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BALANCE AND CHANGE IN THE SHRUB-STEPPE
A Holistic View of a Semi-Arid Terrestrial Ecosystem

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December 1987

Prepared for
the U.S. Department of Energy
under Contract DE-AC06-76RLO 1830

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PREFACE

Eighteen years ago, senior scientific staff of the Pacific Northwest Laboratory embarked on a long-range program of research on ecosystems at the Hanford Site. A master plan guided the initial development of work, with the advice, during the first four years, of a scientific advisory committee composed of university colleagues. Subsequently the plan was modified, as our understanding of the ecological system progressed. Throughout the later period, three objectives were emphasized: quantitative characterization, examination of ecological responses to perturbation, and inferences based on modeled system-level events, such as water balance or recovery from stress.

The Hanford Site[a] is among the largest land holdings of the Department of Energy, approximately 1482 square kilometers (570 square miles). It represents an undeveloped segment of the once extensive shrub-steppe vegetation characteristic of the intermountain regions of the northwestern United States.

Typically, most ecosystem research is hampered both by a lack of funding continuity and by the unavoidably long time frame required for data collection--many of our colleagues maintain that in ecosystem research, one year's data is only one data point! We have not been immune to these problems, but we have been fortunate that most of our senior staff have remained at

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(a) The entire Hanford Site was declared a National Environmental Research Park by the Energy Research and Development Administration, predecessor of the Department of Energy, in March 1977. Its purpose is to encourage university access to the Site and to laboratories where environmental research is conducted.

the Pacific Northwest Laboratory (PNL) throughout this time period and have been able to provide a thread of continuity in a changing research program. We have been fortunate, also, in having university colleagues contribute their interest, ideas and time towards developing a more complete understanding of the shrub-steppe ecosystem. Many are continuing their associations with the research. We are indebted to colleagues who have made useful contributions and whose work is described in this synthesis. Several hundred faculty and graduate students have participated in these studies since 1968, and well over 75 master's and doctoral dissertation studies in the ecological sciences have been completed.

In long-term research of this kind, it is important to evaluate the ongoing efforts in relation to new issues, and to reassess priorities in the allocation of time and effort. Ecological characterization is never complete, no matter how many years have been involved, for example, in soil profile development and the acquisition of climatological data. But how complete must efforts be before an understanding of ecosystem function is practicable? And at what point can one reasonably believe to have identified the "controlling" processes or ranges of perturbation response in an ecosystem? On the Hanford Site the siting of a major nuclear production facility, with its attendant low-level environmental dispersal of short- and long-lived radionuclides, has prompted the belief that a unique use exists for radioactive materials--as tracers of ecosystem functions. How practicable have such "tracer" studies been? Under what conditions can one expect to gain useful information?

The synthesis undertaken here concerns air, water and land resources and is mostly directly applicable to the 312-square-kilometer (120-square-mile)

Arid Land Ecology Reserve. Studies were coherently planned to focus not only on biological variables, but also on the chemical and physical factors that control the regional ecosystem events. Such system-level features as water balance and mineral cycling, which, for example, underlie currently major

engineering concerns in waste barrier design and soil stabilization of contaminants, were evaluated by realistic models on a quantitative basis. The needed multi-year databases so seldom available elsewhere were established for biotic and abiotic variables, and they were developed on a concurrent basis as required for advanced modeling and theoretical development. In the course of the studies, significant quantitative information about wildlife and habitat was developed.

In light of this investment of time and effort in ecological research, what information has proven most useful in understanding semi-arid ecosystems? Twenty years ago, with far fewer systematic data available, it was difficult to associate phenomena of the semi-arid region with such concepts as watershed dynamics, nutrient dynamics, or even energy dynamics. Today, with benefit of a considerable base of "hard" data--and hindsight! --such concepts have taken on real meaning for the region, and their interrelationships can be better understood through quantitative research. Without attempting to answer all of the questions suggested, we would like to leave to the reader's judgement this summary and synthesis.

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September 1987

CONTENTS

PREFACE iii

CHAPTER 1. INTRODUCTION: SHRUB-STEPPE LANDS
(L. E. Rogers and W. H. Rickard)

HISTORY 1.1

The Lewis and Clark Expedition 1.1

Trappers and Traders 1.4

The Oregon Trail 1.4

Settlement 1.4

THE ARID LAND ECOLOGY RESERVE: STUDY SITE
FOR THIS BOOK 1.6

History of the Arid Land Ecology Reserve 1.9

Climate 1.11

Geology 1.12

Soils 1.13

Springs and Streams 1.13

Dryland Vegetation 1.14

Animals 1.15

THE ARID LAND ECOLOGY RESERVE AS A STUDY SITE 1.17

REFERENCES 1.18

CHAPTER 2. CLIMATE OF THE HANFORD SITE
(W. H. Rickard)

Section I. Meteorological Data Base 2.3

Section II. Climatic Patterns at the Hanford Site 2.4

PRECIPITATION 2.4

Snowfall 2.7

Dendrochronology and Precipitation 2.8

SOLAR RADIATION AND AIR TEMPERATURE 2.8

WIND 2.10

REFERENCES 2.13

CHAPTER 3. SOILS: CARBON AND MINERAL CYCLING PROCESSES
(R. E. Wildung and T. R. Garland)

Section I. Occurrence and Distribution of Soils 3.2

DISTRIBUTION OF SOILS 3.4

PROFILE DESCRIPTION 3.6

Section II. Physiochemical Properties 3.9

ORGANIC COMPONENTS 3.10

MINERAL COMPONENTS 3.12

Section III. Carbon Cycling: Influence of
Environmental Factors 3.15

SOIL TYPE 3.16

CARBON SOURCE 3.18

SOIL TEMPERATURE AND WATER. 3.20

LIVESTOCK GRAZING 3.26

IRRIGATION 3.28

HERBICIDES 3.32

METALS. 3.33

Section IV. Relationships of Carbon Cycling to Mineral
Weathering and Mobilization 3.39

MINERAL WEATHERING 3.40

MOBILIZATION OF TRACE ELEMENTS AND RADIONUCLIDES 3.44

REFERENCES 3.56

CHAPTER 4. WATER BALANCE
(G. W. Gee, P. A. Beedlow and R. L. Skaggs)

Section I. General Principles Applicable to Arid Sites 4.2

WATER BUDGET 4.2

PRECIPITATION 4.4

RUNOFF 4.5

EVAPOTRANSPIRATION 4.8

Section II. Microclimatology of the ALE Reserve: Data Bases 4.11

MICROCLIMATES 4.11

THE ROLE OF PLANTS 4.14

TRANSPIRATION 4.14

EFFECTS OF PLANTS ON MICROCLIMATE 4.16

EFFECTS OF PLANTS ON WATER INFILTRATION 4.18

COMPARISON OF WATER USE BETWEEN PLANT COMMUNITIES 4.18

THE ROLE OF SOILS 4.19

Section III. Model Simulations 4.21

THE MODEL 4.21

CRITERIA FOR DATA 4.21

THE MICROCLIMATE DATA 4.23

SOIL DATA 4.24

THE MOISTURE DATA 4.27

THE VEGETATION DATA 4.28

RESULTS OF THE SIMULATIONS 4.29

Section IV. Conclusions 4.33

REFERENCES 4.34

CHAPTER 5. SPRINGS AND STREAMS
(C. E. Cushing and B. E. Vaughan)

Section I. Physical and Chemical Characterization 5.1

SOURCE 5.1

FLOW VOLUME 5.2

TEMPERATURE 5.3

LIGHT 5.3

WATER CHEMISTRY 5.5

Section II. Biological Investigations 5.7

DESCRIPTIVE STUDIES 5.7

PRODUCTIVITY STUDIES 5.14

ENERGY BUDGET STUDIES 5.25

BIOENERGETIC STUDIES 5.29

DECOMPOSITION STUDIES 5.32

Section III. Radionuclides as Indicators of Aquatic Ecosystem Processes 5.34

Section IV. Summary 5.37

REFERENCES 5.38

CHAPTER 6. PLANT COMMUNITIES: CHARACTERISTICS AND RESPONSES
(W. H. Rickard and B. E. Vaughan)

Section I. Characteristics of Contrasting Shrub-Steppe Plant Communities 6.2

STANDING CROP AND SHOOT PRODUCTION IN A SAGEBRUSH-BUNCHGRASS COMMUNITY 6.2

STANDING CROP AND SHOOT PRODUCTION IN A CHEATGRASS COMMUNITY 6.13

PHENOLOGY OF SELECTED PLANT TAXA IN A SAGEBRUSH-BUNCHGRASS COMMUNITY 6.20

NITROGEN AND PHOSPHOROUS 6.26

MINERAL ELEMENTS IN SHRUB LEAVES 6.42

WEIGHT LOSS OF DEAD PLANTS IN A CHEATGRASS COMMUNITY 6.48

INFLUENCE OF GREASEWOOD ON SOIL CHEMISTRY AND GROWTH OF CHEATGRASS 6.51

CATIONS IN HALOPHYTES AND GLYCOPHYTES 6.56

Section II. Responses of Plants and Plant Communities to Disturbances 6.60

EXPERIMENTAL CATTLE GRAZING 6.60

EXPERIMENTAL PLOWING, RECOVERY OF CHEATGRASS COMMUNITIES 6.67

RESPONSES TO WILDFIRE: SAGEBRUSH-BUNCHGRASS AND CHEATGRASS COMMUNITIES 6.71

RESPONSE TO WILDFIRE: GREASEWOOD AND SPINY HOPSAGE 6.78

EXPERIMENTAL MANIPULATION OF MICROCLIMATE AND THE RESPONSE OF PLANTS 6.82

Section III. Radionuclides as Indicators of Biological Fate and Transport of Materials 6.88

RADIOACTIVE STRONTIUM AND CESIUM IN THE SOIL PROFILE 6.88

PLUTONIUM RESUSPENSION AND FOLIAR IMPINGEMENT 6.94

IODINE IN DESERT PLANTS AND SOIL 6.98

CARBON-14 DENDROCHRONOLOGY IN SAGEBRUSH 6.101

Section IV. Summary 6.104

REFERENCES 6.109

CHAPTER 7. TERRESTRIAL ANIMAL HABITATS AND POPULATION RESPONSES (L. E. Rogers, R. E. Fitzner, L. L. Cadwell, and B. E. Vaughan)

Section I. Mammals and Reptiles 7.3

LARGE MAMMALS: HABITATS AND POPULATIONS OF DEER AND ELK ON THE HANFORD SITE 7.6

MID-SIZED MAMMALS 7.10

Coyotes, Bobcats and Badgers 7.10

Black-Tailed Hares and Cottontails 7.13

SMALL MAMMALS: POPULATION RESPONSES TO DISTURBANCES 7.14

Relative Abundance in Undisturbed Sagebrush-Bunchgrass Communities 7.15

Comparative Data for Cattle-Grazed Plots 7.17

Response to Summer Wildfire 7.19

Response in a Cheatgrass Successional Community 7.21

Relationships to the Larger Shrub-Steppe Region 7.24

Conclusions 7.28

SNAKES AND LIZARDS ON THE HANFORD SITE 7.29

Section II. Birds 7.31

PASSERINE BIRDS IN A SAGEBRUSH-BUNCHGRASS COMMUNITY 7.32

LONG-BILLED CURLEW 7.36

RAPTORS IN SHRUB-STEPPE AND MEADOW-STEPPE REGIONS 7.39

Butenoid Hawks, Prairie Falcon and Golden Eagle 7.39

Northern Harrier Nesting 7.46

Nesting Owls 7.48

Bird Populations Associated with Surface Waters 7.51

Streamside Thickets 7.51

Columbia River 7.53

Artificial Ponds 7.59

UPLAND GAMEBIRDS 7.64

CARRION EATERS (MAGPIES, CROWS AND RAVENS) 7.67

Section III. Insects and Related Arthropods 7.69

BIOMASS IN A SAGEBRUSH-BUNCHGRASS COMMUNITY 7.70

RESPONSE TO WILDFIRE 7.74

RESPONSE TO CATTLE GRAZING 7.79

INSECTS AND RELATED ARTHROPODS IN A CHEATGRASS COMMUNITY 7.84

BEETLES ON THE HANFORD SITE 7.87

GRASSHOPPERS (ACRIDIDAE) OF THE HANFORD SITE 7.95

Section IV. Animals as Indicators of Radionuclide and Chemical Contamination 7.97

INSECTS 7.98

BIRDS 7.103

MOBILE MAMMALS 7.107

REFERENCES 7.112

CHAPTER 8. THEORETICAL PERSPECTIVE ON ECOSYSTEM DISTRUBANCE AND RECOVERY (P. A. Beedlow, P. Van Voris, and L. E. Rogers)

Section I. Concepts of Response and Recovery 8.2

THE STABLE SYSTEM 8.4

THE RECOVERY PROCESS 8.6

Section II. Characterization of Disturbance and Stress in the Shrub-Steppe Ecosystem 8.10

WILDFIRE 8.12

LIVESTOCK GRAZING 8.13

FARMING 8.15

CONSTRUCTION 8.16

Section III. Future Research Needs 8.17

REFERENCES 8.21

EPILOG
(L. E. Rogers and W. H. Rickard)

CHAPTER 1. INTRODUCTION: SHRUB-STEPPE LANDS

L. E. Rogers and W. H. Rickard

CHAPTER 1. INTRODUCTION: SHRUB-STEPPE LANDS

L. E. Rogers and W. H. Rickard

The shrub-steppe is the largest of the grassland regions in North America, totaling about 644,716 square kilometers. Shrub-steppe grasslands occupy a large part of the western United States. They extend from western Wyoming into northern Utah and southern Idaho, through eastern Oregon and eastern Washington to the Cascade Mountains, and they reach into the northern portions of California and Nevada. Table 1.1 shows the relative areas of shrub-steppe and other North American grassland types. Their geographical relationships are shown in Figure 1.1.

HISTORY

Since the first contact with Europeans, which occurred when the Lewis and Clark expedition traversed the region in 1805 and 1806, the North American shrub-steppe has undergone substantial and irretrievable change. Unfortunately, of the few written records left by the early explorers, traders and trappers regarding the original, pristine condition, those that have survived are sparse indeed.

The Lewis and Clark Expedition

The Lewis and Clark journals offer the first insight regarding the shrub-steppe. Although the explorers systematically recorded their daily observations, most entries dealt with conditions along the rivers, the Indians they encountered along the way, or descriptions of individual plant and animal

TABLE 1.1. Grasslands of North America (Risser et al. 1981)

Grassland Type	Area in Contiguous United States (km^2)
Annual Grassland	52,688
Shortgrass Prairie	615,223
Mixed-grass Prairie	566,174
Tallgrass Prairie	573,511
Shrub-Steppe	644,716
Desert Grasslands	207,565

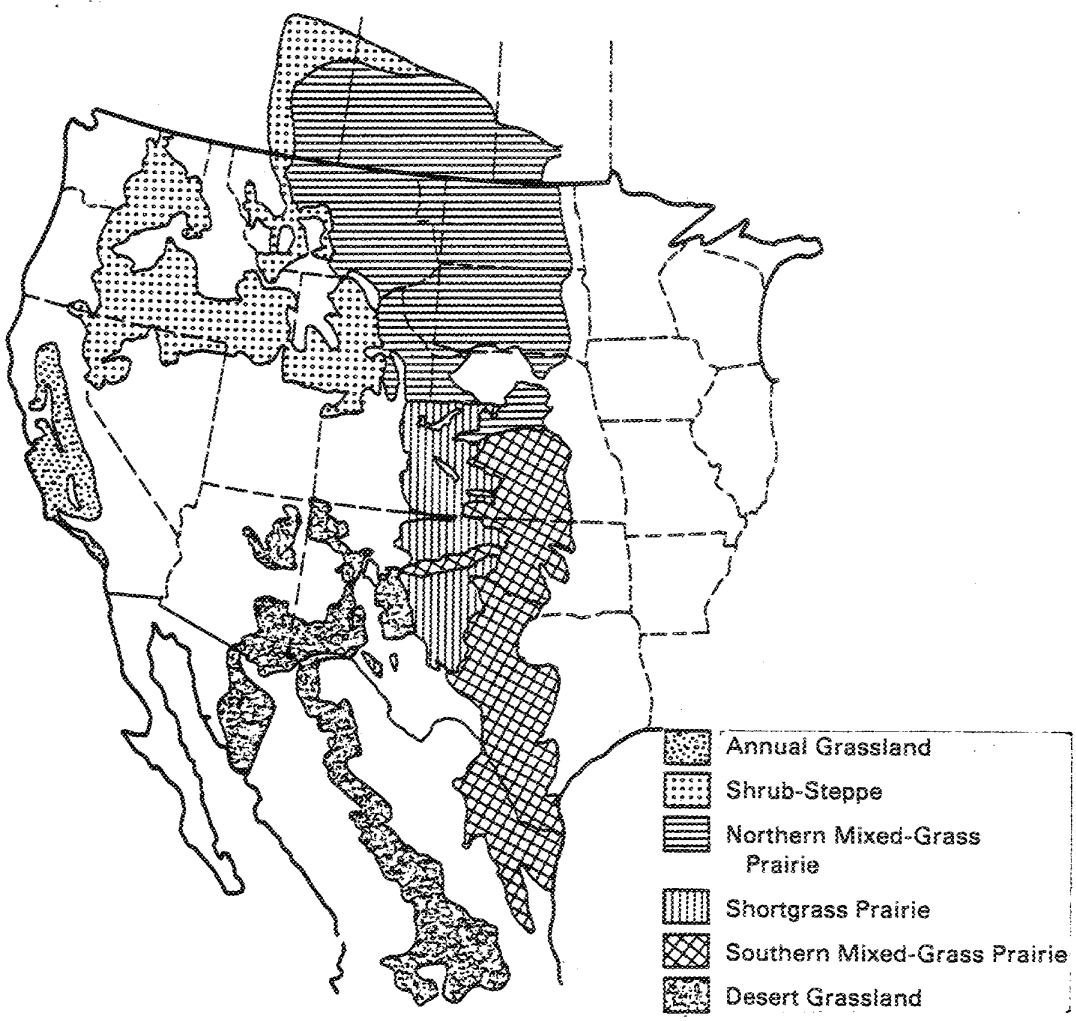

FIGURE 1.1. Major Grassland Types of Western North America (from Risser et al. 1981)

species. The few observations that concerned the surrounding countryside were not particularly complimentary, and dealt mostly with the lack of timber or the scarcity of any large game that might have served as a food source on the open plains. By the time they reached the confluence of the Snake and Columbia Rivers (October 16, 1805), Lewis and Clark had spent several days along the lower Snake River plains. The autumn landscape would have been composed of brown and dry tussocks of bunchgrasses and scattered clumps of sagebrush and other shrubs--little contrast in comparison to the forests and green hills of the Rocky Mountains through which they had recently passed.

They were surprised, however, at the condition of the Columbia Basin on their return trip the following year. Lewis recorded in his log on April 17, 1806, "The plain is covered with a rich virdue of grass and herbs from four to nine inches high and exhibits a beautiful seen particularly pleasing after having been so long imprisoned in mountains and these almost impenetrably thick forests of the seacoast [sic.]." They were also surprised at the condition of the Indians' horses. Lewis entered in his log for April 25, 1806, near present-day Wallula, Washington, "It astonished me to see the order of their horses at this season of the year when I know they had wintered on dry grass of the plains and at the same time rode with greater severity than is common among ourselves. I did not see a single horse which could be deemed pore, and many of them was verry fat; their horses are generally good [sic.]" (Thwaites 1969). This was the first indication that the native flora might support development of a livestock industry.

Trappers and Traders

During the succeeding 40 years, most contact with the shrub-steppe was by trappers and traders. However, they tended to travel along the rivers and streams of the region and had little contact with the open dryland areas (Young et. al. 1978). Their comments dealt mostly with the abundance of forage available for their animals and the lack of water or large animals for food in the open dryland areas (Ogden 1972, Rinehart 1932).

The Oregon Trail

The Oregon trail opened in 1843. Early-day travelers passed through a substantial part of the shrub-steppe region. After arriving at Fort Laramie from Independence, Missouri, they crossed the continental divide at South Pass in Wyoming, dropped south by way of Fort Bridger, then passed down the Snake River to old Fort Boise. From there, they crossed the Blue Mountains near present-day Walla Walla, Washington, and journeyed to the Columbia River near the Dalles.

Earlier in the year, on their way to Oregon country, these early travelers had passed through the tallgrass, mid-grass and shortgrass prairies. By the time they reached the shrub-steppe region, the season was advanced and the shrub-steppe appeared dry and barren. Consequently, their journals tend to stress sagebrush, dust and the lack of available forage (Tisdale et al. 1969, Young et al. 1978).

Settlement

Substantial pioneer inhabitation of the shrub-steppe was initiated by the Mormons, who settled in Utah in 1847. Herds of introduced cattle

flourished on the native bunchgrasses, the first time that large herbivores had been present in the shrub-steppe since the close of the Pleistocene epoch 10,000 years ago, (Young et al. 1976). By 1869, there were several thousand head in Owyhee County, Idaho, alone (Oliphant 1968). The introduction of large numbers of cattle, and later of sheep and feral horses, into an area that had little previous exposure to heavy grazing resulted in rapid reduction of the native perennial grasses and in alteration to the soil surface. The shrub-steppe, unlike the great plains to the east, lacked sod-forming grasses. The soil surface was covered by a fragile crustose-lichen layer that proved sensitive to the trampling activity of large concentrations of ungulates (Mack 1981).

During the last half of the nineteenth century, many individuals traveled down the Columbia River, examining the area with an eye toward the future. Colonel Thomas William Symons surveyed the Columbia and surrounding country for the Army. His report, published in 1882, described navigational and agricultural possibilities of the southcentral region. Symons was impressed by the quality of the land, especially the vast areas of bunchgrass. He wrote: "'Bunchgrass' has become the synonym for things good, strong, rich, and great: the bunch-grass country is the best and finest country on earth; bunchgrass cattle and horses are the sweetest, fleetest, and strongest in the world; and a bunch-grass man is the most superb being in the universe." He noted that the largest species of sagebrush were found on rich soil and remarked on a local expression that "the bigger the sagebrush the better the land." He stressed the value of the hilly regions for growing grain, and he prophesied, with some accuracy, the day "when the whole land shall be a waving field of grain with here and there a village or a city...." (Symons 1967).

Homesteading increased dramatically in the 1880s, following the boom in railroad construction. Where precipitation was adequate, much of the native grassland was plowed and planted to dryland wheat. The combination of soil disturbance associated with livestock and plowing and the generally depleted condition of the range allowed for the rapid spread of several weedy plant species. By the early part of this century, the native bunchgrasses were severely degraded over wide areas and in some places nearly eliminated (Mack 1981). A number of aggressive, alien, annual plants were introduced into eastern Washington from Eurasia with the advent of livestock grazing and farming and are now a permanent part of the flora. The aliens include cheatgrass, tumble mustard, spring draba, jagged chickweed and Russian thistle. These plants are present in variable quantities in all plant communities. Generally, however, those communities with the greatest degree of human-induced soil disturbance show the greatest invasion by alien annuals, usually cheatgrass.

THE ARID LAND ECOLOGY RESERVE: STUDY SITE FOR THIS BOOK

Some remnants of the original shrub-steppe remain. These areas are usually remote from water--or they were in other ways inaccessible to the early settlers. The Arid Land Ecology (ALE) Reserve, located on the Hanford Site in southcentral Washington (Benton County), represents such a remnant (Figure 1.2). It contains the only remaining sizeable acreage of Washington steppe landscape that is still in a nearly pristine state of vegetation.

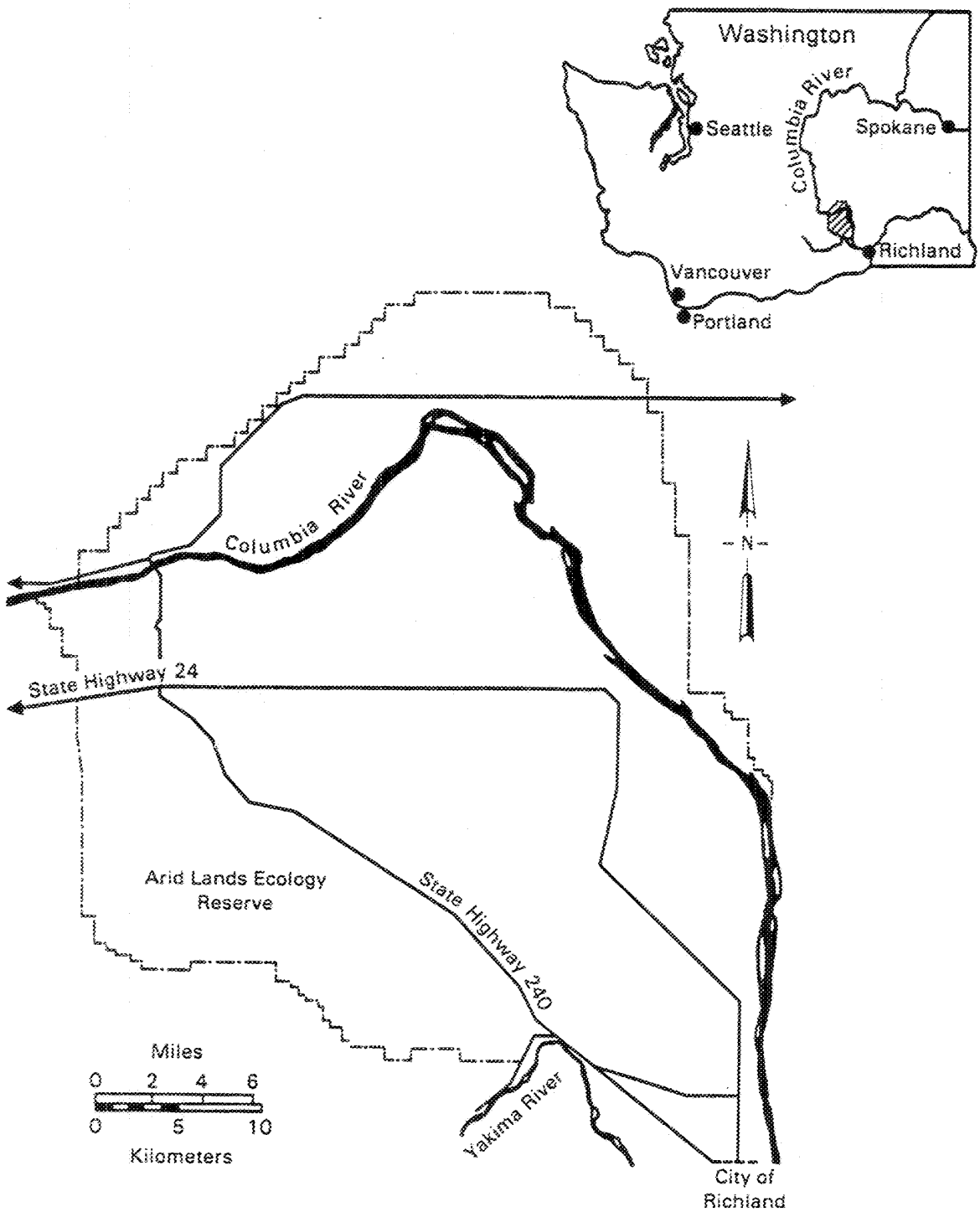

FIGURE 1.2. The Hanford Site, Southcentral Washington

The ALE Reserve is managed for the U.S. Department of Energy by Pacific Northwest Laboratory, a division of Battelle Memorial Institute. The 312-square-kilometer (120- square-mile) Reserve is part of the 1482-square-kilometer (570-square-mile) National Environmental Research Park (Figure 1.3), located on lands near Richland, Washington, that are owned by the Department of Energy. The Park (part of the Hanford Site) offers opportunity for scientists to study relationships between energy-related facilities and the surrounding environment (Vaughan and Rickard 1977).

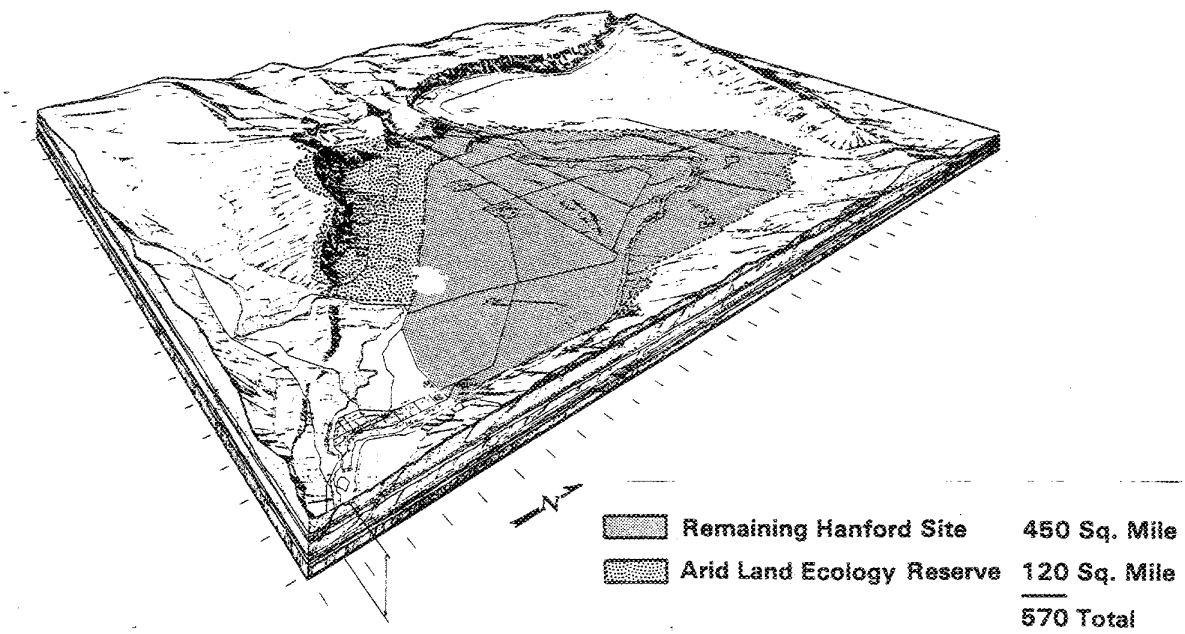

FIGURE 1.3. National Environmental Research Park, Southcentral Washington

As a result of the exceptional research opportunities offered by the Park, and the many and varied research activities that have taken place on the ALE Reserve, a great deal has been learned about the characteristics of a semi-arid ecosystem. Its nature, and the reactions of its components to various natural and human-induced changes, provide the subject matter for this book.

History of the Arid Land Ecology Reserve

In 1967, the U.S. Atomic Energy Commission set aside 33,500 hectares of nearly pristine shrub-steppe on the Hanford Site to preserve portions of vegetation types that once covered a great expanse of the West. Now known as the ALE Reserve, this portion provides a natural research area that is free from the human-related land use pressures common to other parts of the shrub-steppe (Rickard 1972).

The ALE Reserve is situated on the northeast-facing flank of the Rattlesnake Hills. Rattlesnake Mountain (Figure 1.4) is a long anticlinal ridge, with a crest at 1100 meters above mean sea level. Elevations drop to 125 meters on the mountain's southeastern end near the Yakima river. The gently sloping southern side of Rattlesnake Mountain, an area outside the ALE boundaries, supports mostly dryland wheat farming at the higher elevations. The northern slope drops steeply (about 25 degrees) to 650 meters, then eases down to 350 meters and finally slopes gently into the Cold Creek Valley at an elevation of 150 meters.

Settlement of this part of the Lower Columbia Basin took place relatively late. The first recorded immigration into what is now the National Environmental Research Park occurred in 1853, when a party left the Oregon

FIGURE 1.4. Rattlesnake Mountain, a dominant feature of Soutchcentral Washington

trail and turned north to pass through the Yakima Valley (Eastland 1911). Cattle were introduced into the nearby Yakima Valley around 1860 (Meinig 1968) and soon became the mainstay of the local economy.

Interviews with former land users of the ALE Reserve revealed that from about 1880 to 1940, the land was used mostly for homesteading, grazing, some oil and gas production, and road building. Those land use practices associated with grazing and homesteading have left the greatest impact on the landscape. Disturbed sites of such past land use practices are still visible and are dominated by non-native plant species, especially cheatgrass.

Climate

The climate of the ALE Reserve can be characterized as arid, with hot summers and cold winters (Rickard 1972). This part of the Lower Columbia Basin lies within the rain shadow of the Cascade Mountain Range and annually receives only 10-25 centimeters of precipitation. Almost two-thirds of the precipitation occurs during the winter months, about half as snow. Details about the climatological patterns are presented in Chapter 2. Microclimatological studies described in Chapter 4 show basically the same pattern over most of the Hanford Site, although extremes will vary for certain meteorological variables in some locations.

Systematic meteorological observations have been performed by staff of the Hanford Meteorology Station (HMS) from 1946 to the present. The record is supplemented with precipitation and temperature data taken by U.S. Weather Bureau cooperative observers at a site about 10 miles east-northeast of the HMS during the period from 1912 to 1943, thus covering over 70 years. Studies

on water balance modeling (discussed in Chapter 4) and experimental microclimate modification (Chapter 6) have drawn on both the HMS data base and ancillary data developed by the research staff (Thorp and Hinds 1977, Rotenberry et al. 1976).

Geology

The Columbia Basin geologic province covers about 50,000 square miles of what is now southeastern Washington and adjacent parts of Idaho and Oregon. The Basin is underlain by vast lava flows of the Columbia River Basalt Group. Today, those flows and the ground surface above them slope toward the Pasco Basin, where two large rivers, the Snake and the Yakima, enter the Columbia.

The Hanford Site is located at the low point of the Pasco Basin and is bounded to the southwest, west and north by large anticlinal ridges that extend eastward from the Cascade Mountain Range and terminate within the Pasco Basin. Hanford is bounded to the east by the Columbia River and the steep, imposing, west-facing white bluffs of the Ringold Formation. Beyond, gently rising basaltic lava flows lead into the Palouse country of eastern Washington.

Elevations within the Hanford Site range from about 105 meters (345 feet) above sea level to 1093 meters (3586 feet) at the crest of the Rattlesnake Hills. That portion of the ALE Reserve below about 366 meters (1200 feet) and most of the remainder of the National Environmental Park was covered by floods associated with the glacial Lakes Missoula, Columbia, Spokane and similar ice-marginal lakes, and by glacial meltwaters (Brown 1970).

The fauna present during the late Pleistocene epoch indicate the presence of extensive grasslands. Mammoth, bison, horses, deer and other unidentified

species were all present (Fry 1969). Effective precipitation apparently was greater than now, in order to support the vegetation that was grazed or browsed by these populations of large animals. The mammoths, bison and horses are believed to have become extinct between 8,000 and 10,000 years ago, disappearing shortly after the time of the last glacial lake Missoula floods (Brown 1970).

Soils

Soils within the ALE Reserve have been mapped. The Warden and Ritzville silt loams occupy most of the land area; they are found on the lower and middle slopes of the Rattlesnake Hills. Steep slopes, ridge crests, draw bottoms and alluvial fans are mapped as Lickskillet, Kiona, and Scooteney silt loams. The basal plains are mapped as Esquatzel silt loam, Ephrata stony loam, Burbank sandy loam, and Hezel and Koehler sand (Wildung 1977). Physicochemistry of the soils is discussed in Chapter 3, and their hydrological behavior is portrayed in Chapter 4.

Springs and Streams

There are 125 springs or suspected spring sites within an area of 182.5 square miles centered on the Rattlesnake Hills (Gephart et al. 1979). Most of these are of an intermittent nature; only two result in permanent stream flows. One of these is located in Snively Canyon and the other at Rattlesnake Springs. The Rattlesnake Springs are the largest and best known of the permanent springs on ALE. They are located adjacent to the east end of Yakima Ridge and at the northern edge of a large alluvial fan heading in Snively Canyon. Water charged to the perched aquifer from upper Dry Creek and Black

Rock valleys to the west appears as springs where the perched bed is exposed along the canyon bottom (Brown 1970).

Both of the streams associated with the Snively and Rattlesnake Springs support extensive riparian areas. The major species are black cottonwood, various willows, wild plum, sumac, and mock orange (Rickard 1972). Although the riparian areas occupy only a narrow area along the stream banks, they provide important nesting habitats for birds. The springs supply available water for numerous birds and mammals, as well as supporting aquatic fauna. The aquatic biota within an arid environment and the role of its springs and streams are described in Chapter 5.

Dryland Vegetation

The plant communities of the Arid Lands Ecology Reserve are distributed across the landscape according to the physical and chemical properties of the rooting substrate, the micro- and macro-topographic features of the land, and the microclimate. Their characteristics and responses to various disturbances have been extensively studied. Several of these studies are described in Chapter 6.

All plant communities on the ALE Reserve are exposed to wildfire. Extensive fires in 1957, 1973, 1981 and 1984 removed sagebrush shrubs from approximately 80 percent of the Reserve, resulting in an external appearance of simple grassland (steppe) communities rather than shrub-steppe. Chapter 6 provides descriptions and study data concerning the effects of wildfire on shrub-steppe communities.

The inadvertent introduction of cheatgrass has altered the expected pattern of secondary succession by providing an exceptionally long period of

time in the "weedy annual" stage. At this time there is no field evidence to suggest that the native plants can regain dominance on severely disturbed ground within a reasonable time period, e.g., 50 to 100 years.

Cheatgrass has many unpleasant traits. It replaces perennial grasses preferred by livestock growers; it reduces winter wheat yields by competing for water and nutrients; and it significantly augments fuel for wildfires, destroying animal cover and forage. However, cheatgrass also has some desirable characteristics. It is an early colonizer of severely disturbed ground and can stabilize soil against wind and water erosion without human-induced seeding or ground preparation. It produces seeds that are used as food by the native pocket mouse and by the introduced (alien) chukar partridge, an upland game bird. The position of cheatgrass in the shrub-steppe is further discussed in Chapter 6.

Animals

The relatively undisturbed environment of the ALE Reserve provides protected habitats for a variety of native shrub-steppe animals. The interactions of these populations and their responses to a variety of natural and man-related disturbances serve as the focus of Chapter 7. Here, we identify major populations and provide some indication as to their abundance within these habitats.

Mule deer and elk are the largest animals found on the Reserve. Coyotes are common; badgers and bobcats occur occasionally. Blacktailed jackrabbits occur at the lower elevations. The Great Basin pocket mouse is the most abundant small mammal on the Reserve. Others include the deer mouse, northern

grasshopper mouse, Townsend ground squirrel, vagrant shrew, sagebrush vole and the pocket gopher. Least chipmunks occur within limited areas at higher elevations.

The abundant breeding birds include horned larks, western meadowlarks and sage sparrows. Vesper sparrows and Brewer's sparrows are common at higher elevations; loggerhead shrikes occur in low numbers throughout the Reserve. Riparian areas near the springs and streams provide nesting habitat for black-billed magpies, western kingbirds, lazuli buntings, flickers and starlings.

Resident raptors include sparrow hawks, Swainson's hawks, ferruginous hawks, marsh hawks, great horned owls, burrowing owls, short-eared owls and long-eared owls. Both the golden eagle and the bald eagle are occasional visitors.

The reptiles of the area are less well known. The side-blotched lizard, sagebrush lizard and short-horned lizard are common. Other reptiles known to occur here include the Pacific rattlesnake, gopher snake and yellow-bellied racer.

Even less is known about the various invertebrate taxa. The darkling beetle family (Tenebrionidae) is well represented, with 18 separate species known to inhabit the area. Some, such as the fall-dwelling beetles (*Stenomorpha puncticollis* and *Philolithus densicollis*) occasionally occur in outbreak numbers. Grasshoppers (Acrididae) are also abundant; 24 different species are known to inhabit the area. The migratory grasshopper (*Melanoplus sanguinipes*) is very abundant at times. Darkling beetles and grasshoppers serve as a substantial part of the prey base for larger predators. Many of the invertebrate taxa are quite small (e.g., mites and nematodes) and occur in the soil or within the litter layer associated with the grasses.

THE ARID LAND ECOLOGY RESERVE AS A STUDY SITE

The ALE Reserve contains vegetation types that once covered large portions of the western United States. In the 179 years since Lewis and Clark traveled across the shrub-steppe region, substantial changes have taken place. The land has been trapped for valuable fur-bearing animals (mostly beaver), mined, settled and grazed extensively. No one is certain of the pristine condition of the shrub-steppe. Clearly, the records of the early explorers and settlers are far from complete. To a large extent, we depend upon the existence of remnant natural biotic communities to help piece together a picture of a pristine shrub-steppe landscape. Often these shrub-steppe remnants only exist in very remote, hilly or rocky areas; such areas are not really representative of the once-pristine condition of rolling hills covered with sagebrush and bunchgrass. On the ALE Reserve, a relatively undisturbed system, scientists representing various disciplines can gain perspective on the changes that have taken place, and also attempt to resolve questions concerning the responses of this large, unique and fragile landscape to activities related to the generation and transmission of energy, the use of toxic pollutants, and other types of perturbations associated with humans.

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CHAPTER 2. CLIMATE OF THE HANFORD SITE

W. H. Rickard

CHAPTER 2. CLIMATE OF THE HANFORD SITE

W. H. Rickard[a]

Climate and time are master factors in the evolution and geographic distributions of species of higher plants and animals. The reproductive cycles of higher plants and animals that inhabit the Hanford Site are repeated each year, and the timing is predictable to within fairly close tolerances. For example, Say's phoebes arrive on the Hanford Site in late February or early March and begin to nest. Seeds of cheatgrass germinate with the onset of autumn rains, and flowering occurs in late April or early May. Some species of darkling beetles emerge from the soil in September as adults, breed, and lay eggs before the onset of sub-freezing temperatures in December. Mule deer and elk enter the rutting season in October, and most of the births are in early June.

The biochemical and biophysical processes in wild plants and animals inhabiting the earth's temperate regions are strongly regulated by climatic patterns. Solar radiation regimes and carbon dioxide concentrations in air are major contributors to photosynthesis, which provides the chemical energy for animal processes. Ambient temperatures regulate respiration processes in cold-blooded vertebrates, invertebrates and microorganisms. The availability of free water, which is a scarce commodity in arid regions, depends on precipitation patterns. Finally, wind direction and speed affect physical and biological processes and the dispersal of gases and particles released into the air at industrial facilities.

(a) We thank D. J. Hoitink for critically reviewing use of the meteorological data.

The continuous measurement of precipitation, solar radiation, air temperatures and wind speeds, using standardized instrumentation over long periods of time, has provided the scientific basis for climatic descriptions of different geographical regions of the world. In this chapter, climatic data from 30 years of measurement at the Hanford Meteorology Station and various parts of the ALE Reserve are used to illustrate the patterns and to demonstrate the biological effects in a sagebrush-grass ecosystem. Ordinarily, climatic data are summarized at monthly intervals over a calendar year, January through December. On the Hanford Site, however, the annual cycles of solar radiation and precipitation are most meaningful to biological processes when the 12-month period is measured from October of one year through September of the next calendar year. This 12-month period is called the "bioclimatic year."

Section I. Meteorological Data Base

The meteorological data base maintained by the Hanford Meteorology Station consists of hourly data, taken from the ground surface and from a 410-foot tower. The data were collected continuously from 1953 to the present. Since 1955, the information has been stored both on magnetic tape and rigid disk, but the original data from which these were created are still available from records storage. Monthly summaries of these data are also available for the same time period.

Hourly surface observation data consists of the following parameters: cloud type, sky condition, ceiling height, visibility, weather and/or obstructions to vision, sea-level and station pressure, temperatures (dry bulb, wet bulb, and dewpoint), relative humidity, wind speed and direction, total sky cover, precipitation amount, and solar radiation amount. Hourly data from the tower include wind speed and direction at 2, 9, 15, 30, 60, 90 and 120 meters (7, 30, 50, 100, 200, 300 and 400 feet); also aspirated temperature measurements at 1, 9, 15, 30, 90 and 120 meters (3, 30, 50, 100, 200, 250, 300 and 400 feet). Subsurface soil temperatures are measured at about 1, 39 and 90 centimeters (0.5, 15 and 36 inches).

An array of twenty-two 10-meter towers provides hourly wind speed and direction data at the 10-meter level. Data from these towers are radio-telemetered to a central computer at the Hanford Meteorology Station. The towers are primarily located onsite; the few offsite locations are nearby. Data from the earliest of these stations began in early 1979. All data are available on both magnetic tape and rigid disk.

Section II. Climatic Patterns at the Hanford Site

PRECIPITATION

The annual precipitation measured at the Hanford Meteorology Station for the calendar years 1951-1980 averaged 6.29 inches (16 centimeters). Eighty-one percent of the precipitation fell from October through May, the portion of the year in which most plant growth occurs (Figure 2.1). In the 30 years of record, precipitation during the October-May period averaged

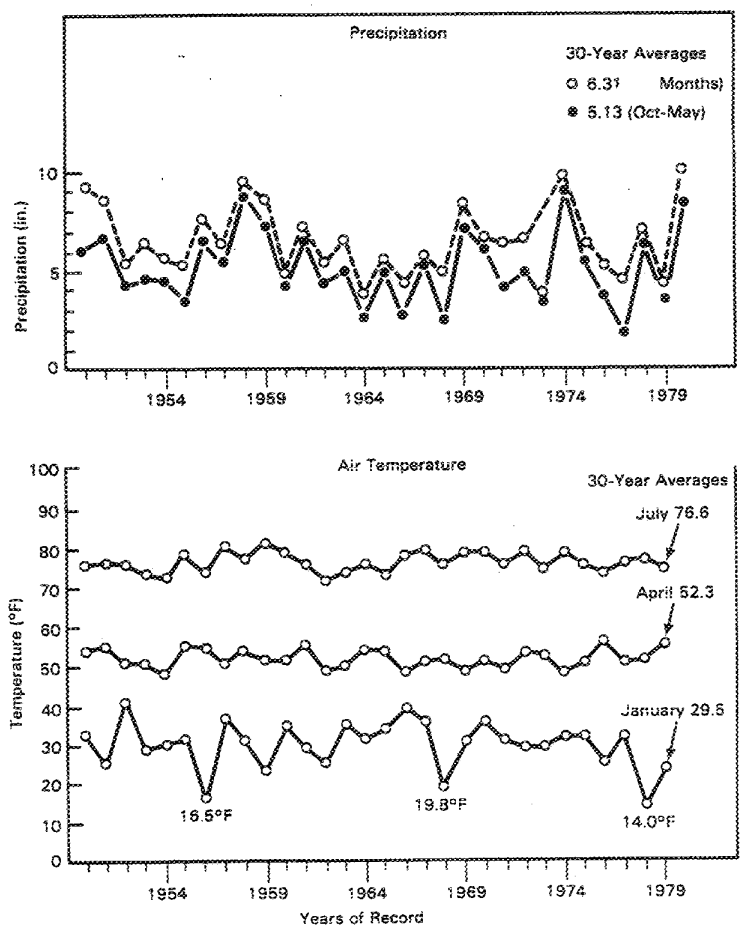

FIGURE 2.1. Precipitation and air temperature on the Hanford Site, in the years 1950 through 1980

5.06 inches (12.8 centimeters). Four of these years, 1964, 1966, 1968 and 1977, had less than 3 inches (7.6 centimeters) of precipitation. The driest period, 1976-1977, had only 1.86 inches (4.7 centimeters). The three wettest years were 1958, 1974 and 1980. The greatest amount of precipitation was 8.95 inches (22.7 centimeters), which occurred in 1973-1974.

The monthly distribution of precipitation is illustrated in Figure 2.2 and shows the three major biological periods of the year, i.e., autumn-winter growth, spring growth and summer dormancy. The first October through January is the time of autumn-winter growth, when precipitation exceeds evapotranspiration, and soil water storage occurs. February through May is the period of spring growth, when most of the plant growth occurs, and when stored soil water is depleted most actively by shoot transpiration. June through September is the period of lowest rainfall, a stressful time of the year for both plants and animals. Most of the plants reduce water losses by dropping some or all of their leaves, or else the shoots die back to near ground level. During this period of summer dormancy, ground squirrels retreat below ground and remain there until October. Pocket mice are active aboveground only during the night.

As shown in Figure 2.2b, the relative humidity is highest from October to January. The average is 71 percent, compared to only 37 percent in the period from June through September.

Although much of the land area of the Hanford Site is gently rolling, the Rattlesnake Hills rise to 1100 meters. This increase in altitude is accompanied by an increase in precipitation. Figure 2.3 illustrates this change with measurements taken at locations on the ALE Reserve. The annual

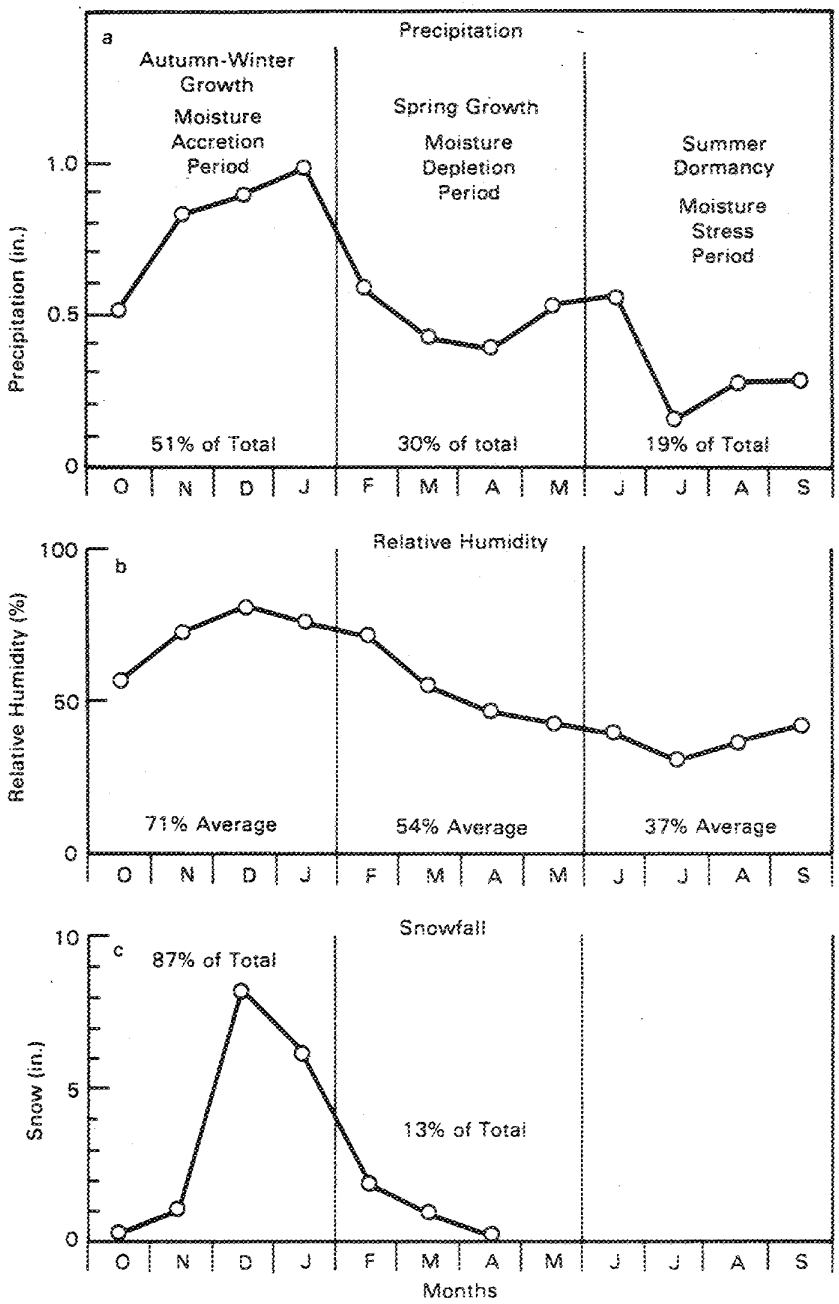

FIGURE 2.2. Monthly Distributions of Precipitation, Including Relative Humidity and Depth of Snowfall, on the Hanford Site During a Typical Bioclimatic Year

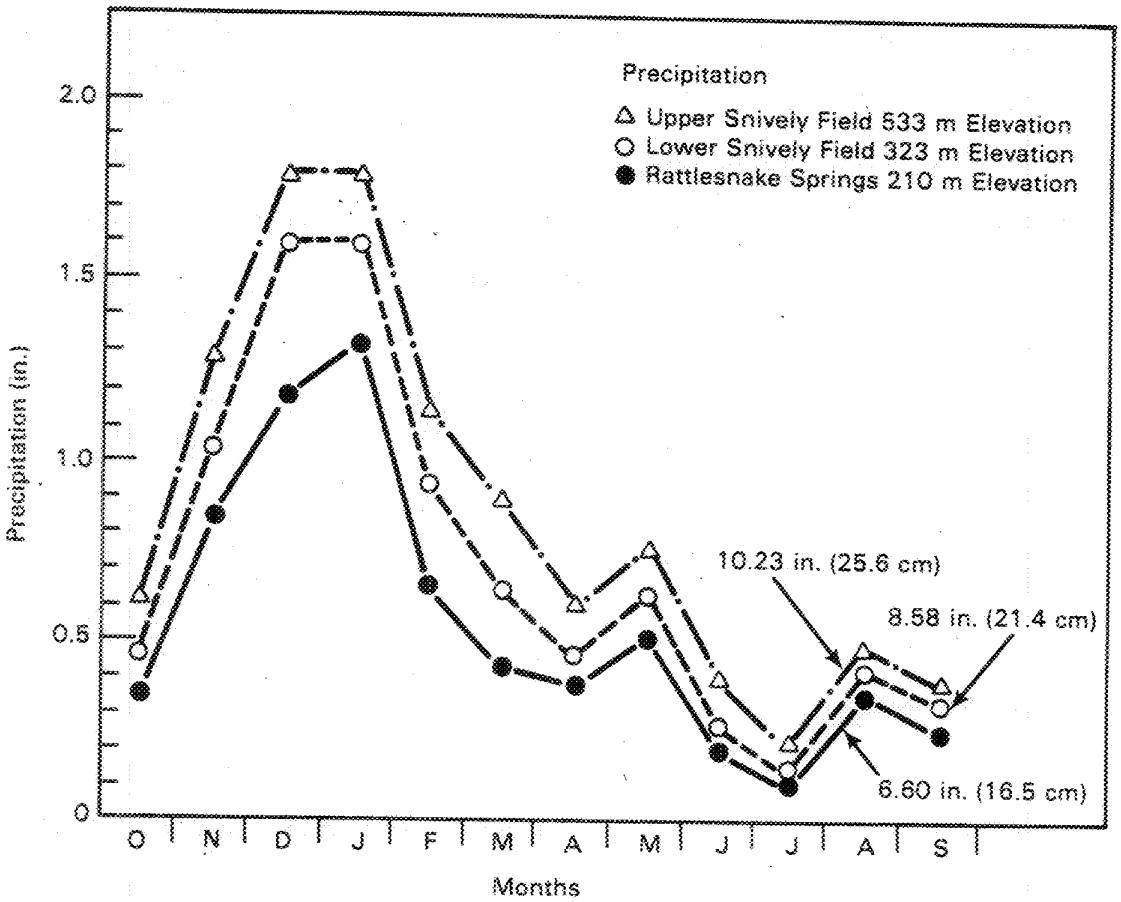

FIGURE 2.3. Changes in Precipitation with Increasing Elevation on the Hanford Site

precipitation at Rattlesnake Springs, situated at an elevation of 210 meters, averages 6.6 inches. Upper Snively Field, elevation 553 meters, averages 10.23 inches. The different altitudes have a pronounced effect on shoot production and plant phenology (Rickard et al. 1973).

Snowfall

Snowfall is an annual event on the Hanford Site. Figure 2.2c shows that 83 percent occurs in the period from October through January, peaking in December. The 30-year norm for the Hanford Site is 13.7 inches

(34.8 centimeters). Snowfall differs from rainfall in that once it is deposited, it can be re-distributed by wind. In this way, soil water storage can be lessened in soils that are swept free of snow by wind and increased in soil upon which the snow is deposited. Monthly snowfall amounts vary greatly from year to year, as shown below.

	Oct	Nov	Dec	Jan	Feb	Mar
Maximum snowfall amount (inches)	1.5	12.7	19.1	23.4	12.7	4.2
Minimum snowfall amount (inches)	0	0	T	T	0	0
Number of years with measurable snowfall (1950-1980)	3	14	29	30	19	12

Dendrochronology and Precipitation

The growth rings of plants can provide clues about the growing seasons during the plant's lifetime. The sagebrush stem shown in Figure 2.4 was growing in the vicinity of the Hanford Meteorology Station. The 1976-77 growing season, which was the driest ever measured on the Hanford Site, is illustrated by a very restricted growth ring for that year. In contrast, the 1973-74 growth ring is very wide, reflecting the above-normal precipitation for that period.

SOLAR RADIATION AND AIR TEMPERATURE

Figure 2.5 displays patterns of solar radiation and air temperature during a typical bioclimatic year. Solar radiation ranges from a low of 89 langleys[a] per day in December to 647 in July. Only 15 percent of the solar

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(a) A langley is equal to 1 small calorie per square centimeter of surface per unit of time.

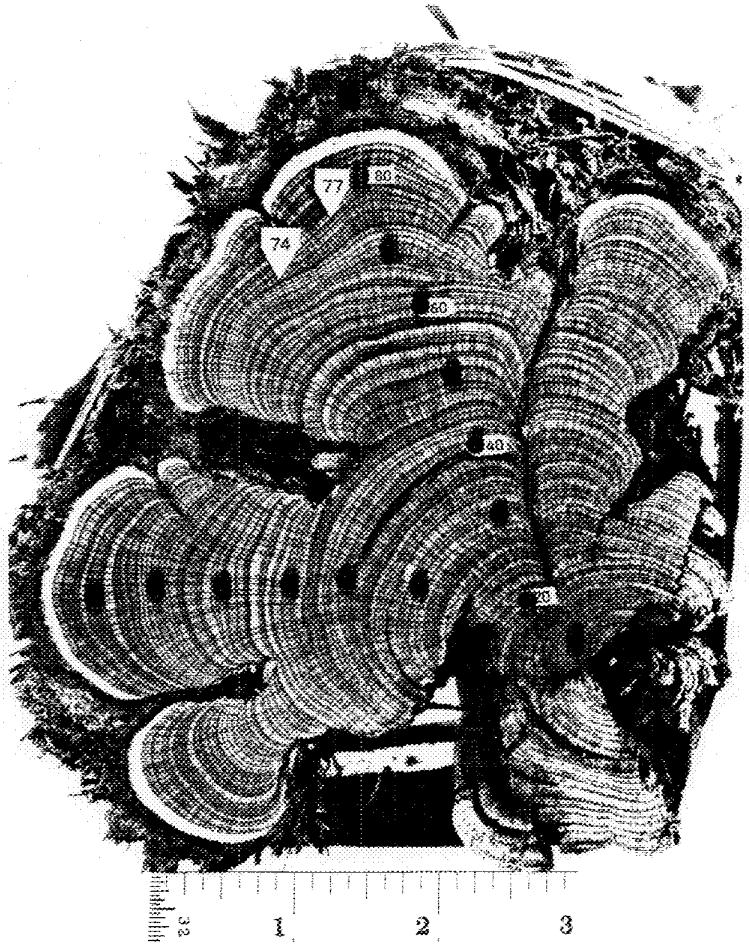

FIGURE 2.4. Growth Rings in a Sagebrush Stem Cross Section, Showing Patterns of Growth for 80 Years. (Numbering is from 1920, #20, to 1980, #80. 1977, the driest in 50 years, is reflected by a very small growth ring, #77. In contrast, 1974 was a wet year, and is represented by a broad growth ring, #74.)

radiation input is received in the October-January period of the bioclimatic year; 50 percent is received in the period from June through September (Figure 2.5a). However, most of the primary production is performed from February through May, which receives only 35 percent of the annual solar radiation input. Clearly, primary production (photosynthesis) is not synchronized with the period of the year in which sunlight is most intense. It is also equally clear that maximal photosynthetic activity is performed during the few weeks when soil water is most available and when air temperatures are moderate (Figure 2.5b).

Winters on the ALE Reserve can be quite cold. Over the past 30 years, four winters were much colder than normal: 1955-56, 1956-57, 1968-69 and 1978-79, but below-freezing temperatures over extended periods of time are not unusual. This characteristic is probably a major reason for the relatively low species diversity of Hanford Site flora compared to that of the southwestern desert areas of the United States. The flora of the Hanford Site are predominantly comprised of cool-season plants with the C_3 photosynthetic pathway.

WIND

Wind plays major role in the dispersal of seeds and pollen and the re-distribution of snow once it is deposited in the ground. Wind is a chronic force in soil erosion, and it is very important in the spread of wildfire and in the redistribution of burned plant materials and surface soil following summer wildfires. Wind is also an important force in the dispersal of industrial chemical pollutants released into the air from stacks.

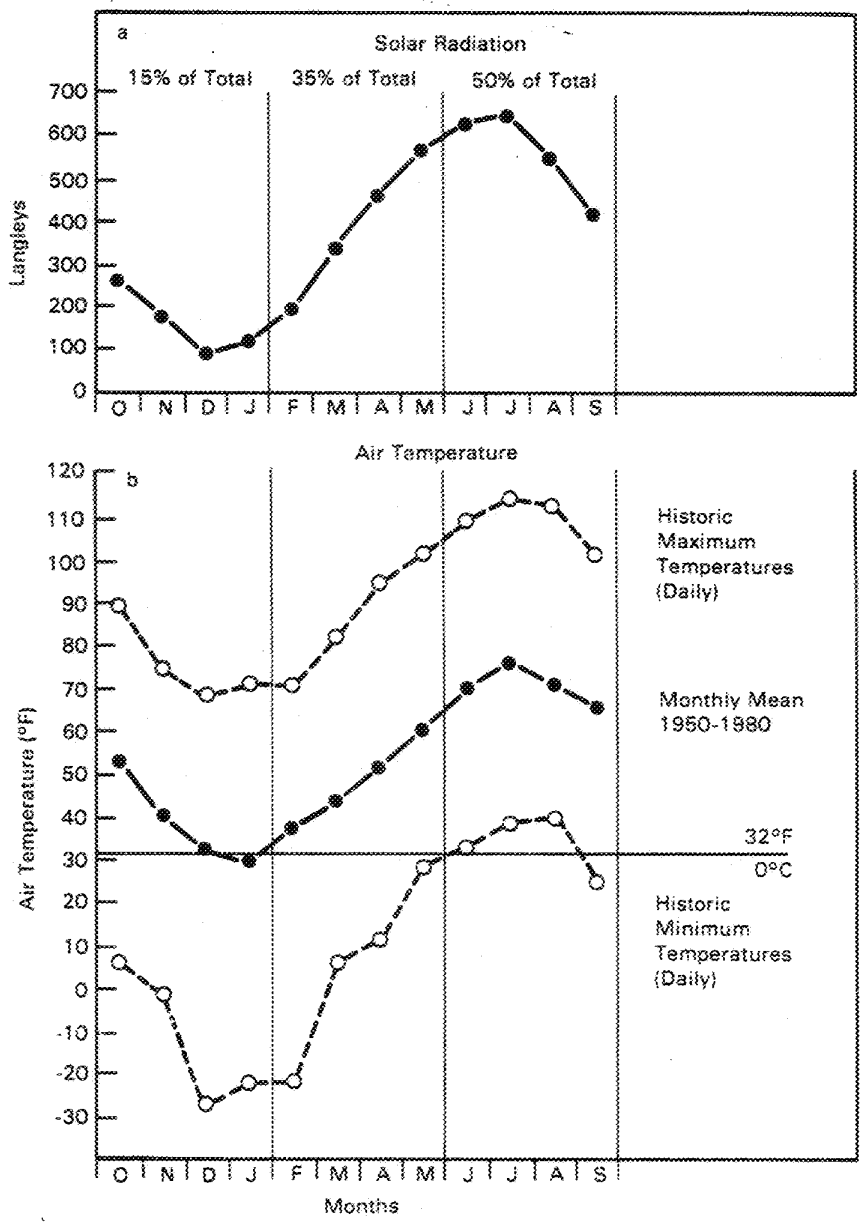

FIGURE 2.5. Patterns of Solar Radiation and Air Temperature on the Hanford Site During a Typical Bioclimatic Year

Figure 2.6 illustrates average and peak wind speeds and directions on the Hanford Site. The prevailing wind directions are from the northwest and

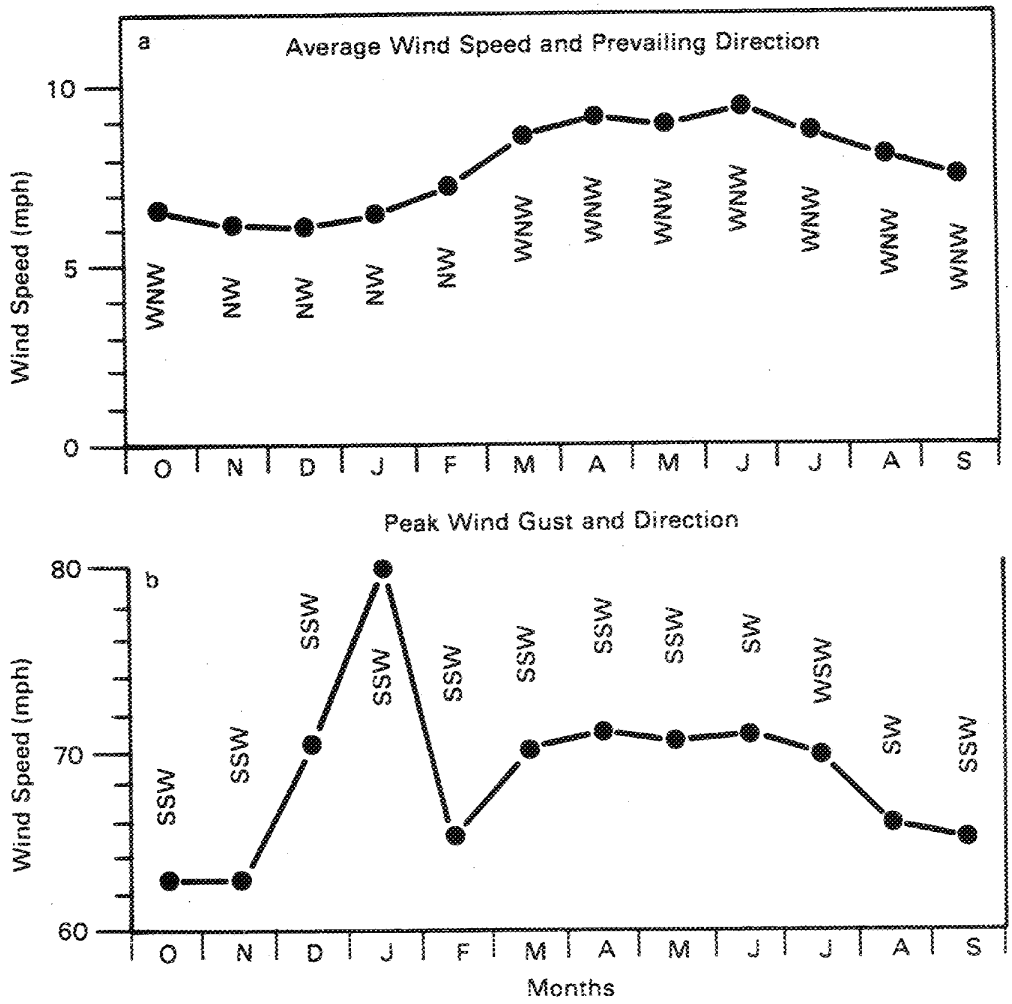

FIGURE 2.6. Average and Peak Wind Speeds and Direction on the Hanford Site During a Typical Bioclimatic Year

west northwest. However, peak gusts are from the southwest or south southwest. Wind speeds tend to be lowest during the autumn and winter months (October through January).

The relatively low wind speeds associated with the months of October and November are probably favorable to the germination of seeds and the establishment of seedlings following the onset of autumn rains by helping to slow evaporation losses from the wetted soil surfaces.

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CHAPTER 3. SOILS: CARBON AND MINERAL CYCLING PROCESSES

R. E. Wildung and T. R. Garland

CHAPTER 3. SOILS: CARBON AND MINERAL CYCLING PROCESSES

R. E. Wildung and T. R. Garland

Soil serves as an integral part of the shrub-steppe ecosystem and often plays a controlling role in its structure and function. The nature and extent of this role, however, is highly dependent upon soil physicochemical and biological properties. These properties and the unique character of the soil, in turn, are dependent upon the combined effects of the principal soil-forming factors including its parent material, topography, climate, biological processes, time, and to a variable extent, human activities (Jenny 1941, Barshad 1965).

This chapter describes the general occurrence and distribution of soils in the Pacific Northwest shrub-steppe as influenced by soil-forming factors, and summarizes the results of research to define carbon (C) and mineral cycling phenomena as influenced by seasonal changes in temperature and moisture and physical and chemical stresses. Particular emphasis was given to research establishing the relationship between C and mineral cycling. The research was conducted on the Arid Land Ecology (ALE) Reserve and, when linked with studies of water and plant relationships, provides information integral to understanding the complex controls on C, mineral and energy flow in this system.

Section I. Occurrence and Distribution of Soils

The Pacific Northwest shrub-steppe, encompassing vast acreages in the upland regions of eastern Washington, eastern Oregon, and southern Idaho, includes a diversity of soils. However, the soils of the shrub-steppe are typified by those existing on the Columbia Plateau, bordered by the northern Rocky Mountains on the east, the Cascade Mountains on the west, the Okanogan Highlands on the north and the Blue Mountains on the south. The plateau functions as a large inland basin comprised of a series of smaller basins. The surface of the plateau has been modified initially by glacial abrasion and redistribution and later by wind and water. A significant portion of the basin section has developed on a mantle of loess and Pleistocene outwash sediments. The soils of the Columbia Plateau supporting shrub-steppe vegetation are principally in the drier upland regions of 120 to 1,060 meters in eastern Washington, northwestern Idaho, and northern Oregon.

The ALE Reserve (Figure 3.1) lies in the western portion of the Columbia Plateau on the northeast-facing slopes of the Rattlesnake Hills, adjacent to the Columbia River Plains, in southeastern Washington. The region is subject to low precipitation, as Pacific storms lose most of their moisture when air is cooled crossing the Cascade Mountains to the east. The presence of the Cascade Range also results in a lack of any moderating influence of the Pacific on temperatures, which are high in the summer and low in the winter (Hinds and Thorp 1969).

The ALE Reserve encompasses about 310 square kilometers. The crest of Rattlesnake Mountain, at 1,060 meters, serves as the western boundary of

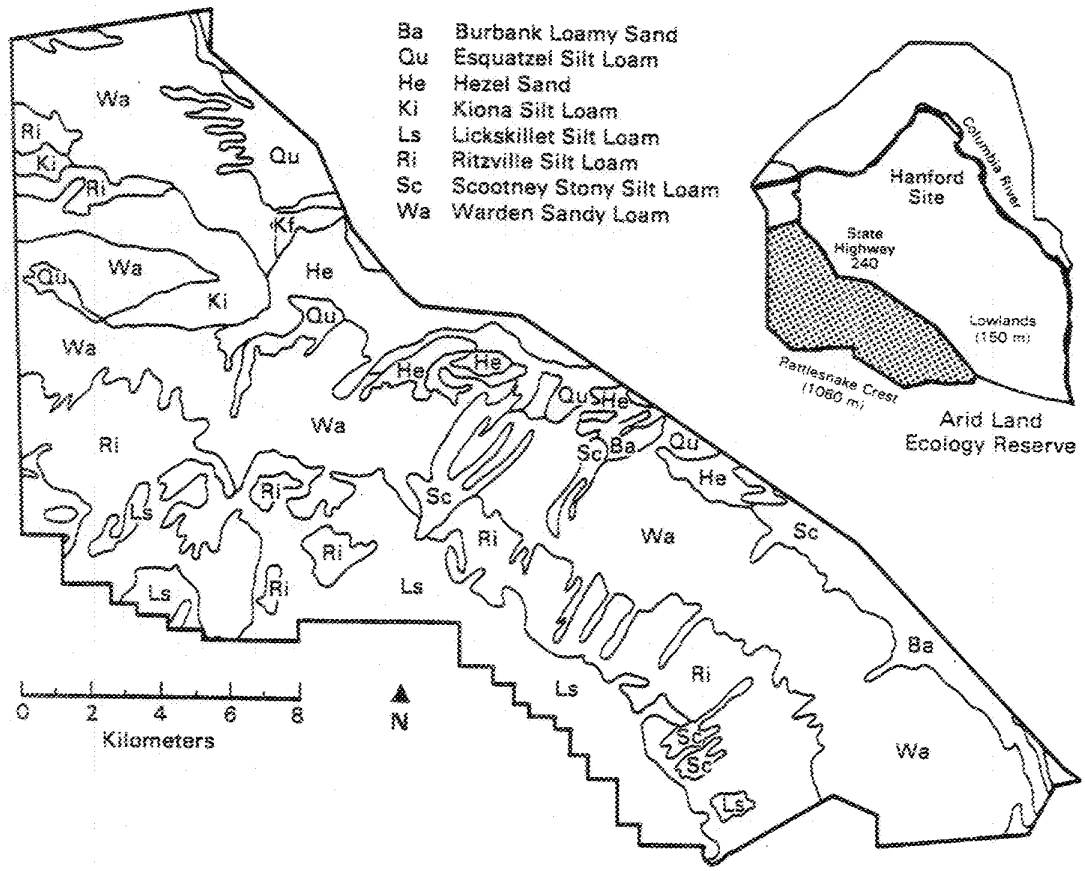

FIGURE 3.1. Soil Distribution of the Arid Land Ecology Reserve (based on Hajek 1966)

the Reserve. The northeast slope of Rattlesnake Mountain is abrupt, dropping to 150 meters on the adjacent plains where the eastern boundary of the Reserve is located. This altitudinal gradient is responsible in part for differences in mean annual temperature range of approximately 9 to 10°C and differences in mean annual precipitation of approximately 18 to 30 centimeters. These factors, in conjunction with differences in parent material, have resulted in a diversity of soils.

DISTRIBUTION OF SOILS

The ALE Reserve is underlain by a series of basaltic layers which are part of the Columbia River lava field. The lava is generally level in the valleys and plains, but folded, steeply inclined layers from part of the canyon walls, benches, terraces and rocky outcrops of the region. The basalt is often overlain by unconsolidated materials of loessial, eolian lake-laid and stream-laid origin that serve as the parent material for soils of the Reserve.

The crest of Rattlesnake Mountain down to approximately 750 meters, consists principally of basalt overlain by a 25 to 50-centimeter layer of loess with numerous rocky outcrops and breaks. The higher precipitation and lower temperatures at this elevation have led to the presence of a variety of forbs as well as bluebunch wheatgrass. The combination of these factors has, in turn, resulted in very dark brown soils of up to 7 percent organic matter content for this region, particularly in protected areas on the north face where snow fields may persist in the spring. The shallow nature of the soils, however, necessitates their classification as a Lithosol. These soils are typified by the Lickskillet series (Figure 3.1).

The soils comprising the major portions of the ALE Reserve occur adjacent to the crest and extend to an elevation of approximately 180 meters. They are derived from loess, are usually greater than 150 centimeters deep, and are probably deposited when the velocity of westerly winds is reduced at the mountain crest. Above 360 meters, mean annual temperatures of 9°C and mean annual precipitation of 23 to 30 centimeters have led to the development of

Brown soils underlain by basalt with dark, grayish-brown A horizons (approximately 20 centimeters thick) and with a calcareous horizon below 90 centimeters. These soils are typified by the Ritzville series on which the intensive study site is located. At approximately 360 meters' elevation, the Brown soils grade to Sierozems which developed under a lower precipitation regime (15 to 23 centimeters) and, perhaps, at higher temperatures. These soils, underlain by reworked lacustrine deposits, extend to a lower elevation of approximately 180 meters. They have been subjected to less leaching, and a highly calcareous layer has developed at approximately 50 centimeters. This soil is typified by the Warden series. Both the Brown and Sierozem soils include occasional basalt outcrops.

At lower elevations on the north, eastern, and southern boundaries of the Reserve, the soils are derived from lacustrine and stream-laid deposits which have been redistributed by wind. The mean annual precipitation here is 15 to 23 centimeters, and the mean annual temperature is 10°C. These soils, which do not occupy large areas of the ALE Reserve, are principally Regosols, Sierozem-Regosol intergrades or Alluvial soils.

The Regosols, typified by Burbank and Hezel series, are developed principally in unconsolidated, wind-blown sands which are usually less than 100 centimeters deep, and are underlain by gravely alluvium in the Burbank series or lacustrine sediments in the Hezel series. The latter occupy the largest portions of the nonloessial soils of the Reserve. They are hummocky, and the hummocks may be stabilized by shrubs and associated grasses. In the swards between hummocks, the underlying, finer-textured sediments are often exposed by wind action in the late spring and early fall when overlying sands

are dry. These soils are poorly developed, reflecting the properties of the parent material, but the slightly acidic surface horizons indicate that some leaching of salts has occurred.

The Sierozem-Regosol intergrade or Alluvial soils, typified by the Scootney series, lie in intermittent stream bottoms and alluvial fans from these streams. Although finer textured than the Regosols, they have weakly developed profiles, distinguishing them from the Warden series and are severely eroded.

The Alluvial soils are formed in recent alluvium derived from loess and lacustrine sediments. Surface horizons are very dark brown. Profile development is generally lacking on the ALE Reserve soils, but the texture of the subsoil varies in the stratified alluvium.

PROFILE DESCRIPTION

Soil profile descriptions for four soils representative of the principal Great Soil Groups present on the ALE Reserve are summarized by Wildung (1977). They occur along an altitudinal transect of the northeast-facing slopes of the Rattlesnake Hills; their distribution is mapped in Figure 3.1. The soils of the ALE Reserve were mapped in an early Bureau of Soils soil survey of Benton County (Kocher and Strahorn 1919). However, the ALE Reserve, as part of the Hanford Site, was not included in the latest Benton County soil survey (Rasmussen 1971) by the Soil Conservation Service. The representative profile descriptions are largely from the most recent survey, but are modified, as appropriate, to more precisely reflect the profiles of the noncultivated soils on the ALE Reserve.

The Lickskillet loam, a Lithosol, is located at the crest of the Rattlesnake Hills. It is stoney, containing numerous basalt fragments, and is located among basalt rock outcrops. The stoniness and the number of rock outcrops vary widely within short distances. The depth to basalt bedrock ranges from 25 to 50 centimeters; the average depth is about 46 centimeters. The shrub, big sagebrush (Artemisia tridentata), is present at low density, whereas the understory consists primarily of bluebunch wheatgrass (Agropyron spicatum) and low-growing forbs, typical of Prairie soils.

The Ritzville silt loam, a Brown-Regosol intergrade, is generally located at elevations below the Lickskillet loam and above the Warden sandy loam. It overlies basalt bedrock as in the case of the Lickskillet, but it is deeper than the Lickskillet and contains less organic matter in the surface horizons. Generally, the depth to bedrock is more than 150 centimeters, but in places it is as little as 75 centimeters. Occasional rock outcrops occur, principally at the edges of gullies. A calcareous C horizon is commonly present at a depth of more than 90 centimeters, but it is shallower in some of the areas where bedrock is within 150 centimeters of the surface. A significant portion of the surface is occupied by lichen mats, which tend to stabilize the soil to wind erosion. The soil is well-drained. Firm aggregates of silt from overlying horizons have been deposited in insect burrows. These aggregates, as much as 1 centimeters wide and 10 centimeters long, are common in the C horizon. The vegetation consists of big sagebrush, in generally higher density than on the Lickskillet, and bluebunch wheatgrass. Forbs generally do not represent a significant part of the total aboveground biomass.

The Warden sandy loam, a Sierozem-Regosol intergrade, is located adjacent to the Ritzville, at lower elevations of the Rattlesnake Hills above the

basal plains. It is usually greater than 150 centimeters deep and overlays lacustrine deposits known as the Ringold sediments. The texture may vary from a fine sandy loam to a silt loam. It includes small areas of Hezel fine sand. In places the horizon is stratified with loamy sand. The depth to the calcareous layer is commonly about 70 centimeters. The depth to bedrock is more than 150 centimeters in most places, but it is about 100 centimeters in some areas. In places, granite cobbles are present. The principal shrub species is big sagebrush, but in contrast to the Ritzville, the primary understory is Sandberg bluegrass (Poa sandbergii).

The Burbank loamy sand (Figure 3.1), a Regosol, occupies the basal plains of the ALE Reserve adjacent to the Warden and in geographical association with the Hezel sand and the Esquatzel silt loam. It includes areas previously classified (Kocher and Strahorn 1919, Hajek 1966) as Ephrata. The soil developed in stoney alluvial deposits mantled with mixed alluvium and windblown sand. The depth to sandy gravel is more than 50 centimeters. A layer of gravely fine sandy loam, 5 to 15 centimeters thick, may directly overlie the sand gravel. In some places the calcareous C horizon is sufficiently developed that the gravel and stones are weakly cemented by lime and silica. The principal shrub species is big sagebrush and the understory consists primarily of cheatgrass (Bromus tectorum).

Section II. Physicochemical Properties

The principal characteristics (Wildung et al. 1971) of the soils along a 13-kilometer altitudinal transect from 155 to 1060 meters elevation on the northeast-facing slopes of the Rattlesnake Hills are summarized in Tables 3.1 and 3.2. The representative soils and sampling sites on the ALE Reserve were selected on the basis of their altitude, vegetation, and surface-soil characteristics.

TABLE 3.1. Representative Soils of the Arid Land Ecology Reserve (Wildung et al. 1971)

Classification			
7th Approximation	Great Soil Group	Vegetative Understory	Elevation m
Lithic Haplustoll (Lickskillet 1)	Lithosol	Agropyron	940
Andic Aridic Haplustoll (Ritzville sil)	Brown	Agropyron	445
Andic Mollic Camborthid (Warden sl)	Sierozem	Poa	190
Typic Torripsammet (Burbank ls)	Regosol	Bromus	155

TABLE 3.2. Characteristics of Representative Soils of the Arid Land Ecology Reserve (Wildung et al 1971).

		Contents[a] of				
Classification	pH	Organic Carbon	Sand (>50μ)	Silt (50 to 2μ)	Clay (<2μ)	CEC at pH 7.0
						meq/100 g
Lickskillet 1	6.2	3.62	42.6	41.1	16.3	40.3
Ritzville sil	6.2	0.66	23.3	64.1	12.6	22.5
Warden sl	7.0	0.52	55.5	34.1	10.4	18.1
Burbank ls	6.9	0.46	76.8	16.8	6.4	11.2

(a) Percent organic carbon based on total soil, other values based on total minerals.

ORGANIC COMPONENTS

The primary influences of altitude on soil organic matter deposition and transformation may be expected to arise from differences in vegetation, temperature, and moisture (Table 3.1). Big sagebrush (A. tridentata) is the principal overstory shrub species throughout the altitudinal sampling range, whereas the grass understory consists primarily of cheatgrass (B. tectorum) at elevations below ≈180 meters, Sandberg's bluegrass (P. sandbergii) at approximately 180 to 270 meters, and bluebunch wheatgrass (A. spicatum) at elevations above 270 meters.

The C content of the intact soils (Table 3.2) generally decreases with decreased elevation, probably as a result of 1) decreased plant understory biomass and soil deposition of organic matter with decreased rainfall and 2) increased soil organic matter degradation rate with increased mean annual temperature (Rickard 1968, Hinds and Thorp 1969). The decreased soil C content occurring with decreased elevation may also reflect a smaller quantity of aromatic substances, resistant to microbial decomposition, deposited on the soil as lignin in associated grass tissues. Investigations by Wildung et al. (1968) have shown that the lignin content of mature A. spicatum, P. sandbergii, and B. tectorum tissue amounted to 4.5, 3.6, and 2.7 percent, respectively.

The soil clay contents range from 6.4 to 16.3 percent and also decrease downslope. Cation exchange capacities (CEC) of the Lickskillet, Ritzville, Warden, and Burbank soils at pH 7.0 are 40.3, 22.5, 18.1, and 11.2 meq/100 g, respectively, thereby increasing with decreased soil clay and organic C

content. The observed increase in CEC results from increased surface area and solid-phase coulombic charge associated with higher concentrations of colloidal mineral and organic matter.

The C, which may be removed from soil as humic colloids or accessory components (alcohol/benzene soluble), ranges from 4.0 16.5 and 1.7 to 7.8 percent, respectively (Wildung et al. 1968). On a basis of total weight, yields of sodium hydroxide and alcohol/benzene soluble materials from soils are less than 0.5 percent; therefore, comparisons of the yields of soil extractives would be tenuous. The C, hydrogen and nitrogen contents of isolated soil humic colloids are quite similar and range from 54.3 to 58.1, 5.7 to 6.2, and 4.8 to 5.8 percent, respectively (Table 3.3). These data are comparable with values reported by other investigators (Kononova 1966, Wildung et al. 1970) for humic components from a wide variety of mineral soils developed under different climatic conditions.

TABLE 3.3. Elemental Composition and Cation Exchange Capacity of Humic Acids from Representative Arid Land Ecology Reserve Soils (Wildung et al. 1971)

Acids	Contents of				Ratio of		Cation Exchange Capacity	
	Ash	Carbon	Hydrogen	Nitrogen	Carbon/ Nitrogen	Carbon/ Hydrogen	pH 4.0	pH 7.0
	(%)	(% of dry, ash-free sample)					(meq/100 g)	
Lickskillet 1	1.2	56.6	5.7	5.3	10.8	9.9	117	200
Ritzville sil	2.9	57.8	6.1	5.8	9.9	9.4	132	190
Warden sl	1.6	58.1	6.2	5.6	10.3	9.3	196	260
Burbank ls	1.9	54.3	6.0	4.8	11.4	9.1	93	270

Although elemental compositions of the humic colloids were similar, the Warden sl and Ritzville sil humic acids exhibited significantly higher C and nitrogen contents and lower C/nitrogen ratios than the Burbank humic colloids, whereas the Lickskillet humic colloid gave intermediate values (Table 3.3). The C/hydrogen ratios were also similar ranging from 9.1 (Burbank ls) to 9.9 (Lickskillet 1).

Cation exchange capacities of soil humic colloids (Table 3.3) at pH 4.0 and 7.0 ranged from 76 to 196 and 190 to 270 meq/200 g, respectively. The CEC of the Warden sl humic acid amounted to over twice that of the humic acid from the Burbank ls at pH 4.0. The Ritzville and Lickskillet were intermediate between the Warden and the Burbank humic acids at the low pH. At pH 7.0, the Warden and Burbank samples gave the highest CEC; the Ritzville and Lickskillet humic acids exhibited the lowest values.

The comparatively high CEC of the Warden humic acid, particularly at pH 4.0, may reflect the high CEC of the associated P. sandbergii lignin at 7.0 (Wildung et al. 1968). It may be speculated that the lignin contains a larger number of acidic groups ionizing near pH 7.0 than the other lignins; and these groups are strengthened during soil decomposition, resulting in a humic acid comparatively higher in CEC at pH 4.0.

MINERAL COMPONENTS

The major minerals present in the clay fraction (Table 3.2) of the ALE Reserve soils are given in Table 3.4. The minerals reflect the varied parent materials of the region and, to a lesser extent, the effects of different mineral weathering rates and processes. Weathering processes probably do not serve as a major control on the clay mineral composition of these

TABLE 3.4. Mineralogical Analysis of Representative Soils of the Arid Land Ecology Reserve (Routson et al. 1977)

Soil	Lickskillet l	Ritzville sil	Warden sl	Burbank ls
Fine Clay (<0.2μ)				
Montmorillonite	M	M	M	M
Illite	M		m	m
Kaolinite		m	t	m
Quartz	m	t	t	m
Vermiculite	M			M
Mica		m		
Interstratified	t			t
Coarse Clay (0.2-2μ)				
Montmorillonite	M	M	M	M
Illite	M		m	m
Kaolinite	m	m	t	m
Quartz	m	m	m	m
Feldspar		t	t	m
Vermiculite	M			m
Mica		m		
Interstratified	t			t

M = major component (>20%)
m = present (5-20%)
t = trace (2-10%)

relatively young soils. Where larger surface areas facilitate more intensive weathering conditions, quartz and feldspar in the finer particle size fractions have normally weathered to extinction. The persistence of quartz and feldspar in the clay fractions of the soils of the ALE Reserve indicates that, in general, the combined effects of weathering intensity and time have failed to alter qualitatively the mineralogy of the soil clay fraction. Mineral weathering sequences will be further discussed in Section III. In contrast, major differences exist in the quantities of oxidic iron, aluminum, and manganese in these soils (Table 3.5). Citrate-bicarbonate-dithionite is generally considered to extract inorganic oxidic iron and

TABLE 3.5. Quantity of Oxidic Iron, Aluminum, Manganese and Silicon in Representative Soils of the Arid Land Ecology Reserve (Wildung 1977)

	Extractant and Element (μg/g)				
	Citrate-bicarbonate dithionite[a]		Potassium Hydroxide[a]		Acidic hydroxylamine[b]
Soil	Iron (Fe_2O_3)	Aluminum (Al_2O_3)	Aluminum (Al_2O_3)	Silicon (SiO_2)	Manganese (MnO_2)
Lickskillet 1	2,900	265	300	2,440	410
Ritzville sil	2,040	170	250	2,420	510
Warden sl	2,040	94	250	690	710
Burbank ls	1,440	94	210	810	240

(a) Jackson (1969)
(b) Chao (1972)

aluminum, including crystallized oxides, amorphous-aged hydrous oxides and amorphous gel hydrous oxides (Bascomb 1968). There was a general decrease in citrate-bicarbonate-dithionite extractable iron and aluminum downslope from the Lickskillet to the Burbank ls, generally corresponding to decreased clay content (Table 3.2). This pattern likely reflected the decreased weathering rate and reactive surface area of the soils downslope. The potassium hydroxide extractant was used to compare extractable aluminum and silicon. The ratios of aluminum to silicon ranged from 2.8 to 9.7, and the soils would be classified as "very siliceous aluminosilicate" types (Jackson 1969). Values exceeding 4.5 are rare in the literature. Oxidic manganese did not exhibit altitudinal trends but the coarse-textured Burbank ls was among the lowest as in the case of the other elements. The relationship between the amorphous fractions of these soils and others representing forests and grasslands of the United States and surface chemical reactivity influencing ion sorption have been further defined by Wildung et al. (1986a,b).

Section III. Carbon Cycling: Influence of Environmental Factors

The soil is the principal medium for return of photosynthetic energy to the atmosphere. Soil microorganisms may be represented as receiving reduced forms of C in plant and animal residues and ultimately oxidizing the carbonaceous materials to the lowest energy state of C, i.e., CO_2. Thus, it is important to understand the environmental factors influencing this process and the possible impacts which may result from human activities.

The rate of CO_2 evolution from soil, the soil respiration rate, is largely a function of the respiration of soil microorganisms, soil invertebrates and plant roots (D'yaKonova 1961). From comparative studies with oat-cropped and fallow soils, it has been estimated (Lundegardh 1927) that respiration by live roots accounts for less than one-third of total respiration from mineral soils. Soil respiration rate and the relative contributions of live roots to soil respiration rate may be expected to vary with soil, plant and environmental factors. However, in arid, non-calcareous grassland soils where the total root biomass is relatively small, respiration by the soil microflora and soil fauna is likely to be the principal mechanism for the return of C to the atmosphere.

Of the potential environmental factors influencing respiration rate in the shrub-steppe, previous research in other systems (Stotsky 1965) indicates that the most important variables would be the quantity and type of decomposable organic matter, climatic factors governing soil temperature and water, and stressors which may affect these parameters or exhibit direct toxicity to the soil microflora. A series of laboratory and field investigations was therefore undertaken to determine the affects of natural and

human-induced stressors on soil respiration rate. These included the effects of soil type, C source, integrated seasonal variations in soil temperature and water, livestock grazing, and applications of irrigation water, herbicides and heavy metals.

SOIL TYPE

Soil type may influence microbial activity through differences in available C and nutrients, particle surface area, water content, and aeration. Untreated Burbank ls, Warden sl and Lickskillet 1 representing the range in soil properties on the ALE Reserve (Table 3.2) were incubated at 18 percent moisture for 30 days and soil respiratory activity measured. After 30 days of incubation, degradation ranged from 7 to 21 mg C/100 g of soil amounting to 0.6 to 2.4 percent of the total soil C present (Figure 3.2a). Evolution of C as CO_2 increased with increased soil C content, but the percentage of degraded soil C was inversely related to initial soil C content.

Amendment of the soils with A. spicatum shoot tissue at the 1-percent concentration level resulted in increased CO_2 evolution (Figure 3.2b). Correction for degradation occurring in the unamended soils allowed estimates of the degradation rate of the added tissue. After 30 days of incubation, degradation amounted to 34 to 106 mg C, or 8 to 24 percent of the C initially applied. The rate of tissue degradation was a direct function of soil type and organic C content. Differences between soil types likely reflected differences in microbial types and numbers, with microfloral activity enhanced in the finer-textured soils containing higher concentrations of organic matter.

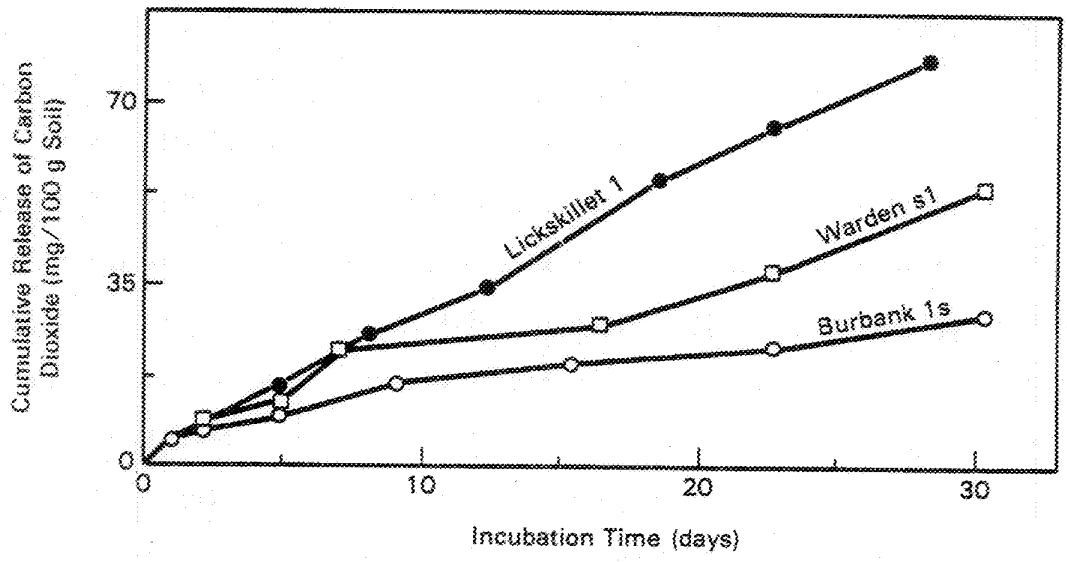

FIGURE 3.2a. Release of Carbon from Untreated Soils

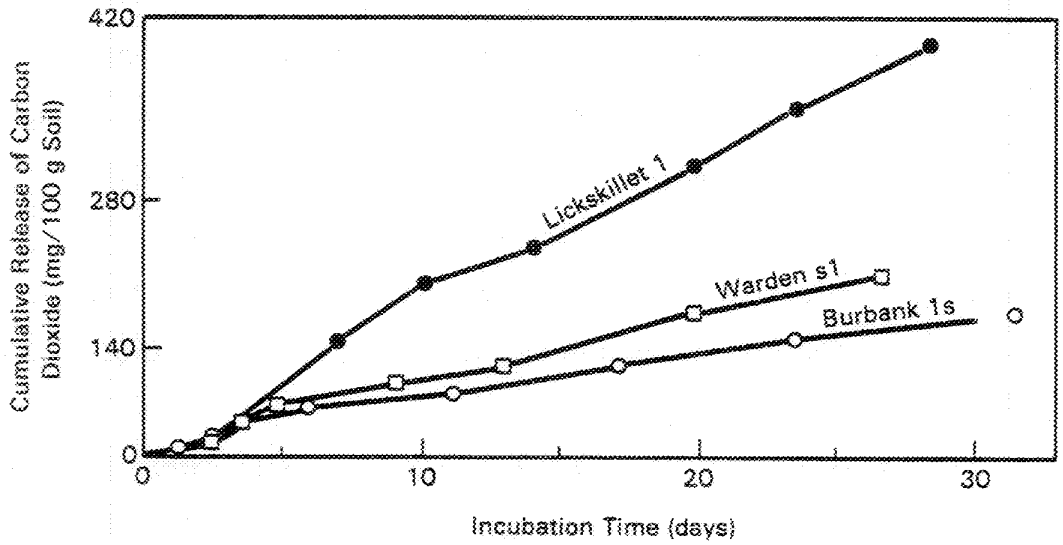

FIGURE 3.2b. Release of Carbon from Soils Amended with 1 Percent *Agropyron spicatum* Shoot Tissue (corrected for release of residual C, Figure 3.2a)

CARBON SOURCE

Carbon enters soils in the form of plant and animal residuals, but in the semi-arid shrub-steppe much of the nonliving, aboveground C is in the form of standing dead plant shoots. Litter layers occur largely in microcosms associated with shrubs or grass clumps. That which does enter soil will decompose successively, beginning with readily degradable materials (proteins, carbohydrates) and culminating with the more resistant components (carbohydrates, lignins). Thus, the rate of decomposition will differ between plants and plant components, depending upon relative composition.

To determine the influence of plant residue type and composition on the degradation rate of plant residue in soils of the ALE Reserve, Warden sl (Table 3.3) soil was amended with P. sandbergii shoots and roots at levels of 1 and 2 percent (by weight of dried plant tissue) and incubated at field moisture capacity (18 percent water) and 25°C for a period of 75 days. Soil degradation of P. sandbergii tissue proceeded rapidly during the initial phases of incubation as readily available carbonaceous materials were utilized (Figure 3.3a). After 5 days, degradation continued at reduced rates to 75 days, when the rate of microorganism proliferation apparently neared a stationary phase.

The active role of the soil microflora in organic matter degradation was substantiated by a marked increase in CO_2 evolution (Figure 3.3b) following reamendment of the soil system with P. sandbergii shoots and roots. A second re-amendment at 84 days with P. sandbergii shoots during exponential microfloral growth extended the phase of accelerated degradation without a lag phase, reflecting the ability of the adapted population to

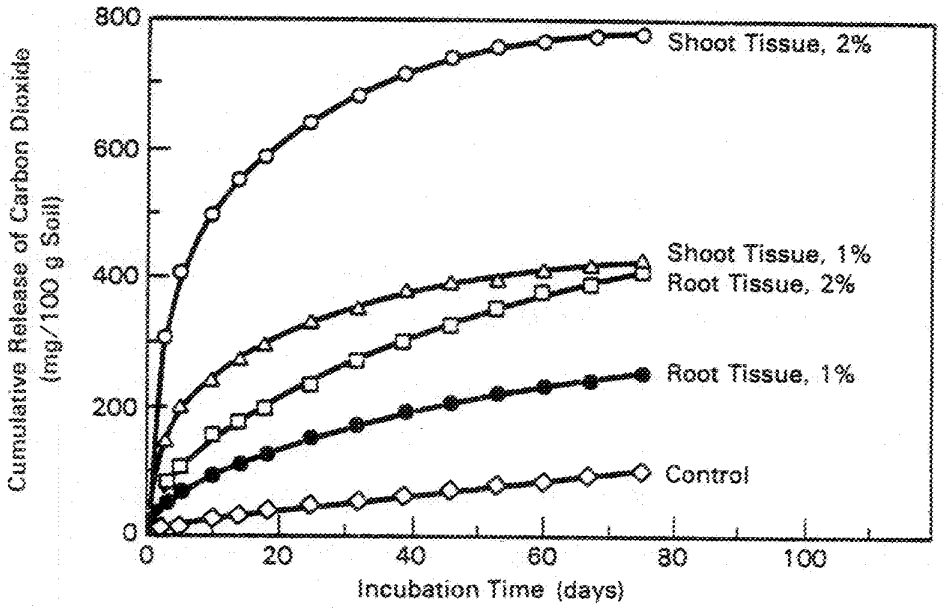

FIGURE 3.3a. Release of Carbon Dioxide from Warden sl Amended with *Poa sandbergii* Shoot and Root Tissue at Two Concentration Levels

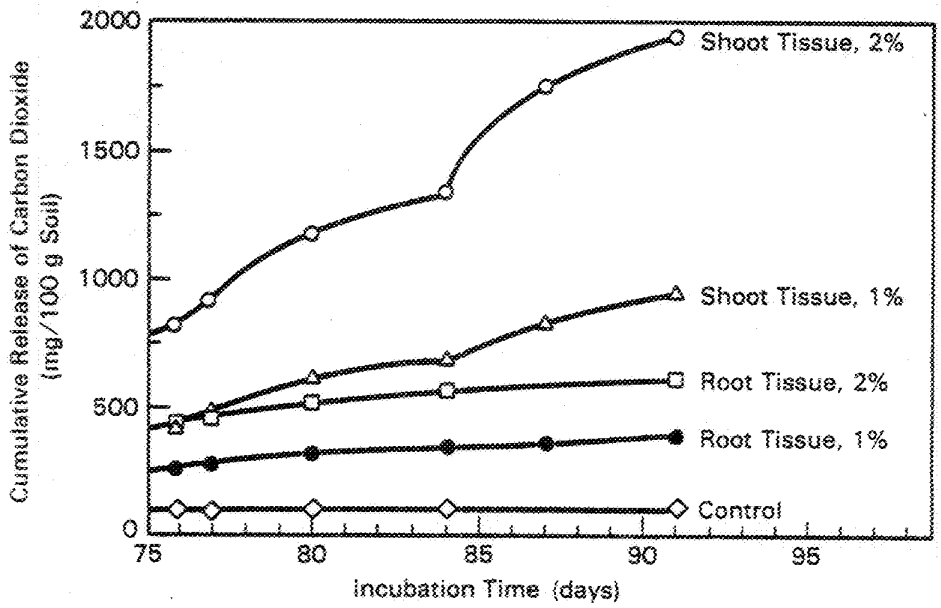

FIGURE 3.3b. Release of Carbon Dioxide from a Warden sl Soil Re-amended with *Poa sandbergii* Shoots and Roots After 75 Days of Incubation and *P. sandbergii* Shoots After 65 Days of Incubation

utilize the available C sources and the ability of the soil to provide other essential nutrients such as nitrogen. The potential of the soil to decompose the material was further exemplified by the proportional increases in decomposition when tissue amendment levels were increased. This pattern suggests that the soil microflora were capable of decomposing concentrations of tissues considerably higher than those employed.

The decomposition rates of P. sandbergii shoots exceeded those of roots by a factor of two (Figures 3.3a,b), suggesting major differences in the composition of readily degradable components. During field studies in which A. spicatum root and shoot tissues were buried in nylon mesh bags and retrieved at periodic intervals, the decomposition rate of A. spicatum shoots approximated that observed in laboratory studies and was also at least a factor of two higher than the roots (Wildung et al. 1973). The difference may reflect the larger fraction of more resistant cell wall material in roots. In contrast, shoot tissues from A. spicatum (Figure 3.2b) and P. sandbergii (Figure 3.3a) were approximately equivalent in their initial degradability, probably reflecting the similarities in readily soluble organic C (Wildung et al. 1968), although the higher lignin content of A. spicatum shoots might be expected to decrease the ultimate degradation rate relative to P. sandbergii shoots.

SOIL TEMPERATURE AND WATER

Soil temperature and water content, as well as the source and availability of nutrients, concentration of salt, pH, soil structure and texture, and atmospheric pressure, may be expected to have complex, interdependent effects on the rate of soil CO_2 production and diffusion (Baver 1959,

Witkamp 1966, Clark 1967, Kramer 1969, MacFadyen 1971, Alexander 1971). However, the incubation of P. sandbergii shoot and root tissues in soil under near-optimum temperature and moisture conditions resulted in decomposition of 20-35 percent of the organic C (Figures 3.2 and 3.3). Thus, during times of the year when sufficient moisture is available, a considerable portion of residual plant C will be lost to the atmosphere, accounting in part for the relatively low C content of these soils and illustrating the important influence of these variables on C cycling in the shrub-steppe. Comprehensive investigations were therefore undertaken to quantify the effects, in the field, of major seasonal changes in soil temperature and water content on soil respiration arising from the decomposition of plant roots, the primary direct source of C to the soil microflora in these systems.

The studies were conducted on a field plot located on the ALE Reserve (Figure 3.1) at an elevation of approximately 445 meters. The understory was dominated by Agropyron spicatum, whereas the principal overstory shrub species were Artemisia tridentata. The soil was a Ritzville silt loam (Tables 3.1 and 3.2). Soil CO_2 evolution, temperature and water content were monitored over a 2-year period, and the influence of changes in soil water and temperature on changes in respiration rate was quantified using multiple regression techniques. The experimental and statistical methodology have been described by Wildung et al. (1975).

The investigations were designed to measure the respiration rate of soils in cylinders, driven to a depth of 2 decimeters, which remained in place for 1-year periods. Thus, the roots present initially were killed, and new root growth to this depth was largely eliminated during the period

of placement. The quantities of roots potentially available for decomposition in the cylinders by soil organisms at the time of cylinder placement amounted to approximately 40 percent of the total biomass to a depth of 10 decimeters. Ancillary studies demonstrated that physical diffusion of CO_2 or live root respiration from areas outside the cylinders thus did not contribute significantly to respiration rates in cylinders placed at this depth. Respiration measured in these studies was, therefore, primarily due to decomposition by the soil microflora and fauna of dead roots and other organic matter in the upper 2 decimeters of the soil profile.

Over the 2-year monitoring period, soil respiration rates ranged from 0.18 to 1.21 g C/m^2/day. Respiration generally increased in the spring to annual maxima in the summer and decreased during the fall to minima in the winter (Figure 3.4). An estimate of the quantity of C evolved during respiration was obtained by integration of the area under the curves representing respiration rate as a function of time. This must be considered an approximation because of the infrequency of measurements at times during the year. However, using this integration technique, approximately 165 g C/m^2 were evolved from the cylinders each year. The soil in the cylinders did not contain recognizable root fragments after 1 year, and no root biomass was detected during the washing and screening technique employed (Rickard et al. 1972). The roots were apparently either decomposed or in advanced stages of decomposition. If it is assumed that the roots to 2 decimeters' depth (240 g C/m^2) represented the major source of organic C available to the soil organisms, then respiration by the soil organisms accounted for approximately 70 percent conversion of root C to CO_2 on an annual basis.

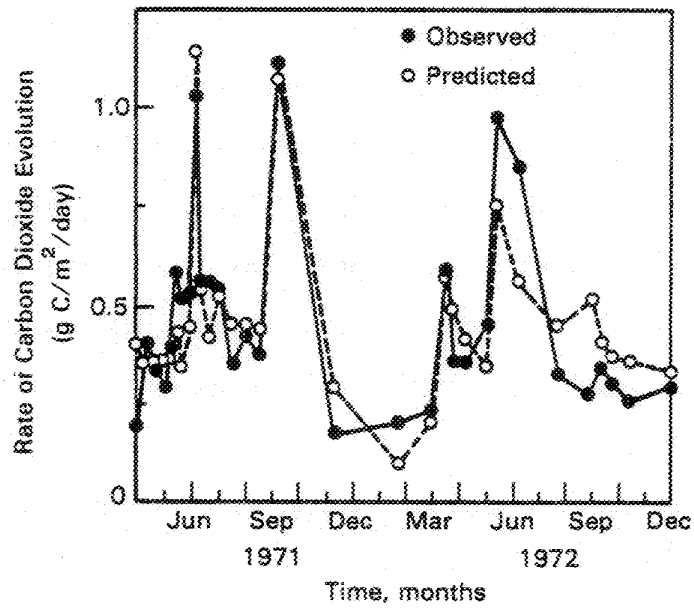

FIGURE 3.4. Seasonal Changes in Soil Respiration Rate [Range in standard errors was 2.3-10.6 percent (n = 12). The predicted values were derived from a simple regression which included only a soil temperature-water interaction term. Wildung et al. 1975]

The relative influence of soil water content on respiration rate differed with soil temperature. To assess the influence of soil water content on respiration rate over different temperature ranges, the ranges were selected on the basis of frequency distribution (Sturges 1926). The relationship of respiration rate to soil water content at the selected temperature ranges was described by the equation $y = a(1-e^{-bx})$, where y, a, b and x were the respiration rate (g C/m^2/day), a constant representing the asymptotic or upper limit of respiration, the nonlinear rate of increase in respiration, and the observed soil water content (percent), respectively. Nonlinear least-squares estimates of the parameters were obtained using the linearization method (Draper and Smith 1966).

Although respiration rate was generally limited by soil temperature in the fall, winter and early spring and by soil water content in the late spring and summer, temperature and water content interacted to affect soil respiration rate. Soil organisms responded to changes in soil temperatures at water contents as low as 1-2 percent (106-88 bar suction). Above approximately 6°C, increased soil water content resulted in increased soil respiration rate, but the extent of the increase was nonlinear and dependent upon soil temperature. Respiration rate approached a maximum at soil water contents of 6-10 percent (35-13 bar suction), depending upon soil temperature, and was generally optimum at temperatures above 15°C.

The interdependence of soil water and temperature in influencing changes in soil respiration rate during the study indicated the need for interaction terms in regression analyses. In order to determine the influence of soil water and temperature on respiration rate, regression equations were constructed using the data obtained over the 2-year monitoring period. The dependent variable (y) was considered to be soil respiration rate, and the principal independent variables were taken as soil water (w) and soil temperature (t). The contributions of the independent variables and an interaction term to the regression were expressed as percentages of the total variation about the mean soil respiration rate as defined by the regression and were calculated by squaring the multiple correlation coefficient (R) and multiplying by the 100. The mutual regulation of soil respiration rate by temperature and moisture during this study was best described by a soil temperature-water interaction or multiplicative term, and regression equations which included this term served to accurately

predict seasonal changes in soil respiration rate. Using a simple regression equation which included only the interaction term, it was possible to account for 70 percent of the total variation in soil respiration rate during the monitoring period (Wildung et al. 1975). The equation was

$$y = (0.88 \pm 0.15) + (0.013 \pm 0.002)\ (w)\ (t)$$

where y, w and t were expressed as

g C/m^2/day, percent and °C, respectively.

The simple regression equation appeared to have excellent predictive capability, being sufficiently versatile to describe the response of the soil microbiota to changes in soil water content at different temperatures. This versatility was most evident in the description of the marked changes in soil respiration rate which resulted from summer rains (Figure 3.4). The studies indicated that respiration rate was generally greatest at soil temperatures above 15°C and at water contents above 6-10 percent (35-13 bar suction). These results are consistent with laboratory studies which have indicated that maximum soil microbial activity occurs above 10-15°C (Richards et al. 1952) and above 40-60 percent of "field water capacity" (Katznelson and Stevenson 1956), which would be equivalent to water contents of 11-17 percent in the Ritzville soil. The positive effect of water content on respiration rate, even at temperatures as low as 6°C, indicated prevalence of aerobic conditions, generally required for heterotrophic decomposition (Raney 1965, Thimann 1967). Furthermore, the dependency of

the effect of water content on temperature suggested that distinct changes in organism types, numbers and metabolic activity (Thimann 1967) occurred in response to changes in temperature.

It may be concluded that over the long term, it is the combined effect of temperature and moisture which is most important in influencing C flow in soil. The importance of developing a means for examining the combined effect of temperature and moisture, i.e., the "hydrothermal" factor, was emphasized by Feher and Frank (1938) and by Kononova (1966). They attempted to define a scheme for seasonal intensity of biological activity in several soil types with a scale derived from meteorological records and from laboratory studies of the effects of temperature and water content on respiration rate. The results of the present studies indicate that a soil temperature-water interaction term would serve a unique purpose in this regard, and the concept of mutual regulation should prove useful in other investigations where it is necessary to examine or predict the effects of these parameters on the activity of soil organisms or on decomposition processes.

LIVESTOCK GRAZING

Grazing may be expected to influence soil respiration rate by altering conditions that influence microbial activity and plant root respiration (e.g., soil fertility levels, availability of readily available sources of C, disturbance of surface soil structure, and plant harvest). These effects should become more pronounced as grazing is continued. However, over the short term, changes in soil respiration rate due to grazing would probably be markedly influenced by changes in soil structure, as this influences soil

water-holding capacity, soil temperature and CO_2 diffusion. Equally influential would be changes in total plant biomass, which is related to consumptive use of soil water and the rate of root respiration.

As part of an effort to determine the influence of grazing on ecological processes, soil respiration rate was measured in grazed and ungrazed sections of the field plot (36 hectares) employed in the investigation described in the previous section (see also Chapter 6, Section II). Cattle (15 head) were allowed to graze alternatively at 7-day intervals on two 18-hectare replicates in the spring of 2 successive years (April 14 to June 10 and April 5 to May 16). Details of the experimental design have been described by Wildung et al. (1973). Soil respiration rate was measured as described earlier.

Soil water content, temperature, and their effects on soil respiration rate were not significantly different on the grazed and ungrazed sites when all data were considered. A t-test comparison (Figure 3.4) of all data on soil respiration rates of grazed and ungrazed plots for both years indicated that the treatments were not significantly different ($P = 0.05$). Use of the sign test indicated that the treatments were not significantly different in the first year, but the grazed site was significantly lower ($P = 0.01$) than the ungrazed site in the following year. In contrast to the "t" test, the sign test accounts for direction of change with time.

The multiple regression model described earlier that was utilized to predict soil respiration rate on the basis of soil water and temperature on the ungrazed site (Figure 3.4) was equally as effective on the grazed site. Since the CO_2 collection devices were inserted at the beginning of the spring each year and the methodology employed was designed to minimize the

contribution of root respiration, it may be concluded that decreases in root respiration on the grazed site were due to decreases in below-ground biomass available for decomposition. The total above-ground biomass of perennial grasses on the grazed and ungrazed sites, which was not significantly different in the spring prior to initiation of the first grazing period, was approximately 25 percent lower on the grazed than the ungrazed sites early in the following spring, prior to initiation of the second grazing period. The differences between treatments were accentuated with grazing and amounted to approximately 50 percent in June of successive years after grazing was terminated. The reduction in above-ground biomass was probably accompanied by a reduction in below-ground biomass, resulting in less available C and accounting for the observed decrease in C recycled to the atmosphere following 1 year of grazing.

IRRIGATION

Investigations to establish the effects of seasonal changes in soil temperature and water on CO_2 evolution from soil (previous section) showed that increased soil water during the spring, summer and fall, when temperatures were above 15°C, markedly increased microbial activity and respiration. Soil water changes resulted from seasonal changes in climatic conditions and moisture use by plants. In the present study, a field plot was established on the Hezel soil (Figure 3.1). Soil moisture was maintained by sprinkler irrigation at approximately 30 percent of field moisture capacity during the spring, ending in June. A selective herbicide was also applied (described in the next section) to examine effects on the productivity of native plants. Its use provided an opportunity to study the

effects of added water and herbicides on soil respiration rate in a different soil-plant system. Soil respiratory activity was therefore monitored for a 16-month period from early June through mid-September of the following year.

The Hezel soil type (described in the previous section) consists of hummocks comprised of wind-blown sand but stabilized by shrubs and associated grasses (primarily B. tectorum). The swards between hummocks consist of finer-textured sediments exposed by wind action with little vegetation. These two areas within the same soil type were shown to respond quite differently. The pattern of changes in soil temperature and water content for controls in both swards and hummocks reflected the patterns observed in the Ritzville sl-Agropyron system (Figure 3.5a). Application of irrigation water in the first spring did not significantly increase surface soil water contents relative to controls, likely reflecting the use by plants of water in the soil, but soil water storage in the late fall and winter increased markedly. Further irrigation in the spring generally maintained increased water levels relative to controls. Reflecting the results of other studies, soil respiration rate responded to temperature and moisture controls. Soil respiration rates (Figure 3.5b) were generally maintained at higher levels in the spring by the addition of irrigation or rain waters when temperatures exceeded 10-15°C. Soil respiration rate in the hummocks during these periods was elevated in both controls and irrigated treatments relative to the swards, undoubtedly reflecting the increased biomass associated with these systems. This system has strong analogies with the Ritzville-Agropyron system described earlier. The swards developed on the Hezel s resulted from soil genesis and erosion processes; on the Ritzville, they resulted from the phenology of bunchgrass. In both systems, microcosm

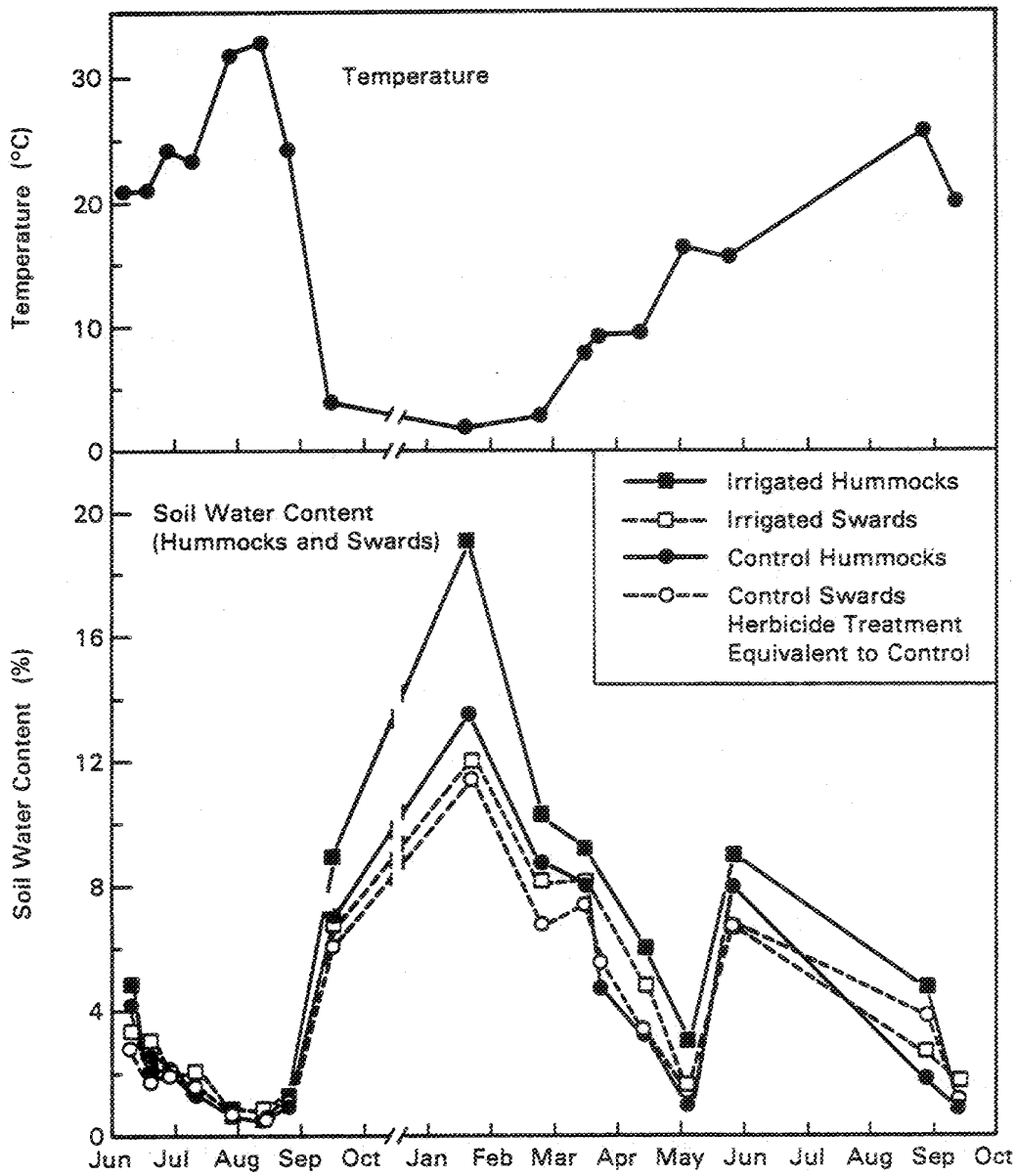

FIGURE 3.5a. Seasonal Changes in Soil Temperature and Water Content on Field Plots Receiving Irrigation Water and Herbicide (The studies were conducted on a Hezel s characterized by coarse-textured hummocks with high biomass and fine-textured swards with minimum biomass.)

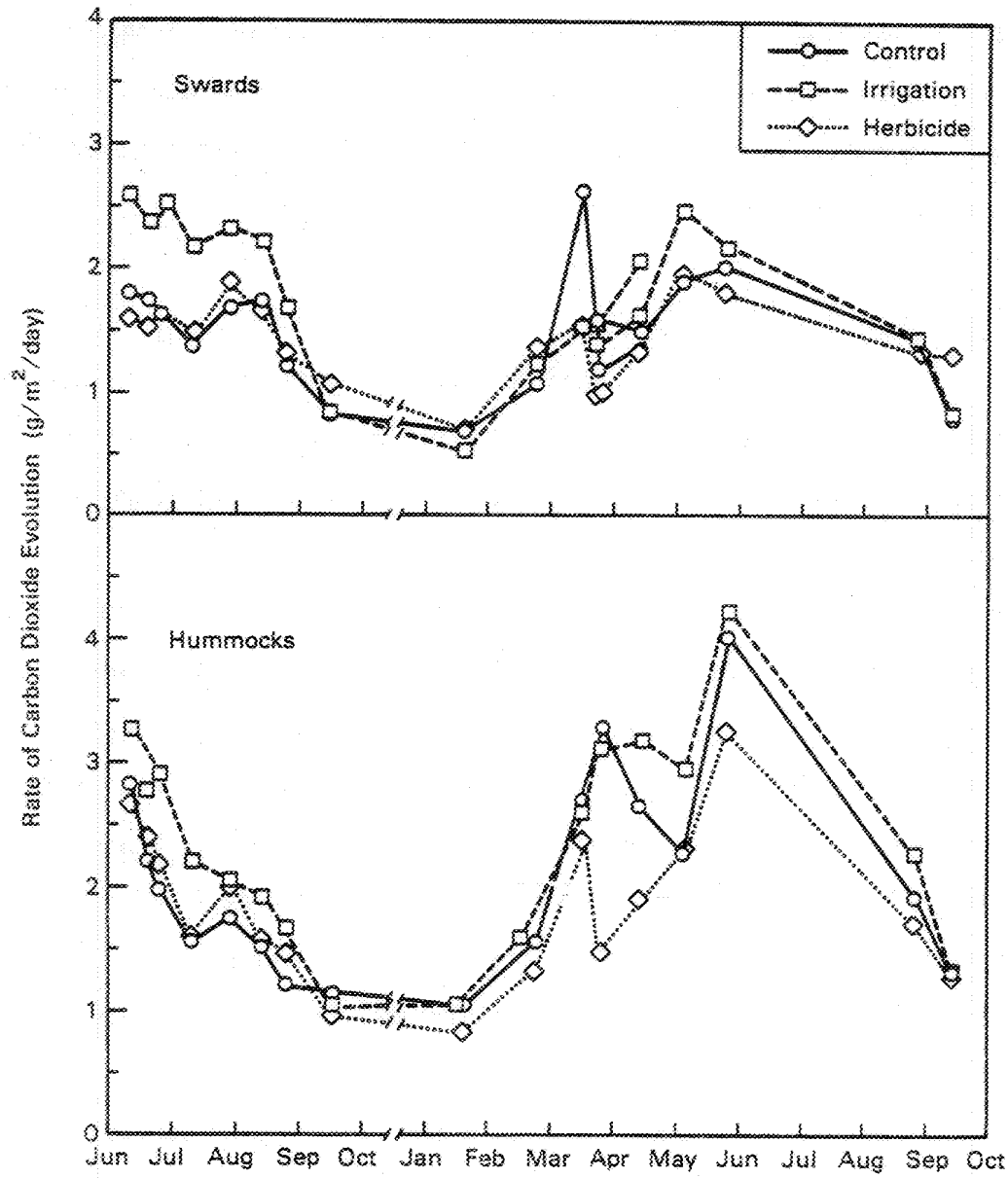

FIGURE 3.5b. Seasonal Changes in Soil Respiration Rate on Field Plots Receiving Irrigation Water and Herbicide (The studies were conducted on a Hezel s characterized by coarse-textured hummocks with high biomass and fine-textured swards with minimum biomass.)

biomass was elevated relative to the associated swards. Hummocks and swards both maintained a base rate of approximately 1 g CO_2/m^2/day during periods when biological activity was restricted by either temperature (<5°C) or water content (<4 percent).

HERBICIDES

Although the irrigation and herbicide studies on the ALE Reserve emphasized the effects on plant and animal communities, the studies offered an opportunity to examine the influence of these parameters on soil respiration rate.

The methods employed on the ALE Reserve for field measurements of soil respiration rate were designed to examine the effects of organic matter decomposition, not the effects of plant root respiration. The same methods were utilized in the irrigation and herbicide studies, and in coarser-textured soils such as the Hezel, some upward diffusion of CO_2 might occur. In that case, selective removal of a plant species should provide insight into the contribution of that species to total soil respiration--if the plant selected made detectable contributions to soil respiration and if herbicide treatment did not influence microbial respiration rate.

The herbicide CIPC was applied to the nonirrigated portion of the field plot described earlier. The herbicide is effective against the *B. tectorum* that comprised the dominant grass understory and exhibits a short half-life in soil (weeks). It was applied in December to kill young *B. tectorum* seedlings, and soil respiratory activity was monitored as in the irrigation plots.

The herbicide was effective in eliminating B. tectorum growth, but soil water content was not influenced (Figure 3.5a). Herbicide treatment did not significantly reduce soil respiration rate in the hummocks until after March 25 in the spring of the second year (Figure 3.5b). At that time, new collection vessels were inserted. Undoubtedly, the quantity of roots placed in June of the previous year decreased as a result of the herbicide application, and effected a corresponding decrease in soil respiration rate. This conclusion is substantiated by the lack of an effect in the swards, which were largely devoid of B. tectorum before herbicide treatment. These studies demonstrated that, as intended, plant respiration was not being measured in this system. The research also confirms that, analogous to grazing, selective removal of a grass species affects belowground biomass sufficiently to reduce C recycling to the atmosphere.

METALS

Trace metals may enter the shrub-steppe through a number of avenues, including deposition as a result of fossil fuel combustion and cooling tower blowdown (Vaughan et al. 1975, Horton et al. 1977), disposal of municipal and other wastes (McCalla et al. 1977) and direct application of fertilizers and other soil amendments (Allaway 1968). The latter have been used extensively in the shrub-steppe in range management programs.

Some of the metals, such as the transition elements, form stable complexes with biological ligands. At elevated concentrations, these complexes then become extremely potent inhibitors of certain cellular enzymatic processes. Since many, such as manganese and iron, are essential for cell reproduction and growth, a delicate balance in concentration must be maintained to avoid

toxicity. The current study was undertaken to assess the potential effects of metals entering soils on soil microbial types and numbers and on respiration rates.

The investigations entailed incubation of a Ritzville sl in glass cells maintained at 22 percent water continuously flushed with moistened CO_2-free air. The evolved CO_2 was continuously determined. Microbial types and numbers were estimated using standard plate counts on stock inocula obtained from periodic subsampling of soils (Wildung and Garland 1982).

The effects of the metals employed in initial screening studies on microbial types and numbers and metabolic activity after a 6-day incubation period are summarized in Table 3.6. Effects were monitored over a 14-day period; however, 6 days was an appropriate time for comparison because most organisms were in the exponential growth phase as measured by cumulative CO_2 evolution from soil.

Both toxic and stimulative effects were observed after treatment with metals. Toxicity among the bacteria and actinomycetes generally increased with increased trace element concentration and was minimal at the 1 μg/g treatment level. This level represented a significant increase in total soil concentration for the elements Ag, Cd, Hg, Mo, Sb, Sn, Tl and W and a very pronounced increase for all elements compared to soluble levels.

The fungi were the most resistant microorganisms to the trace elements examined (Table 3.6), except for Ag and Cr at the 100 μg/g treatment level and Ni at the 1 μg/g treatment level. The latter does not appear commensurate with other observations. The general enhancement of fungal growth for 10 of the 17 elements at the highest treatment level is consistent with the increased toxicity to, and reduced competition by, other organisms such as the aerobic bacteria, generally the least resistant of the microbial classes examined.

TABLE 3.6. Effects of the Additional of Trace Element Salts on Types and Numbers of Microorganisms and Their Metabolic Activity in Soil[a,b]

	Ag	As	Cd	Co	Cr	Cu	Fe	Hg	Mn	Mo	Ni	Pb	Sb	Sn	Tl	W	Zn
	1 fg element/g soil																
Aerobic Bacteria[c]	0.84	1.0	1.4	0.88	0.81	0.97	0.20	0.66	1.1	0.61	1.1	0.82	0.38	0.22	1.1	0.90	1.1
Anaerobic Bacteria[c]	1.7	0.83	3.5	1.2	0.77	1.2	1.1	0.56	1.9	1.0	0.91	0.81	0.92	0.97	0.90	2.3	1.1
Spore-Forming[c] Aerobic Bacteria	1.7	0.73	1.1	1.3	0.94	1.4	0.78	0.94	1.2	1.0	0.53	0.94	1.0	0.68	0.89	2.4	1.3
Spore-Forming[c] Anaerobic Bacteria	2.4	1.0	1.6	1.1	0.62	1.4	0.81	0.94	1.5	1.1	1.2	0.71	1.2	0.68	1.1	2.8	1.4
Actinomycetes[c]	1.1	0.51	0.88	0.57	0.69	1.1	0.33	1.2	1.8	0.65	1.1	0.90	1.3	0.27	1.2	1.0	0.91
Fungi[c]	1.0	1.3	0.90	0.76	0.76	1.3	0.68	4.8	1.2	1.0	0.27	1.0	1.1	0.89	1.5	0.70	1.2
Rate[d]	1.9	1.3	1.1	1.0	0.59	1.0	0.60	1.8	1.0	1.0	1.2	0.90	1.1	0.80	1.0	0.90	1.4
Total Evolved[d]	1.5	0.96	1.0	1.0	0.83	1.1	0.88	1.7	1.1	1.0	0.90	0.90	1.0	0.87	1.0	1.0	0.97
	10 fg element/g soil																
Aerobic Bacteria[c]	0.25	1.2	1.0	0.79	0.69	1.1	0.64	0.048	1.2	0.25	0.84	0.65	0.47	0.46	1.0	1.3	1.1
Anaerobic Bacteria[c]	1.5	0.75	0.55	0.96	0.17	1.3	1.2	0.67	1.7	0.72	0.59	0.82	0.81	1.1	1.9	2.3	1.2
Spore-Forming[c] Aerobic Bacteria	2.6	0.90	2.1	1.1	0.27	1.0	0.73	0.13	1.0	1.0	0.50	1.3	1.0	0.94	1.7	1.6	1.6
Spore-Forming[c] Anaerobic Bacteria	4.7	1.2	0.71	0.93	0.067	0.75	0.72	0.15	1.4	1.2	1.3	0.84	1.0	0.92	2.4	1.3	1.7

(a) After 6 days' evaluation
(b) Effects are significant at $p < 0.01$ for ratios of microbial numbers <0.5 (toxicity) and >1.5 (stimulatory effect). Effects are significant at $P < 0.01$ for ratios of carbon dioxide evolution, <0.8 (toxicity) and >1.2 (stimulatory effect).
(c) Ratio of microbial colony-forming units to untreated controls.
(d) Ratio of carbon dioxide evolution to untreated controls.

TABLE 3.6. (contd)

	Ag	As	Cd	Co	Cr	Cu	Fe	Hg	Mn	Mo	Ni	Pb	Sb	Sn	Tl	W	Zn
	10 fg element/g soil (contd)																
Actinomycetes[a]	0.26	1.6	0.53	0.47	0.62	1.5	0.61	0.22	1.5	0.46	1.0	0.79	0.89	0.72	1.8	1.3	0.88
Fungi[a]	0.85	1.2	1.5	0.67	1.2	1.4	0.91	7.7	>2.0	1.1	0.58	0.90	0.99	1.1	>2.0	1.4	1.0
Rate[b]	0.70	1.3	1.2	1.0	0.50	0.90	0.70	2.5	1.1	1.1	0.90	0.90	1.1	0.70	0.90	0.70	1.5
Total Evolved[b]	0.64	1.0	1.2	1.0	0.81	0.95	0.88	0.95	1.1	1.0	0.92	0.94	0.98	0.90	1.0	0.93	1.0
	100 fg element/g soil																
Aerobic Bacteria[a]	0.0034	0.98	0.11	0.32	0.12	0.53	0.12	0.0050	0.72	0.46	0.21	0.82	0.53	0.34	0.073	1.0	0.55
Anaerobic Bacteria[a]	0.011	1.3	0.22	1.1	0.038	0.081	0.15	0.011	1.2	0.73	0.33	0.97	0.83	0.030	2.1	1.8	0.83
Spore-Forming[a] Aerobic Bacteria	0.016	1.6	0.080	1.0	0.080	0.14	0.19	0.042	0.78	1.0	0.13	1.0	1.0	0.017	1.0	2.1	0.70
Spore-Forming[a] Anaerobic Bacteria	0.030	2.4	0.16	0.63	0.015	0.045	0.12	0.016	2.6	0.70	0.043	0.69	0.90	0.0030	2.2	1.3	0.41
Actinomycetes[a]	0.0039	0.93	0.025	0.33	0.20	0.042	0.14	0.013	1.2	0.74	0.32	0.72	1.9	0.26	0.10	1.2	0.75
Fungi[a]	0.038	1.9	3.0	0.76	0.41	3.3	1.4	12	>2	0.64	1.9	0.76	0.68	2.6	>2.0	3.8	32
Rate[b]	0.30	1.9	0.90	0.80	0.50	0.80	0.50	0.70	1.2	0.50	2.6	0.70	1.3	0.50	0.60	0.80	2.5
Total Evolved[b]	0.39	1.4	1.3	0.95	0.42	0.78	0.82	0.57	1.0	0.88	1.2	0.82	1.1	0.76	0.88	1.0	1.3

(a) Ratio of microbial colony-forming units to untreated controls.
(b) Ratio of carbon dioxide evolution to untreated controls.

As is the case of microbial numbers, soil CO_2 evolution reflected the dynamic microbial system: successive changes occurred in individual classes with growth and in response to metals. However, the microbial classes examined do not constitute all the organisms that may contribute to respiration, and taken individually, they would not be expected to significantly influence respiration. The accumulative CO_2 (Table 3.6) correlated with total microbial numbers, as both increased with incubation time. The CO_2 evolution rate generally reflected the effects of increasing trace element concentrations on the microbial numbers.

The effects of Cr on respiration rate were particularly pronounced. Chromium was the only element that significantly reduced soil respiration rate at the 1 $\mu g/g$ treatment level (Table 3.6). It was postulated that Cr inhibited the conversion of starch to glucose through a reduction in extracellular anylase in soil. To determine the validity of this hypothesis, a series of experiments were undertaken. The results are described by Drucker et al. (1979). In summary, it appeared that Cr inhibition of amylotic enzymes was not a major factor limiting metabolic activity. Alternatively, the studies suggested that in the presence of Cr, there was a selection with time (24 days) for Cr-resistant organisms capable of metabolizing glucose by a pathway qualitatively different from organisms in the controls. Over the shorter periods of measurement employed in comparative studies (Table 3.6), the principal impact was on the decomposition of glucose and its conversion to CO_2.

From measurements of microbial numbers and soil respiration, the general order of toxicity for most classes of bacteria and the actinomycetes was determined to be Ag > Hg > Cr > Cd > Ni > Cu > Tl > Co > Mo. The fungi, as the most resistant organisms, tend to dominate at the expense of the other

organisms when toxic metal concentrations are reached. Toxicity of the metals will depend on the concentration and chemical speciation of the elements in solution, which, in turn, will be a function of metal source, soil properties and environmental factors (Wildung and Garland 1980). However, it appears that the most toxic elements alter microbial ecology and inhibit C flow at 10 μg/g and that major impacts might be expected between 10 and 100 μg/g. At the higher concentrations, the fungi tend to dominate, with corresponding effects on a number of microbially mediated decomposition and mineral cycling processes.

Section IV. Relationship of Carbon Cycling to Mineral Weathering and Mobilization

Although representing less than 1 percent of the total soil volume, the living portion of the soil is intimately involved in the cycling of nutrient elements and the flow of energy in the environment. The soil contains numerous small animals (Burges 1967), but the fate of C, N, S and P entering the soil in plant and animal residues, fertilizers and wastes depends most upon the activities of soil microbes. In addition, plant root and microbial decomposition processes may indirectly influence mineral weathering and the behavior of other elements through alteration of the soil atmosphere and soil solution composition (Routson and Wildung 1969, Cataldo and Wildung 1983).

Under aerobic conditions, soil microflora and plants, as part of their life cycles, convert energy in the form of reduced compounds of C to the lowest energy level, that is, CO_2 and water (Delwiche 1967). As a result of this process, CO_2 is present in the soil at levels several hundred times that of the atmosphere. When CO_2 reacts with soil water, carbonate, bicarbonate and carbonic acid, a dynamic equilibrium forms, the nature of which is a function of the partial pressure of CO_2. This system has marked influence on mineral stabilities and soil solution chemistry. In addition, intermediate products excreted during the decomposition process are as complex as life itself and have the potential for interacting with soil minerals and solutes, forming complexes which influence subsequent elemental biological availability and mobility of elements in soil. These processes have been the subject of intensive study in laboratory and field studies on soils of the shrub-steppe.

MINERAL WEATHERING

Primary rock-forming silicate minerals compose over 95 percent of the earth's crust. These rock-forming minerals, which have generally crystallized in higher temperature and pressure environments than those of the earth's surface, are thermodynamically unstable relative to the clay minerals (Garrels and MacKenzie 1967, Routson and Kittrick 1971). Unstable minerals weather at the earth's surface, forming the more stable clay minerals and releasing mineral components to solution. This process serves as a control on the solute composition of the soil solution, and, ultimately, of groundwater. Understanding the weathering process is therefore requisite for understanding the total plant-nutrient cycle in natural ecosystems and the chemical behavior of pollutants entering soil systems.

To define mineral weathering processes, sequences and controls operational in the arid shrub-steppe, a study was undertaken (Routson et al. 1977) on a closed, 71-hectare watershed located over an elevational range of 760-1060 meters near the crest of the Rattlesnake Hills on the ALE Reserve (Figure 3.1).

The watershed has an estimated mean rainfall of 22 cm/yr (Hinds and Thorp 1974). Soils of the selected watershed belong primarily to the Lickskillet sl series (Tables 3.2-3.5), which grades into a very stony loam and basalt talus, as well as rock outcrops at the upper elevations. The silt loam texture is largely attributable to loessal deposition of primarily felsic origin (Table 3.2).

The soils of the watershed were developed from parent materials of mixed mineralogy, necessitating an empirical approach to definition of the weathering schema (Routson et al. 1977). This entailed (1) measuring the solute composition of a perennial spring, which is likely the sole groundwater effluent

from the watershed, (2) measuring the influent solutes from precipitation, and (3) theoretically back-reacting the solutes estimated to arise from weathering [obtained from the difference between (1) and (2)] with the secondary clay minerals of the watershed to identify the primary rock-forming minerals responsible for controlling the watershed effluent water composition.

The average watershed spring water concentration from six samplings encompassing a period of approximately three years is given in Table 3.7. Standard deviations for all components were about equal to the variation found for duplicate analyses for all solutes. Thus, little of the variation is likely caused by seasonal variation. No seasonal trends in the data were evident. Total mean cation concentration was 1.9×10^{-3} eq/L compared to a total mean anion concentration of 2.0×10^{-3} eq/L, indicating analytical consistency.

TABLE 3.7. Mean Chemical Composition of Perennial Spring Water Draining an Arid Watershed from South-Central Washington State[a] (Data from Routson et al. 1977)

Component	Concentration ($M/L \times 10^4$)
Na^+	2.8 ± 0.8
K^+	0.41 ± 0.02
Ca	4.1 ± 0.3
Mg	4.1 ± 0.04
SiO_2	5.4 ± 0.1
HCO_3	17 ± 0.7
Fe	<0.04
Al	<0.05
SO_4	0.81 ± 0.14
pH	7.9 ± 0.1

(a) Mean of seven analyses over 3 years ± standard deviation

The mean equilibrium partial pressure of the soil gaseous phase was calculated from the solubility of CO_2 in solution, pH, and ionic strength (Garrels and MacKenzie 1967, Hem 1970). The CO_2 partial pressure was found to be $10^{-2.8}$, compared to a partial pressure of the atmosphere of $10^{-3.5}$. Thus, this is an aggressive water, which may be expected to react with carbonate minerals and weather crystalline minerals as discussed in previous sections. The source of excess CO_2 is probably the respiration of soil organisms such as plant roots, microflora, and macrofauna, which may ultimately control the weathering dynamics in such a system (Garrels 1968).

An estimate of the contribution of primary rock-forming minerals to the composition of perennial spring waters can be inferred by calculating the weathering reactions in reverse (Garrels and MacKenzie 1967, Garrels 1968). This is equivalent to constituting the original rock-forming minerals from a back reaction of the drainage water solutes with the solid-phase products of weathering. These products include the secondary clay minerals, i.e., montmorillonite and kaolinite, as well as amorphous hydrous-oxides of Fe and Al (Table 3.8). A proposed weathering scheme based on these and other assumptions and data is shown in Figure 3.6.

From the calculations, it was evident that soluble SiO_2 (H_4SiO_4) in the watershed was derived from the weathering of plagioclase, biotite, and pyroxene, even though quartz is a major mineral in the parent material (Table 3.4). Comparisons with other watersheds indicated elevated Mg levels and reduced Na/Ca ratios, reflecting, respectively, the weathering of the dominant plagioclases and of the Mg-pyroxenes present in basalts. The Fe and Al were largely conserved in the solid phases of the watershed. In additiona, the data suggest that the reaction of CO_2 with rock-forming minerals is reasonably

TABLE 3.8. Summary of the Theoretical Back Reaction of Perennial Spring Water Solutes and Solid-Phase Weathering Products to Reform Primary Rock-Forming Minerals in an Arid Watershed[a,b]

	Na	K	Ca	Mg	SiO_2	HCO_3^-	SO_4^-
Initial solutes	2.8	0.41	4.1	4.1	5.4	17.0	0.81
-Snow (corrected for evapotranspiration)	2.7	0.39	4.1	4.1	5.3	15.3	0
Kaolinite[c] biotite	2.7	0	4.1	2.9	4.5	12.6	0
Kaolinite[d] plagioclase	2.5	0	3.8	2.9	4.1	11.8	0
Montmorillonite[e] plagioclase	0.5	0	0.9	3.5	4.2	5.2	0
"Ions" + hydrous iron oxide[f] pyroxene	0.5	0	0.9	0	0.2	-1.8	0

(a) Mean of seven analyses

(b) Garrels and MacKenzie 1967, Routson et al. 1977

(c) Kaolinite to biotite: $0.20\ Al_2Si_2O_5(OH)_4 + 0.39\ K^+ + 1.17\ Mg^{+2} + 0.77\ SiO_2 + 2.73\ HCO_3 \rightleftarrows 0.39\ KMg_3AlSi_3O_{10}(OH)_2 + 2.73\ CO_2 + 1.56\ H_2O$

(d) Kaolinite to plagioclase: $0.38\ Al_2Si_2O_5\ (OH)_4 + 0.20\ Na^+ + 0.30\ Ca^{+2} + 0.40\ SiO_2 + 0.80\ HCO_3^- \rightleftarrows 0.5\ Na_{0.40}Ca_{0.6}Al_{160}Si_{2.40}O_8 + 0.80\ CO_2 + 1.15\ H_2O$

(e) Montmorillonite to plagioclase: $3.32\ Ca_{0.22}Mg_{0.18}Si_{3.56}Al_{2.36}O_{10}(OH)_2 + 2.0\ Na^+ + 2.9\ Ca^{+2} + 6.6\ HCO_3^- \rightleftarrows 4.9\ Na_{0.40}Ca_{0.60}Al_{1.60}Si_{2.40}O_8 + 0.6\ Mg^{+2} + 6.6\ CO_2 + 6.3\ H_2O + 0.05\ SiO_2$

(f) Hydrous iron oxide + "ions" to pyroxene: $0.50\ Fe\ OOH + 3.5\ Mg^{+2} + 7.0\ HCO_3^- + 4.0\ SiO_2 \rightleftarrows 1.0\ [Mg_{3.5}Fe_{0.5}(SiO_3)_4] + 7.0\ CO_2 + 4.0\ H_2O$

Biotite [$K\ Mg_3AlSi_3O_{10}(OH)_2$] + carbonic acid ➡ Kaolinite [$Al_2Si_2O_5(OH)_4$] + solutes.

Basaltic plagioclase [$Na_{0.40}Ca_{0.60}Al_{1.60}Si_{2.40}O_8$] + carbonic acid ➡ Kaolinite + solutes.

Basaltic plagioclase + carbonic acid ➡ Montmorillonite [$Ca_{0.22}Mg_{0.18}Si_{3.56}Al_{2.36}O_{10}(OH)_2$] + solutes.

Pyroxene [$Mg_{3.5}Fe_{0.5}(SiO_3)_4$] + carbonic acid ➡ Hydrous oxides of Fe + solutes.

FIGURE 3.6. Proposed Simplified Weathering Scheme for an Arid Watershed in Southcentral Washington State (Routson et al. 1977)

rapid and occurred largely within the soil profile because the pH of the watershed spring water is alkaline and an acid pH would be expected at the calculated partial pressure of CO_2 in this system if no reaction had occurred.

If the proposed reactions represent accurately the weathering sequence that controls effluent water composition of the watershed, a mass balance should be attained; i.e., the calculated residual solutes should equal zero and the actual composition of the effluent spring. These measures were within the standard error of the analyses.

In summary, the composition of perennial spring waters draining an arid watershed of mixed mineralogy appears to be controlled by the weathering of the mafic plagioclase. Respiration resulting from metabolic processes serves as the ultimate control of the dynamics of weathering. Weathering reactions are apparently rapid, occurring within the soil profile.

MOBILIZATION OF TRACE ELEMENTS AND RADIONUCLIDES

The concentration and speciation of elements in the soil solution is controlled simultaneously by both geochemical and biological factors. A great deal is known about the geochemical controls on the solubility of trace elements in soil (Jenne and Luoma 1977, Keeney and Wildung 1977, Lindsay

1979), but consideration of physicochemical factors alone underestimates elemental mobility in natural systems. There is much less understanding of the effects of soil microbiological activity on trace element solubility or of the nature of the complex, dynamic equilibria that exist at the interface between the soil solution and the root symplast, particularly the effects of root secretions on elemental stability. From studies in agricultural systems, it is clear that biological control or regulation is imposed by both soil microbial and plant processes, but the mechanisms are defined insufficiently to develop valid conceptual and predictive models for long-term elemental (nutrient, pollutant) behavior in soil-plant systems. In natural systems such as the arid shrub-steppe, even less is known. The importance of these processes in the shrub-steppe is illustrated in Figure 3.7. As noted previously, Fe is generally conserved in these systems; i.e., as a hydrolyzable element, its mobility is limited by mineral solubility controls. Thus, in the absence of biological activity, Fe is generally uniformly distributed down the soil profile. In the rhizosphere of Artemisia tridentata, however, soluble Fe is present in higher concentrations at the soil surface where plant recycling processes and microbial activity are most pronounced. In addition, the distribution of Fe down the profile is closely related to soluble organic C, which provides an overall measure of biological activity, and which is an indication that organic complexing ligands from plant and microbial metabolism play a role in Fe mobilization. These phenomena, illustrated in Figure 3.8, may therefore control the soil mobility, plant availability and subsequent transfer of elements from plants to animals (Cataldo and Wildung 1978, 1983).

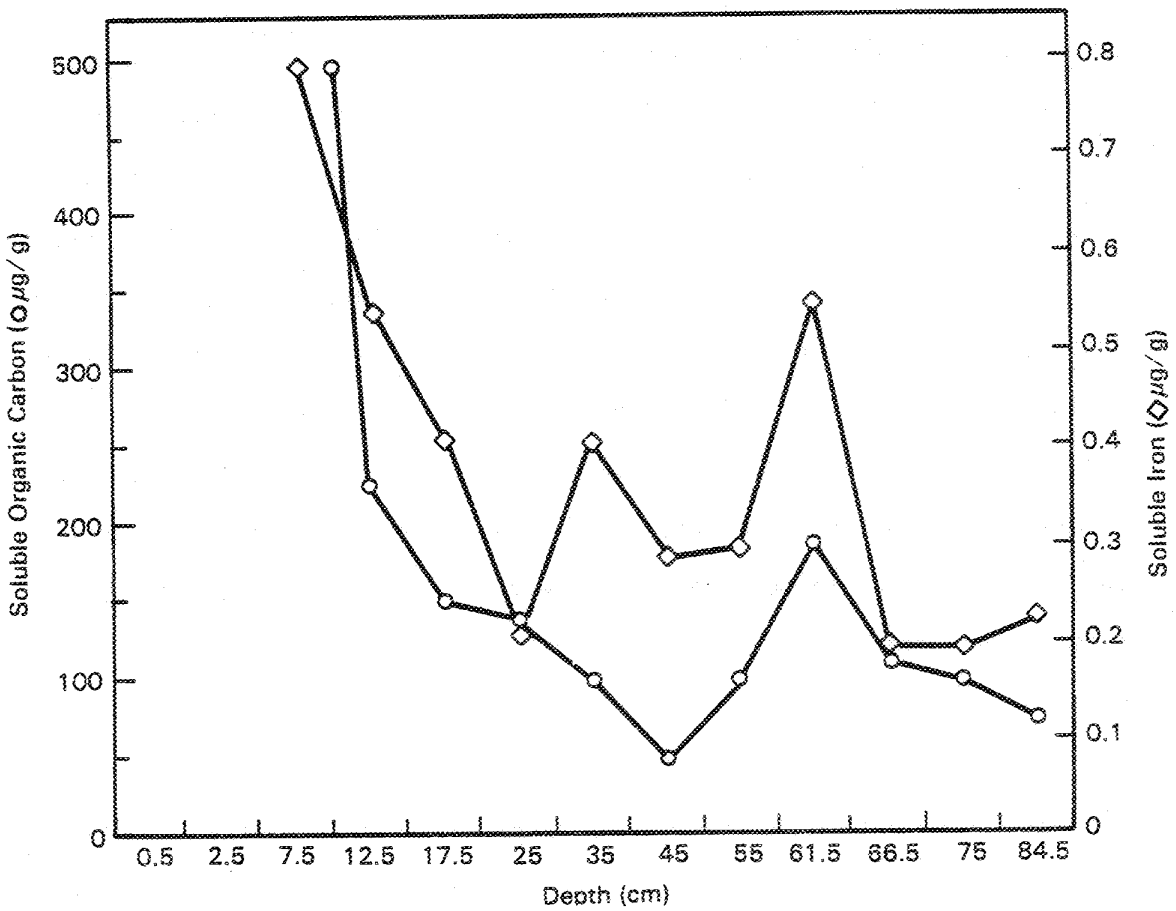

FIGURE 3.7. The Relationship of Soluble Organic Carbon and Iron with Soil Depth in the Rhizosphere of *Artemisia tridentata*

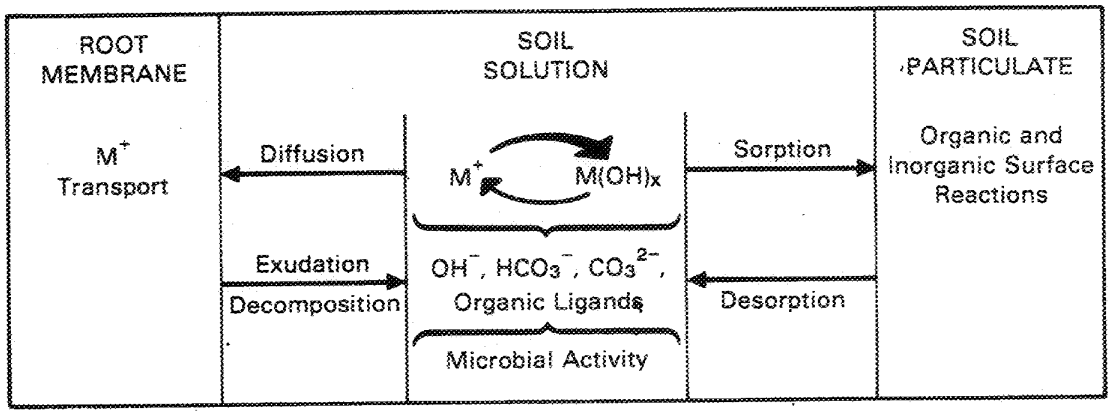

FIGURE 3.8. Metabolic Factors Influencing Hydrolyzable Trace Element Behavior in Soil and Uptake by Plants (Wildung et al. 1986b)

The microbial and plant metabolic processes governing the behavior of trace elements in the rhizosphere and subsequently in plants and animals has been the subject of intensive study for the Department of Energy and the the National Institutes of Environmental Health Sciences over the past decade. Until recently, the research had focused on agricultural plants but employed the soils of the arid shrub-steppe. At the onset of this project, conceptual models were developed to explain possible metabolic phenomena controlling trace metal behavior in the soil-plant system. The soil model (Figure 3.8) was based on the hypothesis that interactions of the hydrolyzable metals with microbial and plant metabolites resulted in metal stabilization against hydrolysis, decreased sorption on solid phases and increased mobility and plant availability. A corresponding plant model hypothesized disassociation of the soil complexes at the root membrane and transport and localization in the plant through interaction with a series of plant-derived organic ligands. This process would facilitate translocation within the plant, and the presence of complexes was postulated to increase gastrointestinal absorption upon consumption by animals. Research progress in defining the behavior of trace elements in plants and animals has been summarized elsewhere (Garland et al. 1981, Cataldo and Wildung 1983, Cataldo et al. 1986).

The soil model was tested with an experimental approach (Figure 3.9) designed to establish which elements were likely to be influenced by soil microbial and plant metabolic processes, to focus research efforts on representative elements and key processes, and to delineate the most important phenomena controlling elemental behavior and form. The approach was based on separate examination of plant and microbial sources of organic ligands,

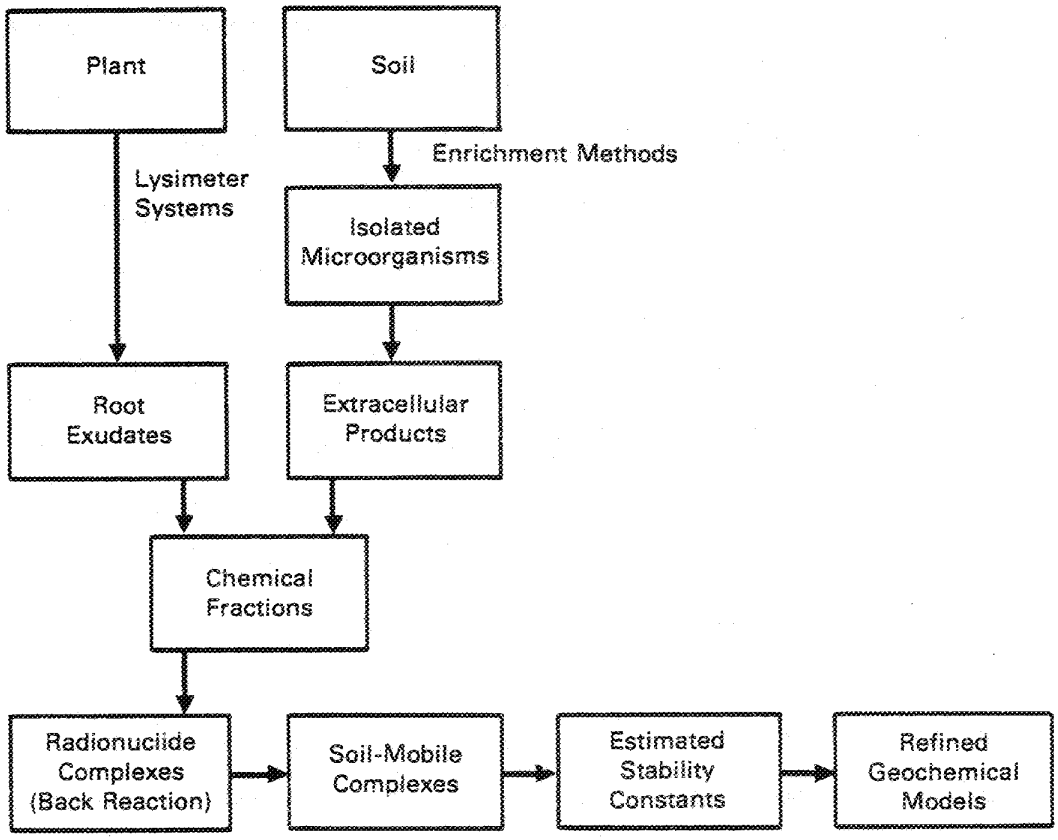

FIGURE 3.9. Overall Research Approach to Delineate the Interactions of Soil Microbial and Plant Root Exudates with Inorganic Elements (trace metals, radionuclides) in Soil

and a comprehensive investigative process that leads to a focus on those ligands most important in governing mobility in soil and definition of their effect through geochemical models.

The plant studies have been only recently been initiated and represent the primary future research direction in these studies. A broad range of soil microorganisms were isolated from soil. Selection was based on their cation requirements, metal tolerance and ability to exocellularly complex metals. Plants are grown in nutrient solutions in sand lysimeters, and the root exudates and microbial exocellular products from selected microorganisms

are subject to chemical fractionation into major classes of organic ligands. Radionuclide-traced complexes are formed by back reaction of the chemical fractions. These are eluted through soil, to identify the soil-mobile complexes which may be further chemically characterized. This information is used, in turn, to identify representative model compounds from which estimated stability constants can be obtained from the literature or experimentally. The final step is to incorporate the stability constants into a geochemical model that defines the distribution of the element between the soil and soil solution on the basis of thermodynamic equilibrium constants and the activities of ions and complexes in solution. This provides a basis for linkage with plant accumulation and hydrologic models to describe solute uptake by plants and mobility in soils.

Soil studies employed the Ritzville sil (Tables 3.2-3.5). All studies were conducted at constant temperature (25°C) and under aerated conditions typical of a surface soil. Thus, the major variable was the different chemical properties of the elements as related to soil chemical and microbial phenomena.

The soluble components of the 17 elements initially under study were determined to represent a small fraction (<0.5%) of the total concentration in soil. Clearly, the plant-available fraction would also be low, but the capacity of the soil solid phase to replenish the element in solution would be large following downward leaching or plant absorption. Measurement of soil solution composition as a function of solid-to-solution ratio and time indicated that most of the trace elements under study were limited by solubility. Thus, for elements subject to hydrolysis in soil, formation of soluble organic complexes with exocellular ligands of microbial origin might be expected to affect soil solution concentration and subsequent availability to plants with time.

The formation of trace element complexes with organic ligands in soil may occur through interactions of the elements with products of normal microbial metabolism or as a result of specific protective actions by the organisms to convert the element to a form that is less capable of entering the cell or is less toxic to it. The type of complex formed may thus be dependent upon the extent and mechanisms of toxicity of the elements.

As a first phase in an investigation to assess the role of soil microorganisms in formation of trace element complexes in soil, experiments were undertaken as described in a previous section to determine the effects of trace element concentration on soil microbial numbers and respiration rate. Investigations were narrowed to the elements Cd, Cr, Ni, Pu, Tc and Tl, which exhibited a range in sources and chemical properties, and (according to preliminary studies), which were solubility limited in soil and metabolically controlled in microbial and plant systems. These elements were subsequently examined in more detail, to determine the role of soil microbial and plant root processes in controlling their behavior. The results of soil microbial studies have been summarized by Wildung et al. (1986a,b). Plant root studies have subsequently been initiated.

Establishing the relative influence of soil microbial type, C source and growth parameters on complexation was a necessary prerequisite to predicting metal behavior in soils. As a basis for this investigation, pure cultures of bacteria and fungi were isolated by enrichment methods and examined as to their ability to produce extracellular metabolites capable of complexing metals during growth in solution and of altering metal sorption in soil.

Based on the patterns of complexes formed and on morphological and physiological characteristics, 19 bacteria and 60 fungi were selected as representative of the collection. To identify complexes with other elements

formed by these organisms and to establish the importance of the organisms in influencing trace element solubility in soil, the solubility and chromatographic and electrophoretic properties of the elements selected for intensive study were also determined after growth and after elution through a column of the soil from which the organisms were isolated. Microbial extracellular metabolites substantially affected the soil mobility of Ni and Pu. Growth of several of the fungi resulted in increases in the concentrations of Ni and Pu in soil eluates by factors of 1000 and 300, respectively, relative to water controls. The importance of these phenomena may be illustrated by examination of the results of Pu studies.

The solubility of Pu(IV) monomerically dispersed in soil is primarily controlled by hydrolysis (Ksp for $Pu(OH)_4 \approx 10^{-50}$) and subsequent sorption on soil particulates (Rai and Serne 1977). Soluble, diffusible Pu(IV) will therefore usually constitute less than 0.1% of the total Pu in soil, but the solid phase serves as a potential long-term reservoir of Pu to replace that removed from solution by downward percolation or plant uptake. The reasons for the effects of fungal growth on soil mobility of Pu(IV) and Pu(VI) are illustrated in Figure 3.10. The organism produced neutral and negatively charged Pu complexes that were not completely removed by the soil. The presence of microbial metabolites and synthetic ligands (DTPA, EDTA, EDDHA) was shown to result in reduction of Pu(VI) to Pu(IV) and formation of anionic Pu(IV) complexes that were mobile in the predominately negatively charged soil.

The role of the soil microbiota in mobilizing Pu and the value of the research approach (Figure 3.9) were verified in intact soil. When Pu mobility and soil respiration rate were monitored in a sterile soil and a previously

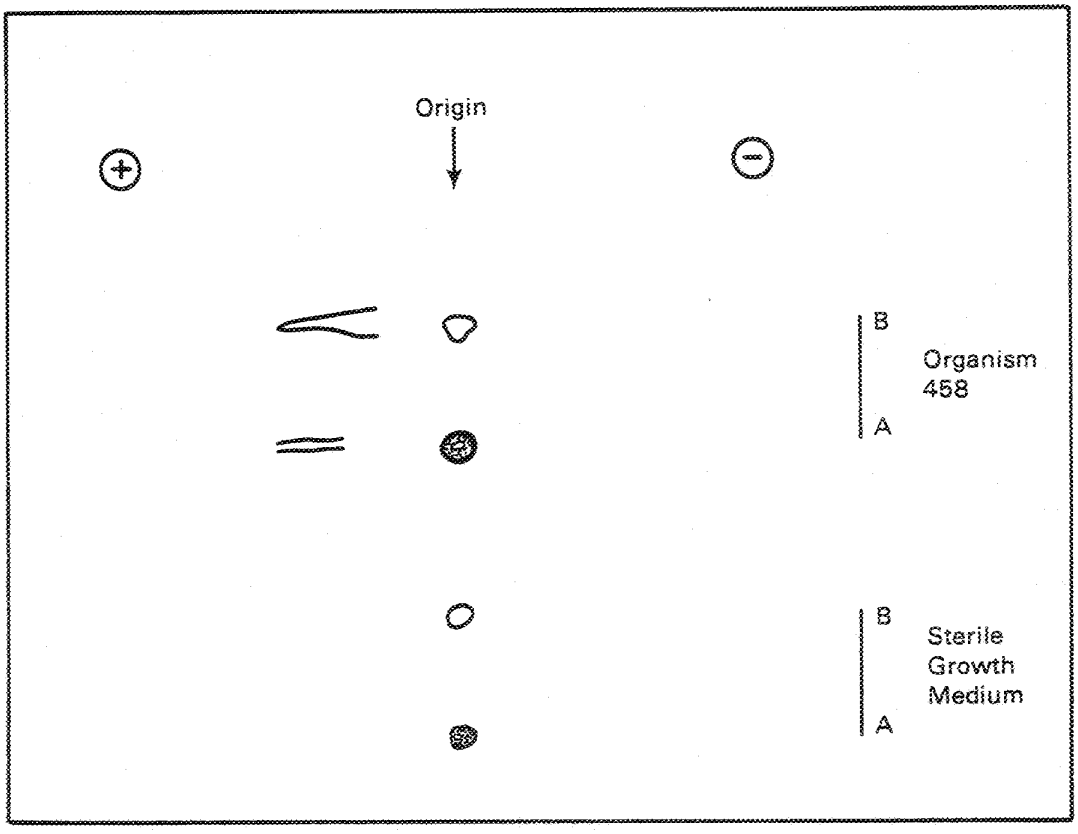

FIGURE 3.10. Thin-Layer Electrophoretic Behavior of Plutonium Complexes with Exocellular Fungal Metabolites in Pu(OH) Solutions Before (a) and After (b) Elution Through Soil (Plutonium was visualized by autoradiography; intensity is directly related to Pu concentration. Wildung et al. 1986a)

sterile soil inoculated with a soil population conditioned to the presence of Pu, Pu solubility increased with increased microbial activity as measured by soil respiration rate (Figure 3.11). The importance of this process is illustrated in Table 3.9.

Prior incubation, which in microbial studies was shown to increase the solubility of Pu in soil, increased Pu uptake by shoots compared with the unincubated controls (Table 3.9). The effect was greatly accentuated in the

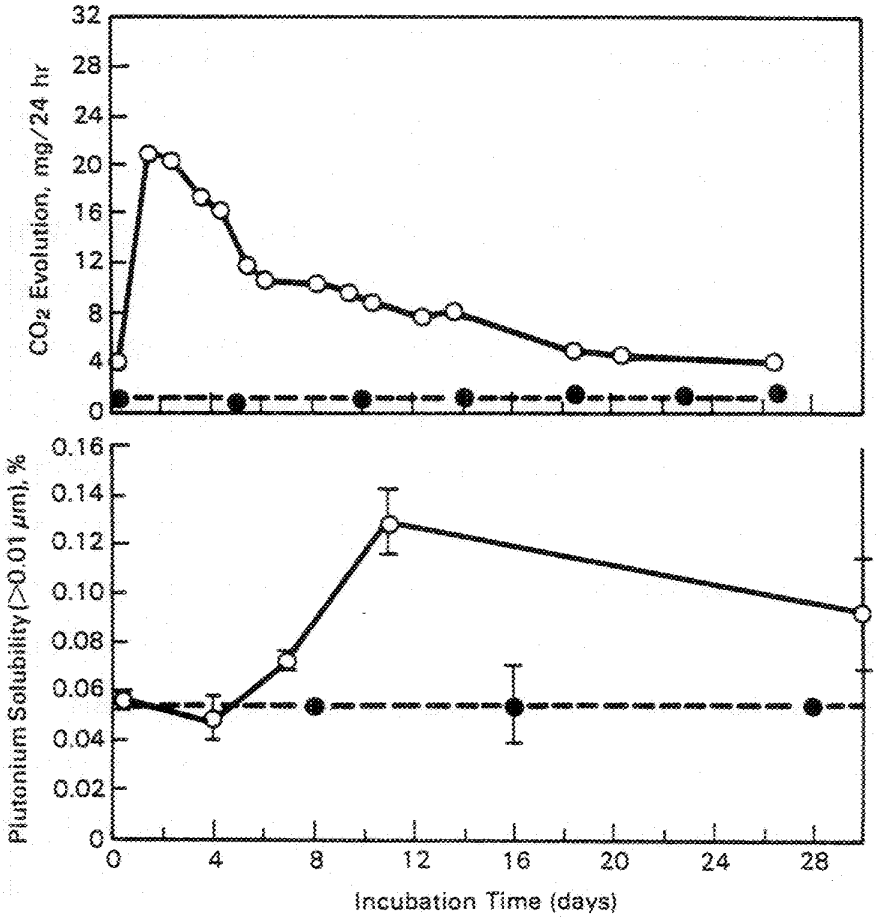

FIGURE 3.11. Changes in Soil Respiration Rate and Plutonium Solubility in Sterile Soil Inoculated with Plutonium-Treated Nonsterile Soil (The soil was a Ritzville silt-loam. Wildung and Garland 1980)

TABLE 3.9. Uptake of Plutonium in Barley as a Function of Prior Incubation in a Ritzville Silt Load Soil (Wildung and Garland 1980.)

Plant Component	Concentration Ratio[a] Unincubated	Incubated[b]
Shoots	0.019	0.071
Roots (soil free)	0.060	2.2

(a) Microcuries of plutonium per gram of over-dry plant tissue per microcuries of plutonium per gram of oven-dry soil) x 10^{-2}. Initial concentration of ^{239}Pu was 0.5 μCi/g on a dry-weight basis. Mean standard error (n=3) was ±39%.
(b) Soil was incubated 30 days after amendment with carbon and nitrogen to provide optimal microbial activity.

case of the soil-free roots, and incubation increased the soil-to-plant concentration ratios by up to 37 times relative to the unincubated control, depending on Pu soil concentration.

Investigations are currently underway to estimate the stability constants of important ligands controlling soil mobility and plant availability of trace elements in soil. The ligands identified at present have exhibited relatively low molecular weights (<1200), strong affinities for metals and a negative charge at soil pH values. The most important ligands have been implicated in complexation of several elements with related chemistries; therefore, information on their behavior may have broad application. In addition, the ligands most important in metal complexation have been products of organisms that predominate in the rhizosphere, suggesting their importance in trace element plant availability and providing impetus for future studies of the role of the integrated effects of plant root exudates and associated microbial processes on trace element behavior. Preliminary studies indicate that classes of compounds in root exudates responsible for complexation are similar to those identified in microbial systems (amino acids, peptides, organic acids), facilitating examination of these processes in concert.

The information developed in these studies is being integrated with other efforts underway at PNL (Figure 3.12). The geochemical model refined with stability constants for key elements with natural ligands is being linked with an organic ligand model to describe the production of important natural organic ligands under different soil and environmental conditions. The linkage of these models provides detailed information on trace element concentration and speciation in soil solution which is central to describing subsequent

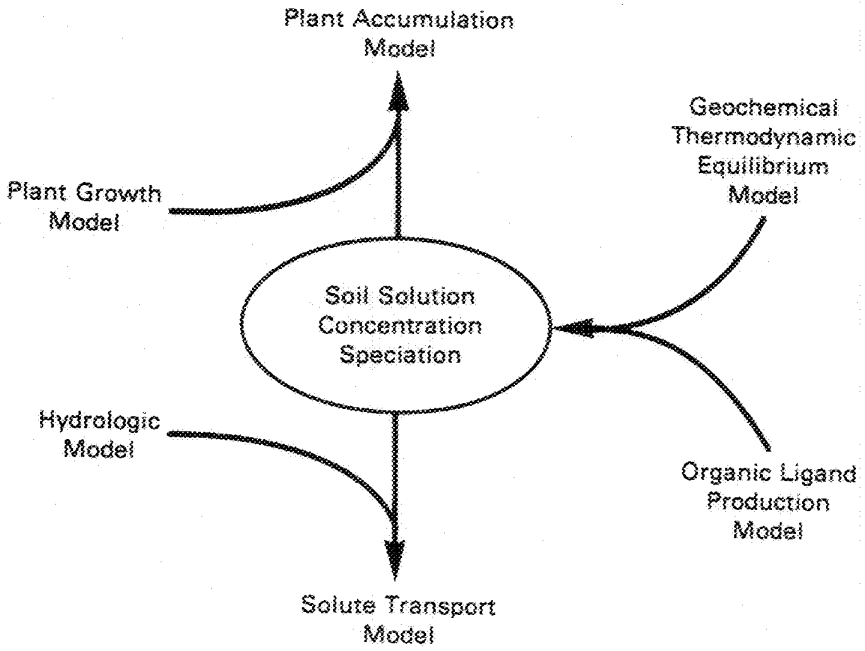

FIGURE 3.12. Integration of Related Reserach Efforts to Provide Capability for Prediction of Trace Element Behavior in Soils and Plants

trace element behavior. The soil solution information, when coupled with a plant growth model, allows estimation of plant accumulation; and linkage with a hydrologic model provides an estimation of solute transport. Together, experimental efforts and model development should provide an integrated view of these complicated processes that can be subsequently employed in predicting the behavior of important trace elements in natural and disturbed systems.

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CHAPTER 4. WATER BALANCE

G. W. Gee, P. A. Beedlow and R. L. Skaggs

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The shrub-steppe ecosystem exists within the arid and semi-arid regions of North America. Water in this ecosystem is limited and is distributed in such a way that plant growth is significantly modified by water stress. Most of the precipitation in these regions is returned to the atmosphere via plant transpiration and evaporation from the soil surface. What is not used by plants nor lost from the surface by evaporation or runoff is stored in the soil or lost as drainage below the root zone. In this chapter the emphasis will be on an approach to modeling water balance components of an arid ecosystem. A specific example of modeling water balance is given for the ALE Reserve, based on data established for this area.

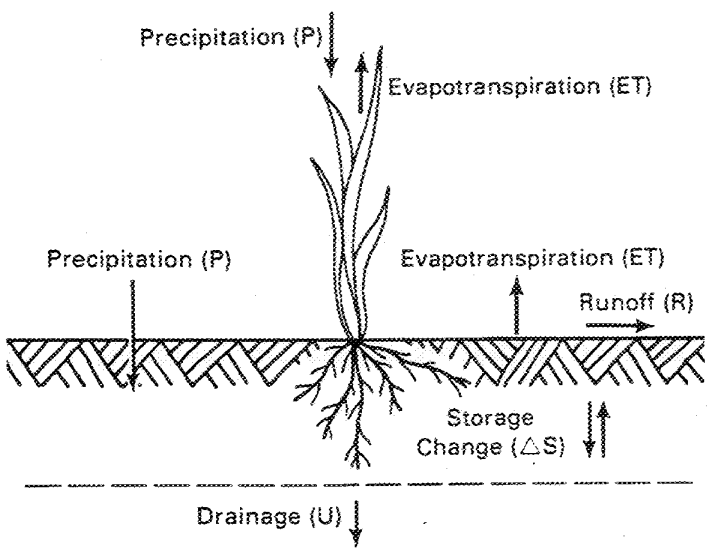
However, even with some data baselines extending over many decades, "patchiness" in the needed data base is inevitable because of costs and other impracticalities of sampling spatially large areas. Information from other arid locations can sometimes be useful in filling the gaps, and will be considered here.

The chapter is organized around the following sections:

* General principles applicable to arid sites
* Microclimatology of the ALE Reserve
* Model simulations
* Conclusions

WATER BUDGET

Figure 4.1 illustrates the primary components of a water budget for an arid site that contains both plants and bare soil. Input to the surface is precipitation (P) in the form of rain, snow and dew. Losses from the surface are by surface runoff (R), evaporation and transpiration, which are commonly expressed in terms of evapotranspiration (ET). Soil moisture changes (W) in the root zone, and deep drainage (U) below the root zone must also be considered for a complete water budget. An excellent review of various components of the water budget for desert ecosystems has been prepared by Evans and Thames (1981).



$$P = ET \pm \Delta S + R + U$$

FIGURE 4.1. Water Balance Parameters for Arid Site Conditions

It is generally assumed that little or no drainage occurs under arid conditions. However, significant quantities of water can be lost to deep drainage if the soil is coarsely textured (low in silt and clay content) so that water moves readily into the soil, particularly during times when little evaporation occurs. If plant roots are inactive during this time, or if the soil texture is coarse enough that the percolating water moves below the root zone, water becomes available for deep drainage.

A number of recent studies have reported water balance and drainage measurements under desert or arid site conditions. Dincer et al. (1974) used tritium tracers to evaluate water balance on sand dunes in Saudi Arabia and concluded that deep drainage accounted for as much as 2 centimeters of the 8-centimeter annual precipitation for their study site. Allison et al. (1985) used natural and radioactive (tritium) tracers to estimate the water balance at a semi-arid watershed in southern Australia and determined that as much as 1.4 centimeters of the 30-centimeter annual precipitation was lost to deep drainage. Gee and Kirkham (1984) have recently reported on water balance measurements at a cheatgrass field on the Hanford Site. From neutron probe measurements, they determined that as much as 8.5 centimeters of a specific precipitation total drained below the root zone. They attributed the large amount of drainage to excessive rains during winter and early spring, coarse soils, and the absence of deeply rooted plants.

Stephens (1985) recently measured the water balance at an arid site in New Mexico. Using field-measured hydraulic gradients and laboratory- measured soil hydraulic conductivities, Stephens concluded that as much as 4 centimeters of the 18-centimeter annual precipitation is lost to drainage below the plant root zone. At a site near Las Cruces, New Mexico, Herbel

and Gile (1973) illustrated the effects of topography and soil type on moisture penetration and drainage. At their study site, where much of the precipitation falls during torrential rainstorms, and where runoff rates are high on steep slopes, they found that depth of moisture penetration was highest on coarse soils in flat terrain and lowest on hill slopes. From their soil moisture data, they concluded that infiltration rate (potential drainage) for surficial soil horizons of sandy material is directly related to precipitation rate, and, thus, that infiltration is most rapid during rainfalls of high intensity.

These studies of drainage and water balance at arid sites clearly show that such factors as soil texture, soil structure, landscape position, vegetative cover, and microrelief can all have marked effects on the water balance at arid sites. Much of the precipitation at arid sites is lost to evaporation and runoff, but each site is markedly different and should be evaluated according to the site-specific controlling processes and factors.

PRECIPITATION

The major source of water to arid and semi-arid sites is precipitation, generally in the form of rain, snow or dew. There is tremendous variability in the microscale distribution of precipitation at a given site. Plant canopies and stems can channel water to soil directly below the plant, so rainfall is often concentrated near the plant stem. Drifting snow can also concentrate water in the vicinity of the plant. Over a period of time, however, water redistribution processes (overland flow, capillary flow and uptake by plant roots) tend to balance the effects of the variable moisture input. Snow and sleet in winter often account for a significant portion of the annual precipitation in shrub-steppe ecosystems located in cold desert

climates. Although snowmelt and sublimation are important mechanisms affecting timing of infiltration and surface water loss, they have received little attention in the modeling of water balance in shrub-steppe ecosystems. No data are available from the ALE Reserve to evaluate the effect of these mechanisms on the annual water balance.

Dew formation and its importance on the water balance at arid sites has been considered by Monteith (1963), Wallin (1967) and Rutter (1975). Montieth has calculated that under appropriate climatic conditions, water input by dewfall can range from 10 to 40 mm/yr. Such amounts may be significant, particularly when total precipitation is low (less than 100 mm/yr). The contribution of dew to total water balance must be viewed as both climatic and plant-controlled. Individual plants such as lichens may maintain an adequate water balance solely on the absorbed water (dew) from the atmosphere during periods of extreme drought when no measurable precipitation occurs (Lange et al. 1975). Although no measurements of dew have been made of the ALE Reserve, the meteorological data suggest that less than 5 percent of precipitation is in the form of dew.

RUNOFF

Typically, in arid/semi-arid regions, only a small percentage of annual precipitation moves as surface runoff to another location. In the shrub-steppe region, runoff occurs in about 1 of every 3 years as the result of intense thunderstorms in the early summer or rain and/or melting snow on frozen ground in the early spring (Cummans et al. 1975). However, runoff is an important component of the water balance because the amount and effects can be substantial during an occasional event.

Runoff amounts vary with space and time. The process is initiated when rain (and/or snowmelt) reaches the earth's surface. A portion of the rainfall is intercepted and held by the vegetation cover and ultimately evaporates. The water that reaches the ground as stemflow or throughfall infiltrates the soil at a rate dependent upon the infiltration capacity of the soil at the time. If the rainfall intensity exceeds the infiltration capacity, the micro-relief surface depressions begin to fill. When the depression storage capacity is exceeded, the water level builds up on the surface and runoff begins. The surface runoff continues to watershed elements of lower elevation, depending upon the rainfall, infiltration capacity, and micro- and macrorelief of successively lower elements. If the rainfall rate exceeds the infiltration rate for a sufficient time, the overland flow successively becomes concentrated in micro-channels, rills, gullies and stream channels (Mitchell and Jones 1978, Chorley 1978).

The most important factors in determining the volume and rate of storm runoff at a site are those related to the infiltration capacity: soil characteristics (texture, structure, depth, initial moisture content, clay chemistry and mineralogy, surface condition), rainfall characteristics (intensity, duration, drop size), and vegetation cover. When water reaches the ground surface, some or all of it is drawn through the soil pores by the forces of gravity and capillary action. In large pores, water moves downward as free gravity drainage. Simultaneously, the water is subject to capillary forces that move water both laterally and vertically (up or down) into fine, intergranular spaces. As the water moves through the pores, it is subject to flow resistance, which increases as the pore diameters decrease (Dunne and Leopold 1978).

During the early part of a storm, the infiltration capacity is high, particularly if the soil was dried out by evaporation prior to the storm. After sustained rainfall, as the soil becomes wet, several processes combine, and infiltration is rapidly reduced to an approximately constant value. Capillary forces are reduced as the small pores are filled. Clay particles become wet, swell, and decrease pore sizes, particularly near the surface where overburden pressures are slight (Dunne and Leopold 1978). Also, raindrop impact can create a crust or seal on the soil surface by breaking up surface soil aggregates and washing fine particles into the pores where they impede the entry of water. Once formed, a surface crust of only a few millimeters' thickness can greatly impede water intake by the soil (Hillel 1982). The latter process is particularly important in arid/semi-arid regions where vegetation is sparse and offers little protection to the soil surface. The combined effects of these processes are demonstrated by Nnaji et al. (1975) who, using a rainfall simulator at the Silverbell site near Tucson, Arizona, measured average initial and final infiltration rates for a gravelly-sandy loam at 90 cm/hr and 4.8 cm/hr, respectively.

Snowmelt is controlled by essentially the same phenomena as is rainfall (i.e., it will infiltrate the soil surface or run off, depending on the relative water flux through the snow and the infiltration capacity of the soil). However, several factors may significantly change the infiltration from that under rainfall at the same site. Normally, snowmelt releases water at a much slower rate than do most rain storms, and infiltration capacity is rarely exceeded. Occasionally, however, a dense layer of ice may accumulate in the topsoil, drastically reducing its infiltration capacity. Significant quantities of surface runoff can result. Pearce et al. (1969) reported that

twice in a 10-year period, the combination of frozen ground, deep snow cover and a period of rapid melting washed out dams and ponds constructed on Dry Creek, near the ALE Reserve.

Interception and depression storage, while of secondary importance to infiltration, play an integral role in the rainfall-runoff process. Interception may account for only 5 percent of the gross precipitation (Evans and Thames 1981), and depression storage can be as low as 0.1 centimeter for steep, smooth hillsides (Dunne and Leopold 1978). Nonetheless, interception and depression storage processes do affect the overall spatial variability of moisture in arid and semi-arid soils following a storm event. Stemflow is channeled to the soil directly beneath the plant, where infiltration rates are usually higher and where local evaporation is reduced by the shade of the plant (Campbell and Harris 1981). Retention of water in surface depressions provides more time for infiltration, thus allowing moisture from a small rain to reach deeper soil depths. Surface retention also serves to reduce soil erosion and may even affect seed distribution (Evans and Thames 1981). At the present time, however, there is no methodology available to predict accurately the amounts of interception or depression storage at a specific site. Until spatial variability of physical processes can be quantified more realistically, mathematical modeling of these processes will require site-specific calibration based on topography, plant cover, type and density.

EVAPOTRANSPIRATION

Processes of water loss from plant and soil surfaces are often considered together and called evapotranspiration. Water loss by evaporation from soil

surfaces is a near-surface process controlled by balances in soil water and energy and characteristics of the soil. Water transpired from plant surfaces is controlled by similar energy and water balances at the plant leaf surface, but the water is removed at-depth by an efficient plumbing system that extracts water from soil at root surfaces and conducts it to the stomates (pores in the leaf) where it is available for evaporation.

Soil water evaporation is a two-stage process. The first stage is considered complete when the soil surface dries, typically accompanied by a distinct color change in the soil from dark to light. Prior to this drying, the evaporation rate of the soil is the potential rate controlled primarily by the atmospheric variables (radiation, humidity, wind and temperature). After drying occurs, the evaporation is controlled primarily by soil factors (soil hydraulic properties, vapor diffusion resistance, etc.). The thicker the zone of dry soil, the slower the evaporation. The rate of water loss after a dry surface has formed is quite low (generally less than 0.1 mm/d).

Plant water losses can approach the potential evaporation rate determined by the climatic factors (often exceeding 10 mm/d), but in arid environments, generally evapotranspiration rates are considerably less than the potential rate. Desert plant surfaces are infrequently wet. Often the plant is subjected to water stress, which causes the stomates to partially or completely close. Evans et al. (1981) reported that maximum evapotranspiration rates at eight arid sites ranged from 2 mm/d to 10 mm/d, depending on the vegetation, water availability and climate. They found that when there was no precipitation for any extended period of time, the evapotranspiration rates generally dropped below 1 mm/d. On the ALE Reserve, Hinds (1975) confirmed these observations using a microlysimeter approach. Measured transpiration was

less than potential transpiration as determinations were over 50 days of the growing season, and the cumulative evapotranspiration over this period was less than 1 mm/d.

Section II. Microclimatology of the ALE Reserve: Data Bases

Regional climates are determined by a few readily observed factors such as distance from oceans or mountains, and latitude. The Arid Land Ecology (ALE) Reserve lies in the dry shrub-steppe region of the Pacific Northwest. However, its quasi-Mediterranean climate differs from other Northwest shrub-steppe areas in that there is a cool wet season compared to the warm wet season found at sites farther east, which have more continental climates. Chapter 2 provides climatological information for the Hanford Site. However, microclimate is affected by local topography and elevation and has special importance to the seasonal growth processes of plants, such as photosynthesis and transpiration.

MICROCLIMATES

The Rattlesnake Hills are largely responsible for the range of microclimates on the ALE Reserve. To determine the extent that microclimates vary on the Reserve, a network of 27 climatological stations was established in 1968, supplementing the Hanford Meteorology Station (HMS), to measure monthly maximum and minimum temperature and precipitation. Data were collected from these stations to characterize the microclimatic patterns (Rotenberry et al. 1976). Elevation primarily determined the microclimate at any given site; the higher sites being cooler and wetter. However, the rolling topography complicated this relationship. The data were analyzed by cluster analysis of similarity coefficients, a technique taken from numerical taxonomy. The analysis of temperature and precipitation data revealed four major microclimate groupings shown in Figure 4.2.

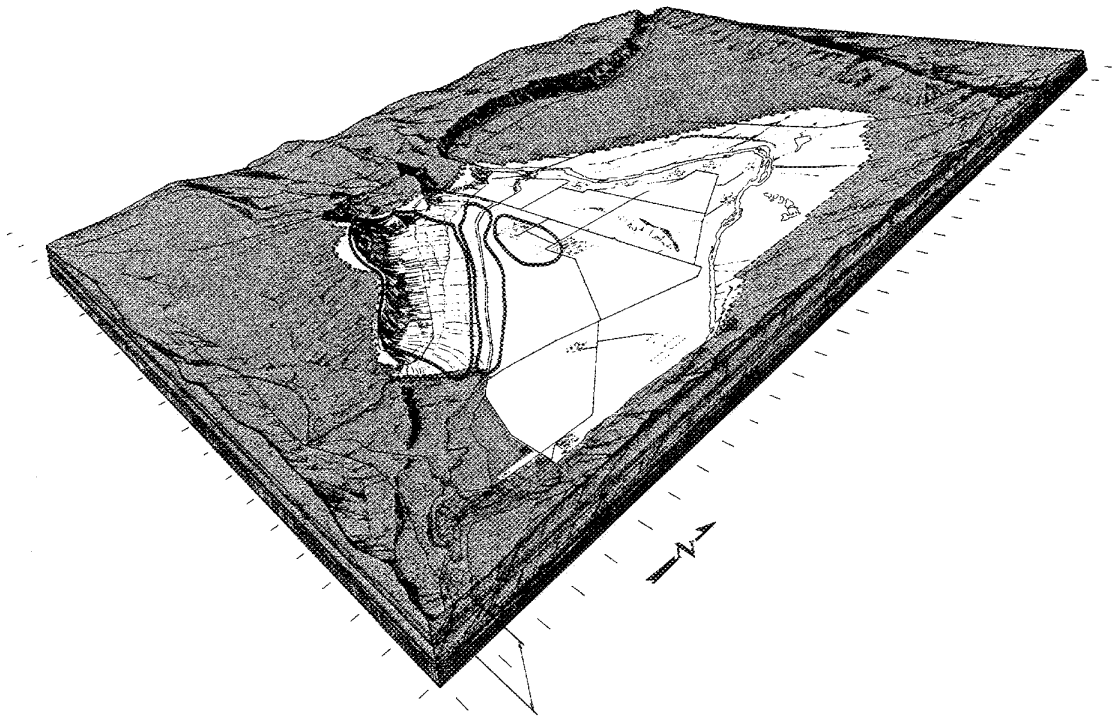


FIGURE 4.2. Major Microclimate Groupings (indicated by isolines around, from left to right, the ridge of Rattlesnake Hills, the plateau of the ALE Reserve, the basin area surrounding the nuclear reprocessing plant, and the remaining areas of the Hanford Site). Similarity coefficients for maximum and minimum temperatures ranged from 0.95 to 0.99 for all groupings.

1. protected, high-elevation grassland (Palouse grasslands)
2. flat, cold, desert shrub-steppe
3. low elevation with concave topography (frost pockets)
4. all other sites (high and low elevations)

The fourth group contained distinct subgroups:

a. high-elevation wind-swept ridges
b. high-elevation southern exposure
c. mid- to high-elevation steep topography

d. mid- to low-elevation moderate topography

e. three stations at the south end of the Rattlesnake Hills (confluence of Yakima and Columbia River valleys).

These observations provided several insights into the patterns of microclimates on the ALE Reserve. The southern end of the Rattlesnake Hills is affected by the confluence of two major river valleys--the Yakima River Valley and the lower Columbia Basin. Low-elevation sites in concave topography produce areas of low minimum temperatures (in the Cold Creek Valley). Ridge-top sites are affected by the frequent strong winds.

Results generally showed that a correlation among the four data sets were quite high, confirming the belief that climatic patterns are basically the same all over the Hanford site; e.g., similarity coefficients for maximum and minimum temperatures were 0.95 to 0.99, and coefficients for precipitation were 0.85 to 0.98 $p < .001$. Despite the high degree of similarity in microclimate pattern across the Hanford Site, unexpected differences were observed in vegetational composition within the major microclimatic cluster (Figure 4.2) for the ALE Reserve. The differences were thought to be related to a critical magnitude for certain of the climatic factors rather than to pattern, per se, but edaphic differences were not ruled out in this study. Some support for this idea is to be found in Chapter 6, in sections on phenology and microclimate modification. A problem in the approach used was that the cluster analysis reflects patterns more sensitively than absolute quantities, i.e., temperature or precipitation. For the future, some way of including relative or absolute magnitudes of these factors is needed in relation to critical plant sensitivities.

Extreme temperatures are certainly more biologically consequential than are the means of high (or low) temperatures generally used for purposes of meteorological characterization. In a further analysis of the 8-year microclimatologic data, Hinds examined the degree of correlation between average monthly maximum (or minimum) temperatures and extreme maximum (or minimum) each month, and the estimation of average of extremes by regression analysis. Results showed that extremes correlated well with the means on the ALE Reserve. For monthly highs, the correlation coefficient r = 0.90 for monthly lows, 4 = 0.881; n = 264 (Hinds and Rotenberry 1979).

THE ROLE OF PLANTS

Plants play a major role in controlling the water balance of shrub-steppe areas (Campbell and Harris 1981). Living plants transpire water stored in the soil. Water that is intercepted on the surface of plants following a rainstorm is evaporated. Additionally, plants affect the temperature of surface soil under their canopies. Thus, they control the microclimate of the site, which in turn affects the rate of water evaporation from the soil. Plant materials, both living and dead, enhance water infiltration to the soil, thereby reducing the amount that runs off the surface. In this section we will briefly review the roles plants play in these processes and the research conducted on the ALE Reserve pertaining to water balance in shrub-steppe plant communities.

TRANSPIRATION

"Transpiration" is the term used to describe plant-controlled soil water loss. Transpiration is the process of water vapor transport along a

concentration gradient from the evaporating sites within the plant to the atmosphere (Brown 1977). Transpiration is the driving force behind the movement of water from the soil to the atmosphere. This movement is from areas of relatively high water potential (soil) to areas of relatively low water potential (atmosphere). The flow of water along this soil-plant-atmosphere continuum is controlled at the point of highest resistance, usually in the leaf (Etherington 1982). The resistance in the leaf is mainly a function of the stomates, which are homeostatically controlled by the plant.

Stomatal opening and closing are affected by the external environment (Etherington 1982). Increased light intensity and reduced carbon dioxide concentration in the leaf usually cause stomatal opening. Stomatal closing can be caused by water stress, high carbon dioxide concentrations in the leaf, low light, and large vapor pressure gradients from the leaf to the air.

A daily cycle of plant water potential in response to transpiration is generally recognized (Brown 1977). Plant water potential declines in response to transpiration during the day because absorption by the roots cannot keep up with transpirational loss. At night, the transpirational demand is reduced, and absorption by the roots replaces the water lost by transpiration. As the soil dries, the daytime plant water potential is reduced to successively lower levels, which increases the internal water deficit. The water deficit continues to increase until wilting occurs.

Arid land plants are adapted to water stress in various ways (MacMahon and Schimpf 1982). Annual plants are often classified as "drought escaping"; when water is available they germinate, grow and reproduce. Succulent species such as cacti avoid drought stress by storing water in their tissues when it

is available. A physiological adaptation, crassulacean acid metabolism, allows succulents to limit the amount of time during which their stomates are open when the air is hot and dry; their night transpiration often exceeds the daytime amount. Species growing in areas where free water is within their rooting zone can spend water freely even in drought conditions; these species are often termed "phreatophytes." Some drought-tolerant species avoid dehydration by dropping their leaves and growing new leaves when water is available. Other species tolerate drought by allowing their tissues to dehydrate or by possessing adaptations, such as thick cuticles and sunken stomates, that protect tissues from dehydration.

EFFECTS OF PLANTS ON MICROCLIMATE

Plants affect microclimate primarily by shading the soil and intercepting precipitation. The degree to which vegetation affects the microclimate in an area is a function of its architecture or structure. The shrub-steppe vegetation is basically two-layered. Shrubs form the upper layer; grasses and forbs form the lower layer. In areas with little soil disturbance, a cryptogamic crust may be found that may be considered a third layer. Horizontally, the vegetation is nonuniform in terms of plant density and type.

Shrubs form an obvious but somewhat restricted element on the ALE Reserve. However, shrubs can markedly affect the microclimate. A study at the ALE Reserve indicated that soil temperatures measured 3 centimeters below the surface around sagebrush showed the effects of shading. Soil on the sunward side of the shrub was found to be 2° to 8°C warmer than the surrounding soil. Warming in this zone is due to solar radiation being reflected from the canopy. A similar analysis of hopsage (*Grayia spinosa*) showed that areas shaded by

the canopy were approximately 10°C cooler than unshaded areas (Hinds and Rickard 1968). In dense shrub stands with 20 percent or more of the surface under shrub canopies, shading could produce large-scale modifications of the microclimate. In areas of sparse shrub cover, the effect is likely to be local, with thermal differences occurring within a few centimeters of the shrub.

Shrubs can also modify the distribution of precipitation. A 3-year study of rainfall interception by sagebrush at ALE showed that an average of 85 percent of the precipitation falling on the canopy penetrated to the soil immediately below; the remaining 15 percent was lost to evaporation via canopy interception. Interception is strongly dependent upon position under the shrub canopy. The central portion of the shrub, out to approximately three-quarters of the distance to the canopy edge, efficiently intercepts rainfall and diverts it away from the area immediately below and toward the periphery of the plant. The amount of the diverted water that flows down the stem is unknown.

Bunchgrass species are dominant in the shrub-steppe ecosystem. The plant architecture and physical features of bunchgrass tend to produce a microenvironment that is in many ways similar to that of shrubs. The microenvironment produced by a bunchgrass includes an area of warmed soil on the sunward side of the bunch as in shrubs, an open but shaded site in the center of older bunches, and very shady sites sheltered by the leaves where densities are about a third of those found in the open.

The effect of bunchgrasses on soil surface temperatures is somewhat different than that produced by shrubs. The soil to the sunward side is warmed similarly to the soil on the sunward side of shrubs, but because of

the vertical openness of grasses, the cooling effect of shading found around shrubs is lacking (Hinds and Rickard 1968).

EFFECTS OF PLANTS ON WATER INFILTRATION

Plants increase water infiltration by increasing soil permeability and reducing the velocity of overland flow. The effects of plants and plant residues on reducing overland flow and soil erosion has been documented (Wischmeier and Smith 1978). Infiltration is enhanced by the organic material added to the soil from the plants. Living plants and litter increase the effective roughness of the soil surface, thereby retarding the flow of surface water, and increasing infiltration. Both shrubs and bunchgrasses affect the distribution of snow. Snow tends to accumulate on the leeward side of plants. Areas with tall bunchgrasses and shrubs can effectively increase water storage because of snow.

COMPARISON OF WATER USE BETWEEN PLANT COMMUNITIES

Water use by vegetation can be expected to differ with respect to the composition of the vegetation and the location of the site because of differences in physiology and root distribution among species. Maximum evapotranspiration rates were found to differ between vegetation types at both hot and cold desert sites (Evans and Thames 1981). Such differences in water use between plant communities may be a function of species interactions. Through time, species interactions for water contribute to the formation of spatial patterns in the vegetation (MacMahon and Schimpf 1981). A clear example of water-species interactions is provided on the ALE Reserve.

Cline et al. (1977) compared soil water use by a 30-year-old cheatgrass community with that of a native bluebunch wheatgrass (Agropyron spicatum) community on the ALE site. Soil water storage was nearly identical in both communities at the beginning of the growing season (1974). The cheatgrass community more efficiently used the soil water in the upper 0.5 meter but did not fully exploit the soil water below 0.5 meter. The bluebunch wheatgrass community, on the other hand, exploited water stored deeper in the profile (Fig. 3 in Cline et al. 1977). Cheatgrass out-competes seedlings of bluebunch wheatgrass on disturbed sites, and once established, it can persist for 50 years or more without re-establishment of bunchgrass (Harris 1967, Daubenmire 1975, Rickard and Sauer 1982). The ability of cheatgrass to prevent the establishment of bluebunch wheatgrass is attributed to its ability to use moisture more efficiently near the surface and thereby prevent the germination of bunchgrass seeds (Harris 1967).

THE ROLE OF SOILS

Soil provides the rooting medium for plants and the storage zone for water accumulation. The amount of water held in the soil at any given time depends upon its hydraulic properties as well as the physical and biological processes that are occurring in the soil. Coarse soils (sands and gravels) tend to drain readily, with little runoff occurring from their surfaces, even after intense thundershowers. In contrast, fine soils transport water slowly and often the fine surface particles (clays and silts) will disperse, acting to seal the surface, reducing infiltration and giving rise to runoff and erosion.

Soils of the shrub-steppe are discussed in Chapter 3, and the ALE Reserve soils have been mapped (see Figure 3.1). However, soils are seldom uniform either with depth or in areal extent. Arid and semi-arid soils (aridisols, entisols, mollisols) are generally alkaline, high in base saturation and often contain carbonate (caliche) layers at depth (Buol et al. 1973, U.S. Conservation Service 1975). These soils also vary widely in physical properties, ranging from silts and clays (found in alluvial surface deposits) to coarse sands and gravels (produced by glacial-fluvial processes). Plant growth in these soils is controlled largely by the amount of water held in the root zone. The water retention characteristics of soil are generally correlated with texture. Fine soils hold more water than coarse soils, and quantitative relationships have been established that correlate textural analysis with water retained at selected water potential levels.

The amount of water available for plants is generally correlated with the amount extracted from the soil, ranging from field capacity to wilting point. This available water range for agricultural crops is often estimated as the difference between the -1/3 bar and the -15 bar water contents. For vegetation native to an arid site, this estimate of available water is inadequate and may significantly underestimate the actual available water. Arid plant communities can extract water at soil water potentials below -70 bars (Campbell and Harris 1977). Moreover, the upper limit of soil water in coarse field soils is often as wet as -0.05 bar (50-centimeter soil suction); hence, predictions of water storage can have considerable error, depending on assumed limits. Field-measured upper and lower limits for soil moisture appear to be the most reliable predictions of the availability of water and capacities for water storage.

Section III. Model Simulations

THE MODEL

In order to correctly describe water balance at an arid site, it is advantageous to use a simulation model that accounts for process of water flow (infiltration, evapotranspiration, drainage, and redistribution). In addition, all factors that influence water input, including climatic and soil variables, need proper accounting. After reviewing the capability of a number of simulation models, we selected UNSAT1D (Gupta et al. 1978), a model that deterministically accounts for climate, soil, and plants and their interrelationships. This approach has allowed us to quantify the influence of changes in various key factors (plants, climate, etc.) on the water balance at a specific site.

CRITERIA FOR DATA

The UNSAT1D computer model (Gupta et al. 1978) was originally developed to describe vertical, one-dimensional, unsaturated water movement under typical agricultural conditions. It was designed as a model for isothermal (i.e., uniform temperature) water flow in the liquid phase. Many models with similar objectives are reported in the literature, (e.g., Nimah and Hanks 1973, Hillel 1977, Feddes et al. 1978, Klute and Heermann 1978, Hanks 1981). All unsaturated flow models depend on the quantity and quality of crucial, site-specific input data. It is impossible to model physical phenomena for which no supporting numerical information is available, regardless of the model's complexity. In view of the continued revisions to unsaturated flow theory and technology, models should be considered as research tools to aid

understanding and should not be interpreted beyond the limitations of input data. A comprehensive review by Molz et al. (1979) provides an outline for the current understanding of unsaturated flow, and a more recent review by Molz (1981) provides a status of plant water uptake models.

We used the UNSAT1D model for this study because it allows us to describe the soil water flow processes clearly and account for time-dependent (transient) behavior that typically controls soil water movement at arid sites.

The following information is necessary in order to simulate unsaturated flow at a specific site:

- depth of the soil profile and location of each soil layer. The maximum depth is the lower boundary condition location.
- type of lower boundary condition specified as a water table or free-drainage situation. Free-drainage conditions are applicable if the water table is actually deep below the simulated profile.
- hydraulic properties of the soil. These are defined by a soil water characteristic curve (water retention relationship) and hydraulic conductivity/water content relationship for each soil type present in the profile.
- the rainfall and potential evapotranspiration for each day of the simulation period, including the pattern of diurnal variation. Rainfall should be by hour, and diurnal variation should be expressed as a fraction of daily amounts for each hour.
- properties of the vapor-diffusion layer that forms on the soil surface when soil has attained air-dry conditions. These properties include layer thickness and characteristic vapor diffusivity. A limit is required for the water content at which the vapor diffusion layer is formed.
- the initial distribution of water over the soil profile as established by a water movement history or direct measurement.
- a soil temperature profile, required if nonisothermal vapor-flow conditions are important. A temperature profile is required for each period in which the temperature alters substantially.
- plant growth and water extraction behavior. This information must include root density distribution as a function of the growth period, and actual transpiration as some factor of the potential value when water is not limited.

The above list represents a considerable amount of data. The difficulty of unsaturated flow modeling is that some of the data usually cannot be measured directly, and so must be estimated by various theoretical methods. The major advantage of an unsaturated flow code is the ability to incorporate known processes (e.g., infiltration, evaporation, redistribution) as we develop a greater understanding of their influence on the water balance of a given site.

We selected a specific site, the Lower Snively Plots (Cline et al. 1977) located on the ALE Reserve, to demonstrate the use of the water balance model in predicting water storage in the surface 1-meter depth of fine-textured soil for a period of 13 years (1968 to 1980). In addition, we looked in detail at two years, 1973 and 1974, using selected boundary conditions and plant transpiration algorithms. We also evaluated the response of the water balance when vegetation was removed (i.e., no plants).

THE MICROCLIMATE DATA

The microclimate description of the ALE Reserve given earlier in the chapter provides general features of the climatic variables. In order to simulate the water balance at this site, hourly climatic data (including solar radiation, precipitation, air temperature, wind speed and humidity) were taken from Hanford Meteorology Tower records for the years 1968 through 1980. The hourly evaporation potential, or potential evapotranspiration (PET), was determined using the FAO-PET subroutine in the UNSAT-1D model (Gupta et al. 1977). Although snowfall conditions were noted for the model simulations, we assumed that the precipitation was in the form of rain, and

that water entered the soil immediately after precipitation occurred. These assumptions tended to overestimate the actual winter infiltration, particularly when temperatures were below 0°C.

Twenty-six sites at five distinct elevation levels were established on the ALE Reserve in 1968 (Thorp and Hinds 1977). Microclimatic measurements included precipitation, soil temperature, maximum and minimum air temperature, and relative humidity. The temperature and precipitation data from these sites were correlated with data from the Hanford Meteorology Station (HMS), located 7 kilometers from the northeastern boundary of the Reserve. The precipitation correlations for sites at elevations above the HMS site show that the intercepts are all positive, indicating that many areas on the Reserve receive precipitation at times when the HMS does not, probably a result of the orographic effects of Rattlesnake Mountain. It is not uncommon for observers at the HMS to report visible showers over the ALE Reserve near the mountains at times when there is no rainfall at the HMS facility just a few kilometers away (Thorp and Hinds 1977). An example of the correlation between the monthly precipitation at a given site and the HMS is shown in Figures 4.3 and 4.4. The R^2 (coefficient of variation) is 0.873 for the Lower Snively site, suggesting that 87 percent of the variation in monthly precipitation is accounted for by the linear regression of precipitation record between the two sites.

SOIL DATA

The soil used in the model simulation was Ritzville silt loam, a dominant soil on the ALE Reserve (further details are provided in Chapter 3). Figures 4.5-4.7 show the particle-size distribution, water retention and hydraulic

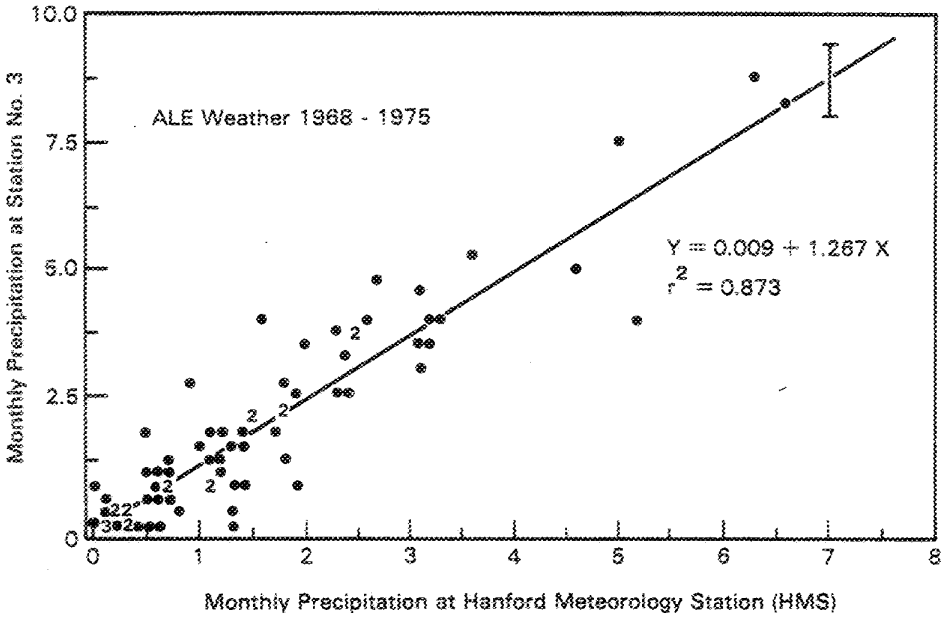


FIGURE 4.3. Correlation Between Precipitation Records from the Lower Snively Site at ALE and the Hanford Meteorology Station (HMS) Located on the Hanford Site (Standard errors: regression 0.697, α 0.103, β 0.052. Data: plotted 88, excluded 0, missing 8)

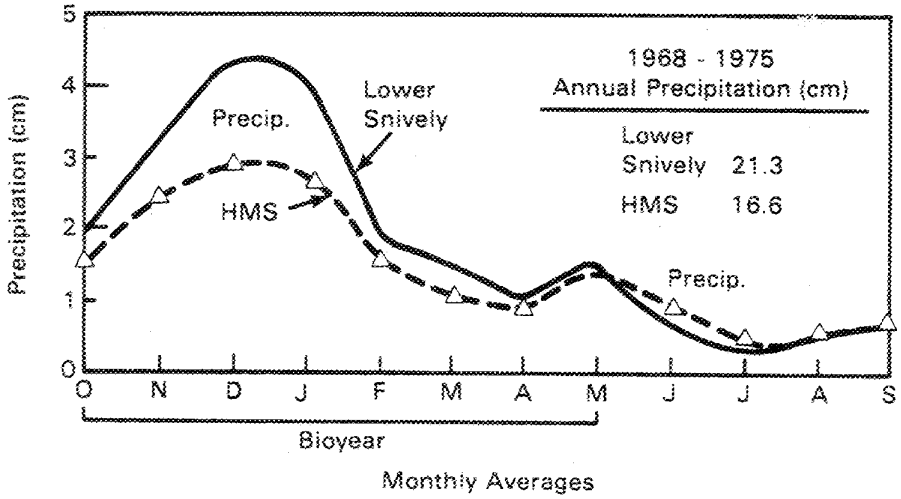


FIGURE 4.4. Comparison Between Monthly Precipitation Averages at Lower Snively and at the Hanford Meteorology Station (HMS)

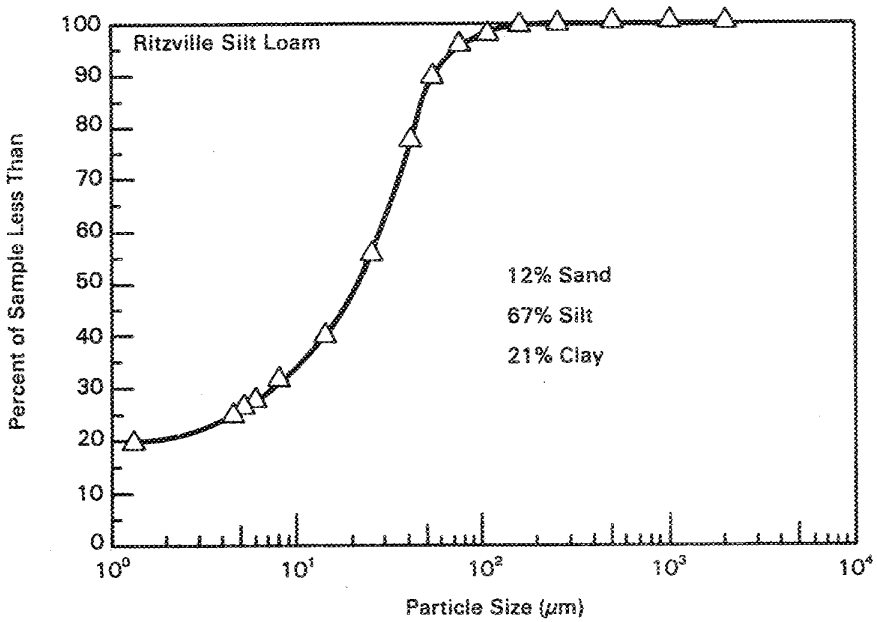


FIGURE 4.5. Particle-Size Distribution Curve for Ritzville Silt Loam

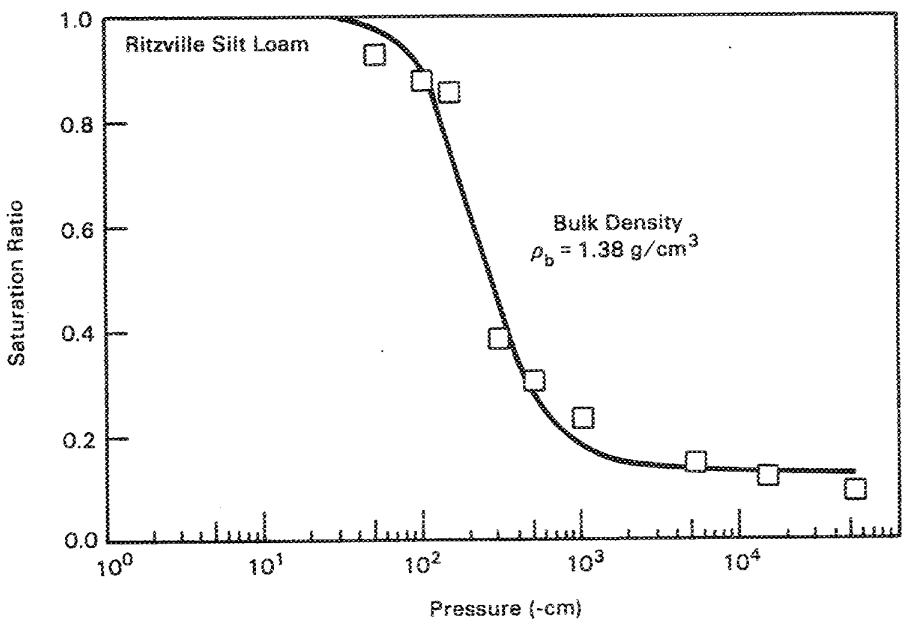


FIGURE 4.6. Water Retention Characteristics for Ritzville Silt Loam Determined from Laboratory Measurements. The fitted curve was constructed using VANFIT procedure described by McKeon et al. 1983.

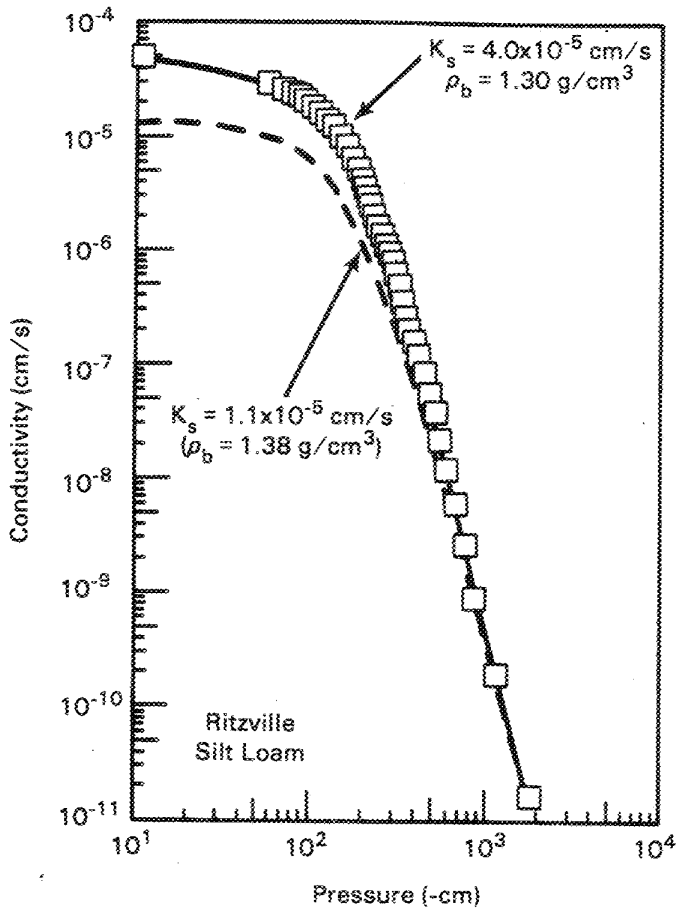


FIGURE 4.7. Calculated Unsaturated Hydraulic Conductivity for Ritzville Silt Loam for Two Bulk Densities

conductivity relationships, respectively, for the Ritzville soil. The water retention characteristics and the hydraulic conductivity relationships are used in the water balance model simulations described in the following sections.

THE MOISTURE DATA

Water content was measured at the Lower Snively site at the ALE Reserve for a 13-year period (1968-1980). These water content samples were taken by

a hand auger in 10-centimeter increments to depths of 1 meter (and occasionally to 2 meters). Samples were taken at least three times each year. Gravimetric moisture contents were determined by oven-drying at 105°C. Bulk density measurements taken by core sample to selected depths were used to convert gravimetric to volumetric water content; and from these data, water storage was calculated by summing incremental volumes over a 1-meter soil depth. Separate measurements (Cline et al. 1977) indicated that the root zone for cheatgrass at this site was less than 1 meter; hence, the calculated storage changes were assumed to reflect values in the active plant root zone.

THE VEGETATION DATA

The Lower Snively site is a 10-hectare area that was farmed (wheat) in the early part of this century but has been abandoned since 1943. A detailed discussion of the vegetation is provided in Chapter 6, it is a continuous cover of cheatgrass (*Bromus tectorum*) with tumble mustard (*Sisymbrium altissimum*) as a codominant (Table 6.27). Peak shoot biomass was measured during each year from 1971 to 1974. The root biomass was largely within the upper 20 centimeters of the soil profile (Figure 6.4 provides an illustration of this data).

Plant simulations were done using two transpiration algorithms modified after the transpiration data of Hinds (1975). This data was taken from direct transpiration measurements of cheatgrass. The "short" algorithm (Figure 4.8) was for plots whose transpiration was simulated starting in January and running for 80 days. The "long" algorithm was for plants whose transpiration was started on October 1 and run for 210 days (through April 30).

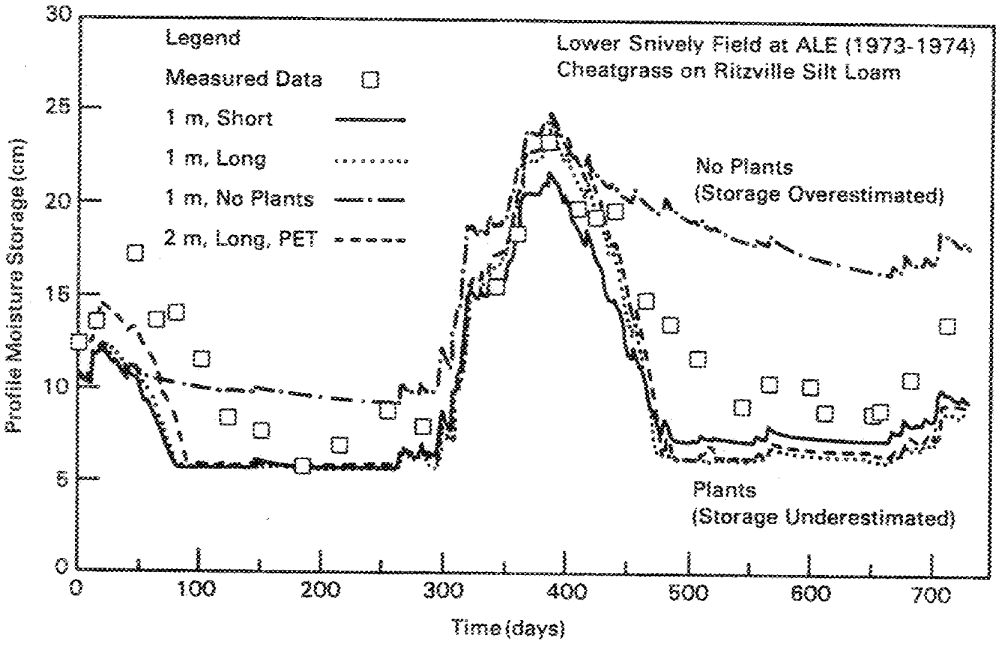


FIGURE 4.8. Measured and Simulated Water Storage Values for Lower Snively Field, 1973-1974. Various simulations represent changes in transpiration algorithm and boundary conditions.

RESULTS OF THE SIMULATIONS

Simulations of water storage for 13 years from 1968 to 1980 (4800 days) are shown in Figure 4.9. These data indicate that the general trend of storage change was simulated in most years, but that the detailed water balance was not adequately described in all years. Several reasons are given for the lack of agreement between measured and modeled water balance.

- Soil hydraulic properties were not adequately simulated. The soil at the Lower Snively site was classed as a Ritzville silt loam, and moisture content samples were taken repeatedly from the site, but neither laboratory nor in-situ hydraulic characterization was done directly on soils taken from this site. The hydraulic properties used in the simulation were taken from soil with a similar classification but from another location on the ALE Reserve, about 10 kilometers from the Snively site.

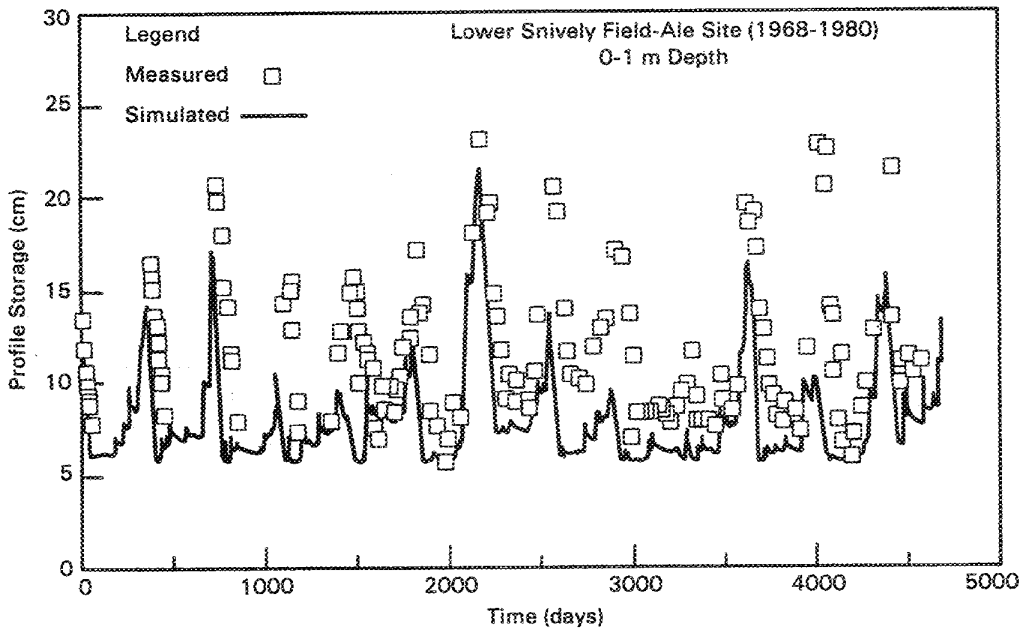


FIGURE 4.9. Measured and Simulated Water Storage Values in the Upper Soil Profile (0-1 meter) at Lower Snively Field on the ALE Reserve, 1968-1980

- Meteorological data were incomplete. Only limited onsite data were available; hence, daily HMS data was used as model input. The correlation of HMS and ALE site data may not adequately describe the Lower Snively climate, particularly in winter months. Differences between estimated and actual rainfall and snowmelt at the site may be sufficiently great that the predicted inputs inadequately describe seasonal and long-term precipitation.

- Estimates of transpiration were incorrect. The plant transpiration algorithm used was not adequate.

To test several assumptions regarding differences in the measured and modeled water balance, several simulations of the water balance were performed for the years 1973-1974. The meteorological data needed to generate potential evapotranspiration (PET) factors were taken from the HMS. Precipitation and temperature data were then scaled to the Lower Snively site using regression

equations published by Thorp and Hinds (1977). The simulated moisture storage in the top 1 meter of the soil profile was compared with measured values of storage. The comparisons are shown in Figure 4.8, where the measured storage values are represented by squares. Four different simulations were conducted:

* 1 meter, short: A 1-meter profile with a short growing season (January 1 - April 30; i.e., the plants were assumed to transpire only during this 4-month period).
* 1 meter, long: A 1-meter profile with a long growing season (October 1 - May 31; i.e., plant transpiration was operative for 6-month period).
* 1 meter, no plants: A 1-meter profile with no plants.
* 2 meters, long, PET: A 2-meter profile with a long growing season (October 1 - May 31). Also, a different version of UNSAT1D was used in which the hourly distribution PET factors were modified so that they summed to 1.0 over a 24-hour period; i.e., the sum of the hourly values equaled the total daily PET.

Initial conditions for the first three simulations were identical. These were the final head values from a simulation of the 1972 year at the Snively site. Initial conditions for the fourth simulation were different. For the top 1 meter of the profile, initial head values were set to the moisture contents measured at the site on January 2, 1973. For the 1- to 2-meter depth of the profile, we used the head value measured at the 1-meter depth.

Figure 4.9 suggests that initial conditions used for the first three simulations were such that the profile moisture storage was about 2 centimeters below the measured value on day 1. Thus, comparisons between 1- and 2-meter-deep profiles are not quite valid for the first 100 days. After 100 days, all profiles with plants were essentially dried out to the -15 bar limit (where plants wilt and transpiration stops) so that the response of each profile to the 1973 to 1974 winter rains could be compared. When there

were no plants, the profile storage did not reach the -15 bar limit of 5.7 centimeters, but was at 10 centimeters for the 1973 summer and 17 centimeters for the 1974 summer.

The measured peak storage value for water of 24 centimeters occurred in January, 1974 (day 380). All four simulations came within 2 centimeters of the peak, with the "no plants" simulation having the highest value (25 centimeters). About 100 days later (day 480), all simulations with plants had storage values near the -15 bar limit (6.1 centimeters), although under the short growing season the storage was 1 centimeter greater (7.2 centimeters). Together, plants and surface evaporation removed about 15 centimeters of water over this 100-day period. When there were no plants, evaporation alone removed only about 5 centimeters of water.

The results from the 1973-1974 simulation runs indicate that with some modifications those 2 years could be adequately simulated using UNSAT1D. One modification would be to simulate actual evapotranspiration as some value between the evapotranspiration rate used for the long PET simulator case and a bare-surface evapotranspiration rate. Such a simulation would likely use soil characteristics that allowed less water to move to the surface so that evaporation could be reduced by 20 to 30 percent. The field characterization of the water retention characteristics appears to be a likely place where corrections could be made. Although the simulations did not predict the exact water balance over a long period of time, it appears that adjustments can be made in input, and that water storage on the ALE Reserve can be adequately predicted.

Section IV. Conclusions

Water balance in the shrub-steppe environment reflects limited water inputs balanced against losses due to surface runoff, evapotranspiration, and drainage. Measurable drainage occurs at some sites while not at others. Site-specific factors such as climate and soil hydraulic properties are needed to predict evapotranspiration and drainage rates at arid sites. Model simulations of the system can elucidate the mechanisms for soil water storage and removal. These models depend on reliable estimates of plant water uptake patterns, which are at present largely unavailable for arid- site plant communities. Conditions of plant water stress make it difficult to correlate plant response with climate (PET) relationships; hence, additional work is needed to elucidate the mechanisms. Water content sampling of the root zone has been helpful in establishing shrub-steppe plant response to climatic variables, but additional data are required to establish plant response functions that will be useful in estimating evapotranspiration under the wide range of conditions that prevail in the shrub-steppe environment. The use of weighing lysimeters and detailed measurements of plant and canopy resistances to water loss, perhaps by micrometeorological methods, will be helpful in more firmly establishing the plant parameter inputs needed for water balance models.

Other difficult problems arise that will require study and evaluation. For example, the soil-hydrological system is dominated by multidimensional, nonlinear processes, and the soil medium is itself spatially variable. Seasonal climatic and microclimatic values are variable from one year to the next, as is vegetational cover, and the overall pattern may not be consistent.

To consider just the climatic variables, one should not base a solution to the water balance model simply on time or space averages. The magnitude and pattern of extreme but infrequent events occurring over several years are probably more meaningful in determining water balance and overall system behavior.

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CHAPTER 5. SPRINGS AND STREAMS

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C.E. Cushing and B. E. Vaughan

This chapter describes the known ecological characteristics of the lotic environments occurring on the Arid Land Ecology Reserve, with one notable exception--the Columbia River, which flows through the Hanford Site.

Schwab et al. (1979) document well over 100 springs and spring locations on a 182 square mile area centering on the Arid Land Ecology (ALE) Reserve. Of these sites, only Snively Springs and Rattlesnake Springs (not included in the Schwab et al. study area) are amenable to extensive study (see Harr and Price 1970); of these two, ecological studies have been done only at Rattlesnake Springs.

Section I. Physical and Chemical Characterization

In the study of any aquatic community, it is important to have information about source, flow volume, temperature, available light, and water chemistry. A number of these physical and chemical characteristics are described below for Rattlesnake and Snively Springs.

SOURCE

Hydrological investigations of both the Snively Springs and Rattlesnake Springs basins indicate that neither is dependent upon surface waters for its perennial flow regime. Price (1972) indicated that the base flow of about 0.005 m^3/s of Snively Springs is not of watershed origin, but comes

from springs trapped between layers of basalt. The perennial flow of Rattlesnake Springs is the result of several springs and seepage areas reaching the surface from a perched aquifer in the area near the toe of the Yakima Ridge; this water originates in the upper Dry Creek and Black Rock Valleys west of Rattlesnake Springs (Brown 1970). Rattlesnake Springs waters remain perched for about 3 kilometers and then seep into the permeable Touchet beds (Brown 1970). About 60 percent of the flow originates in the 190 meter reach above the main spring, 10 percent from the main spring, and the remaining 30 percent between the main spring and gauging weir located 400 meters below the main spring (Harr and Price 1970). Overland flow to Rattlesnake Springs occurs only during the winter when the ground is frozen and snowmelt is accelerated by Chinook winds. These occur at about 3.8-year intervals (Cummins et al. 1983) and can result in catastrophic flash floods. One flood in recent years occurred as a result of extensive rains in the Black Rock Valley-Moxee region in the Dry Creek headwaters area.

FLOW VOLUME

The annual base flow of Rattlesnake Springs is 0.01 m^3/s (Cushing et al. 1980, Cushing and Wolf 1982). Discharge volume ranges from about 840 m^3/d in late summer to 1340 m^3/d in winter (E. G. Wolf, personal communication). Flow measurements, using dyes and ^{86}Rb as tracers, show an average velocity of about 0.5 m/s.

TEMPERATURE

Differing variations in the maximum and minimum water temperatures occur along Rattlesnake Springs, depending upon such factors as distance from the springs and shading by canyon walls. Just below the main spring, water temperatures varied from about 2.5°C in February to 14.0°C in June (Figure 5.1a); this site is located within the canyon (Cushing and Wolf 1984). At a site 400 meters downstream, where the spring-stream emerges from the canyon, water temperatures ranged from 4.3°C in January to 22.1°C in June and July (Cushing and Wolf 1984, Figure 5.1b). This difference is due mainly to warming of the water by solar insolation; water temperature of the main spring is nearly constant.

The only water temperature data available for Snively Springs were taken during July and August 1980. At this time, temperatures varied from 13.9 to 17.8°C in the upper end to as high as 27.8°C at the lower end where the water pools before seeping into the desert.

LIGHT

The annual solar pattern for the Hanford Reservation for the year 1969-1970 is shown in Figure 5.2, taken from Cushing and Wolf (1984). Springs and streams receive intensive solar radiation in this region, with the only exceptions being in locations where the water is shaded by canyon walls or riparian vegetation. Incident radiation (300 to 5000 nm wavelength) ranged from about 24×10^5 J/m^2/d in December to about 300×10^5 J/m^2/d in July.

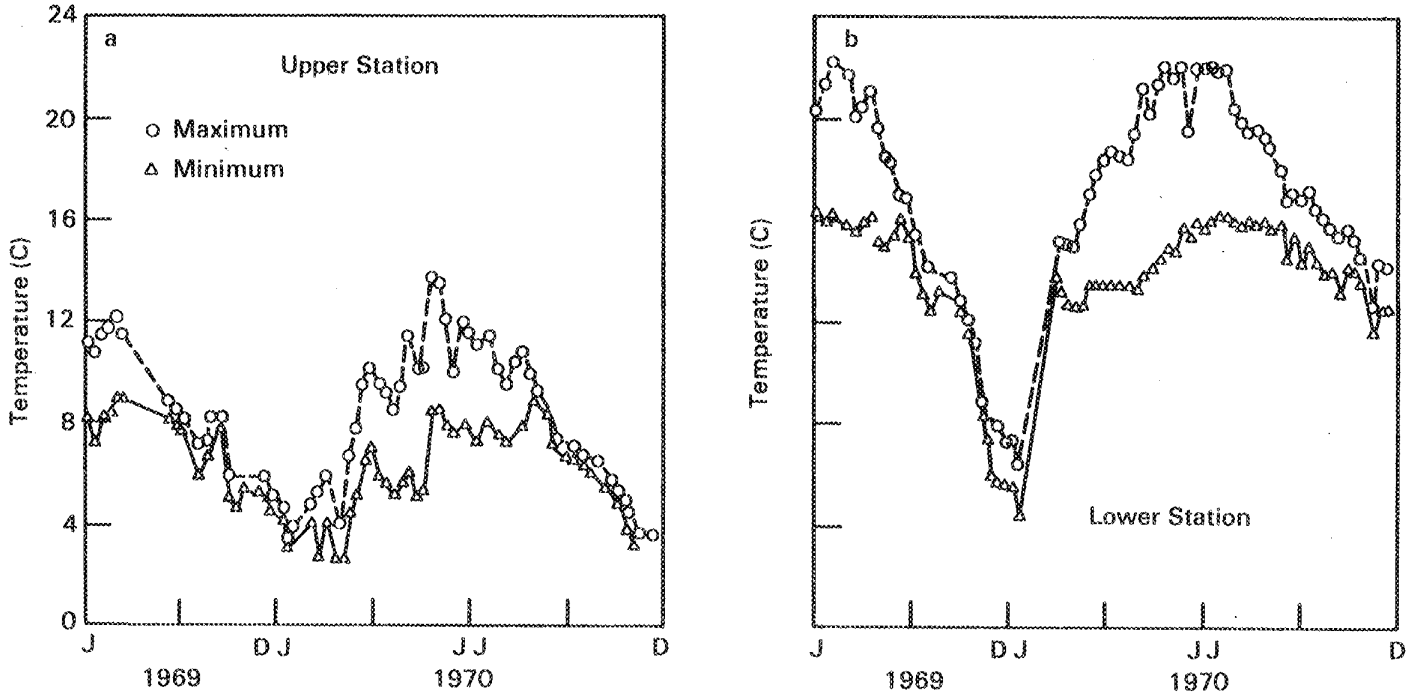

FIGURE 5.1. Maximum and Minimum Daily Water Temperatures at Upper Station (a) and Lower Station (b), Rattlesnake Springs (Cushing and Wolf 1984)

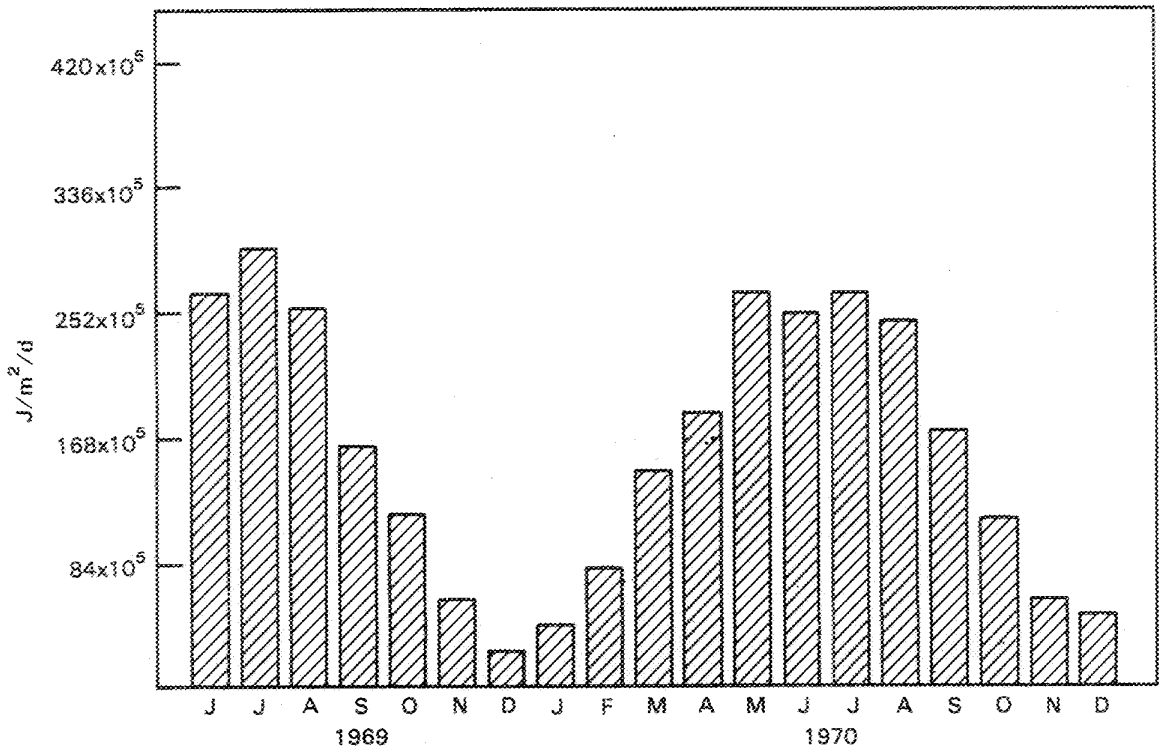

FIGURE 5.2. Annual Solar Regimen, Hanford Site (Cushing and Wolf 1984).

WATER CHEMISTRY

The average annual chemical composition for selected variables is shown in Table 5.1. These data represent the average concentrations from six stations for Wolf's data and a single station for Cushing's.

The only variable which differed markedly between the main spring and the remainder of the spring-stream was dissolved oxygen, which averaged about 2 mg/L less than the open stream. Dissolved oxygen also exhibited the only consistent downstream change, increasing from 8.2 mg/L above the entrance of the main spring, to 10.1 mg/L at the lowest station. Cushing also found the

TABLE 5.1. Average Concentrations for Selected Variables (mg/L)

	1969-1970	1962
Silica	34.8	24
Total phosphate	0.66	
Ortho-phosphate	0.20	0.30
Nitrate	0.28	0.80
Nitrite	0.002	
Ammonia	0.06	
Total dissolved solids	210.3	220
Total alkalinity	128.8	
Methyl orange alkalinity	126.2	132
Dissolved oxygen	8.6	

Section II. Biological Investigations

Descriptive studies of algae, the food habits of a mayfly nymph, and recovery of streamside woody vegetation have been done at Rattlesnake Springs. These are described below along with process studies of the entire stream, energetic studies of certain invertebrates, and a comparative study of leaf decomposition rates.

DESCRIPTIVE STUDIES

A systematic sampling program was carried out in 1972 to collect and identify algae from Rattlesnake Springs and other aquatic sites on the ALE Reserve. Twelve sites were sampled on Rattlesnake Springs and five others at various springs.

During this period, 90 species of algae were identified (Lippert and Cushing 1973). The numbers of species found in the major taxonomical groups are shown in Table 5.2.

TABLE 5.2. Algae From Major Taxonomical Groups

Group	No. of Species
Phylum - Chlorophyta	
Sub-Division Chlorophyceae	22
Sub-Division Characeae	1
Phylum - Euglenophyta	11
Phylum - Chrysophyta	
Sub-Division Xanthophyceae	3
Sub-Division Chrysophyceae	46
Phylum - Cyanophyta	
Sub-Division Myxophyceae	7

The functional group concept proposed by Cummins (1973) has become increasingly used in characterizing invertebrate fauna in streams. Inherent in categorizing aquatic organisms by various functional groups, or trophic relationships (collectors, grazers, shredders, etc.), is knowing the food eaten and how it is obtained. Merritt and Cummins (1978) have summarized a large body of information on trophic relationships of North American aquatic insects; however, the trophic relationships for the mayfly genus Callibaetis (Ephemeroptera:Baetidae) are unclear.

In 1980, we undertook an analysis of the food habits of Callibaetis in Rattlesnake Springs to clarify the trophic relationship of this mayfly (Cushing and Rader 1982). Callibaetis nymphs were collected with hand nets and preserved in 70 percent ethyl alcohol until examination. Gut contents were analyzed by suspension, filtration, and microscopic examination essentially as described by Cummins (1973), Gray and Ward (1979), and Short and Ward (1981). The majority of the particles were spherical, so volumetric calculations were based on the particle size diameters.

Data for 31 nymphs from eight sites are presented in Table 5.3. The number of organic detrital particles per nymph gut ranged from 3270 to 17,600, and varied in size from 111 μm to 230 μm. These particles comprised from 95 to 100 percent of the material present, by number; diatoms comprised one to five percent, and insect parts, probably ingested by chance, less than 1 percent. The calculated volume of the particles per nymph ranged from 7.6 to 22.3 mm^3.

Stations 1 through 17 are in the open desert, and 27, 29, and 31 are in a steep-sided canyon. The unusually high number of particles in the guts of

TABLE 5.3. Detrital Fine Particulate Organic Matter (FPOM) in *Callibaetis* Guts (Cushing and Rader 1982)

Date	Station	n	$\bar{x}$ No. particles (range)		$\bar{s}$ diameter, μm (range)		Part. Volume mm^3 [a]
7 July 1980	1	4	5300	(3440-7070)	140	(110-200)	7.6
8 July 1980	9	4	6600	(5700-7190)	170	(120-210)	17.0[2]
8 July 1980	11	4	3940	(3270-4330)	210	(170-230)	16.5
9 July 1980	17	4	7300	(4900-9090)	150	(130-190)	12.9
10 July 1980	23	3	5300	(4900-5600)	190	(160-210)	19.0
10 July 1980	27	4	7400	(5070-9660)	140	(120-170)	10.6
14 July 1980	29	4	8900	(5750-11,600)	150	(120-200)	15.7
14 July 1980	31	4	15,500	(10,500-17,600)	140	(110-170)	22.3

(a) Volume calculated using mean numbers for particle size and numbers. Since FPOM constitutes 95 to 100 percent of the gut contents observed, similar data for diatoms and insect parts were not calculated.

nymphs from Station 31 may be related to its location at the origin of Rattlesnake Springs in a seepage pool with heavy growths of filamentous green algae.

These data indicate that Callibaetis is primarily a collector-gatherer (sensu Cummins 1973), feeding mainly on fine particulate organic matter FPOM) from the stream bottom. These results differ from those of Edmunds et al. (1976), who state that Callibaetis nymphs are herbivorous, feeding on diatoms and other algae. A rich diatom and algal flora is present in Rattlesnake Springs (Lippert and Cushing 1973); yet these forms make up less than 5 percent of the food ingested in Rattlesnake Springs. The findings are, however, consistent with data on other Baetidae (Cummins 1973, Merritt and Cummins 1978).

Small spring-streams such as Rattlesnake Springs are widely distributed in the semi-arid sagebrush-steppe region of the northwestern United States. They are characteristically bordered by narrow corridors of deciduous trees, especially cottonwoods (Populus spp.) and/or willows (Salix spp.). The value to bird populations of these wooded habitats of limited extent is well recognized and has been especially well documented on the ALE Reserve (Rotenberry et al. 1979; Chapter 7 of this volume). Historically, spring-streams have also been the focal points of human habitation and the congregation areas for herds of domestic livestock that pasture in the surrounding sagebrush-steppe and trek back and forth to the few widely separated spring-streams that serve as watering points. The physiological requirements for drinking water have tended to concentrate livestock at a few places, causing damage and even destruction of riparian woody vegetation (Thomas et al. 1979).

In 1982, we documented the response of the streamside woody vegetation at Rattlesnake Springs following exclusion of livestock grazing in 1963 (Rickard and Cushing 1982). The neo-European history of Rattlesnake Springs is not well documented, but the waterflow at one time was delivered through a series of pipes and ditches from the lower reaches of the spring-stream to a small cultivated field about 6 kilometers downstream. This probably occurred between 1900 and 1940. The land around the spring-stream was intensively grazed by domestic cattle, sheep, and horses during that time, and the spring-stream served as a water source and as a major congregating place for livestock attracted from a wide area. Livestock had an adverse impact on the woody plants. Shoots within reach of livestock were persistently browsed. Some mature trees along the stream were also probably cut by homesteaders for firewood, a scarce commodity in the treeless sagebrush-steppe.

In 1943, the spring-stream and the surrounding land was incorporated into the Hanford Site. The resident human population was relocated and livestock grazing was discouraged. However, a few stray cattle and horses continued to water at Rattlesnake Springs from time to time until 1962, when an 800-acre fenced exclosure was built around the entire spring-stream. Since 1963 there have been no intrusions by livestock.

In the absence of livestock, the woody plants have increased in stature and density and now form a more or less continuous tree corridor along the entire length of the stream, particularly in the canyon section and immediately downstream from it. An aerial photograph of Rattlesnake Springs taken in 1963 (Figure 5.3a) shows the riparian tree/shrub corridor as very sparse and discontinuous. At the time, ground surveys showed only a few widely spaced, broken-topped (wind damage) peach leaf willow trees (Salix amygdaloides).

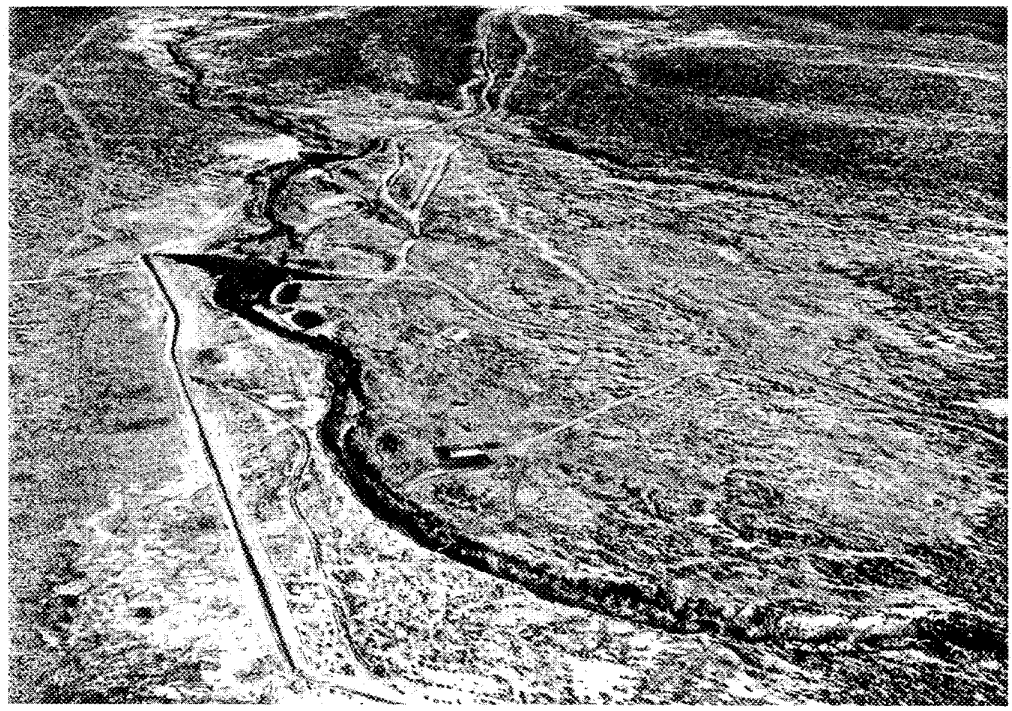

FIGURE 5.3. Contrasting Aerial Views of Rattlesnake Springs in 1963 (a, upper) and 1980 (b, lower)

Tree willows now form a virtually continuous narrow corridor along the length of the spring-stream (Figure 5.3b). The vigorous recovery of tree growth along the spring-stream is attributed to the exclusion of livestock and the absence of a resident human population. In lieu of domestic livestock, the woody plant community is presently utilized by a few head of wild mule deer (Odocoileus hemionus) and elk (Cervus elaphus) (Rickard et al. 1977).

Trees can be important environmental features to small spring-streams because overhanging tree canopies provide shade during the hot summer months and help to keep water temperatures more stable, a feature that is believed to be beneficial to aquatic organisms (Behnke 1979). Tree leaves are relatively rich in biologically essential mineral nutrients, especially nitrogen and phosphorus, and they also serve as a carbon source for populations of small detritivorous aquatic organisms as they fall into the stream during the yearly autumnal leaf fall event (Cushing et al. 1975).

Although shade and mineral nutrients represent positive attributes of tree communities, a potential negative aspect is that trees can act as phreatophytes. If present in sufficient numbers, they may transpire enough water in summer to cause a reduction of stream flow by root tapping the subterranean aquifer. Reduction in flow could be deleterious to at least some stream organisms, and the fauna would be changed dramatically if stream flow became intermittent rather than permanent.

It is clear that riparian tree/shrub communities in an otherwise treeless area play important roles in determining the abundance and species composition of fauna. The total demise of woody plants can be regarded as biologically detrimental; however, revegetation is not especially costly. Seed bed preparation, seeding, or fertilizer applications are not required. In our

case, removal of cattle as a stress was sufficient to allow the development of tree shrub communities.

PRODUCTIVITY STUDIES

Metabolic studies of desert streams have lagged behind similar studies of temperate woodland streams. To date, reported studies have included those of Minshall (1978) on Deep Creek, in Idaho; Cushing and Wolf (1982) on Rattlesnake Springs, in Washington; and Fisher and his colleagues on Sycamore Creek, in Arizona (Gray and Fisher 1981, Busch and Fisher 1981). Duffer and Dorris (1966) presented productivity data on a Great Plains stream in Oklahoma that flows through arid terrain; Prophet and Ransom (1974) studied a similar stream in Kansas, as have Gelroth and Marzolf (1978).

Results from the above studies have added credence to Minshall's (1978) contention that western streams, including desert streams, have a higher propensity for autotrophic production and depend less on allochthonous carbon sources than woodland streams. The general lack of a canopy or lower input of allochthonous organic matter in desert streams may result in positive net daily metabolism (Pg - 24 h R) measurements, or P:R ratios exceeding unity (see Bott et al. 1978 for a fuller definition) in 1st to 4th order reaches (Strahler 1957), rather than farther along the continuum as predicted by the River Continuum Concept (Figure 5.4, based on Vannote et al. 1980).

Primary productivity studies were initiated at Rattlesnake Springs in 1969 (Cushing and Wolf 1984). The study site was the 400-meter reach extending from just below the entrance of the main spring downstream to the emergence

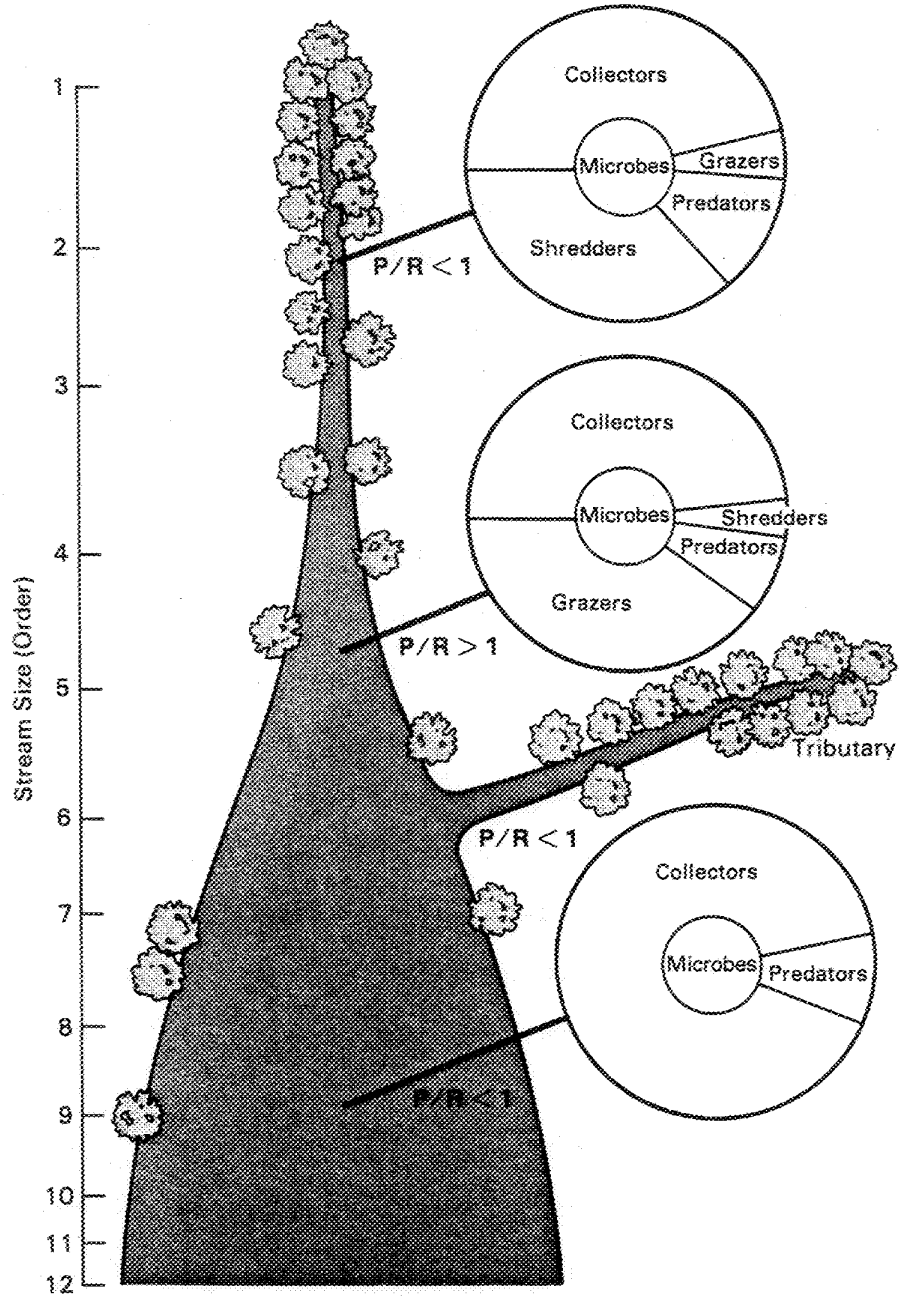

FIGURE 5.4. Hypothetical Functional Group Distribution for Insects and Photosynthesis-to-Respiration Ratio of the River Continuum Concept as Related to Stream Order (Based on Vannote et al. 1980)

of Rattlesnake Springs from the lower canyon. Maximum and minimum daily water temperatures at the upper and lower sites are shown in Figure 5.1 and the annual solar radiation pattern in Figure 5.2. Autotrophic constituents are primarily periphyton [= aufwuchs, sensu Ruttner (1963)], mostly diatoms of which Achnanthes lanceolata, Gomphonema intricatum and Melosira varians are the most abundant (Lippert and Cushing 1973)] and watercress (Rorippa nasturtium-aquatica).

Of the several methods available for primary productivity measurements in streams (see Bott et al. 1978 for discussion), the diel curve for pH-CO_2 method (Odum 1956, refined by Beyers et al. 1963) was selected as the best for Rattlesnake Springs, since little turbulence occurs and CO_2 exchange with the atmosphere was considered negligible and not measured. The method principally relies on changes in soluble CO_2 between an upstream and downstream station. These changes result from CO_2 consumption by photosynthesis, CO_2 release into the water by plant, animal, and aerobic bacterial respiration, and from exchange of CO_2 with air in a direction dependent upon CO_2 saturation in the water. Data were obtained using the automated system described by Wolf et al. (1971) and processed using a computer program described by Wolf and Olson (1974). In essence, the pH-CO_2 curves measured periphyton productivity, periphyton respiration, watercress root and stem respiration, and invertebrate and microbial respiration [invertebrate and microbial respiration probably account for less than 10 percent of community respiration (Minshall 1978)]. Measurements of pH were made using Analytical Measurements Corporation combination electrodes and the automated system which produced alternating 18-minute continuous recordings for each station. Data are presented for the entire stream segment. Watercress productivity was measured

monthly by the harvest method (fifteen 0.1 m^2 samples per month) (Westlake 1969, Vannote and Ball 1972). Ash-free dry weight (AFDW) was obtained after drying samples for 48 hours at 100°C and ashing for 24 hours at 575°C.

Productivity data for periphyton by sample period are shown in Table 5.4. Net primary productivity (Pn) averaged 0.9 $gC/m^2/d$ during the study period and was highest in spring (range - 0.2 - 2.2 $gC/m^2/d$) (Figure 5.5). Daily periphyton gross productivity (Pg) averaged about 8.7 $gC/m^2/d$ (Table 5.4). Watercress is the dominant macrophyte in Rattlesnake Springs, an occurrence common to many springbrooks (Pennak 1971). Isolated patches of _Scirpus_ sp., _Eleocharis_ sp., and _Typha latifolia_ occupied less than 5 percent of the stream area. Following essentially complete removal of the macrophytes by a flash flood in January 1970, the watercress grew rapidly and nearly filled the stream by mid-summer. By November 1970, the watercress covered 93 percent of the stream surface and impeded flow sufficiently to nearly double the total stream surface area. The standing crop increased exponentially (Figure 5.6).

Net productivity data estimated by (1) area covered by watercress, and (2) total stream area, by sample period, are given in Table 5.4. For the growing season, net primary productivity rates averaged 0.3 $gC/m^2/d$ for both the watercress covered area and total stream area basis. If we accept the very rough estimate that 50 percent of gross production is expended as respiration (Odum 1959, Westlake 1969), then the gross production of the watercress would be essentially twice the net production. P_g averaged 0.6 $gC/m^2/d$ for both the watercress-covered area and total stream area. Vannote and Ball (1972) similarly found that macrophyte productivity rates are

TABLE 5.4. Gross (Pg) and net (Pn) primary productivity of periphyton, watercress and total community by sample period, Rattlesnake Springs, $gC/m^2/d$ (Cushing and Wolf 1984)

Sample Period	Periphyton		Watercress: Total stream		Watercress: Watercress covered			Community	
	Pg	Pn	Pg	Pn	Pg	Pn	% covered	Pg	Pn
1 Nov 69 - 14 Jan 70	2.7	0.5	-	-	-	-	0	2.7	0.5
15 Jan - 25 Mar	3.5	0.7	-	-	-	-	0	3.5	0.7
26 Mar - 23 Apr	6.8	2.2	0.02	0.01	0.9	0.5	1.9	6.8	2.21
24 Apr - 22 May	5.1	1.2	0.6	0.3	3.1	1.5	18.4	5.7	1.5
23 May - 17 Jul	6.4	0.9	1.0	0.5	2.1	1.0	49.9	7.4	1.4
18 Jul - 25 Sep	14.0	0.2	0.3	0.2	0.6	0.2	84.7	14.3	0.4
26 Sep - 20 Nov	7.3	1.2	0.8	0.4	1.0	0.5	92.8	8.1	1.6
26 Mar - 20 Nov	8.7	0.9	0.6	0.3	0.6	0.3	92.8	9.3	1.2

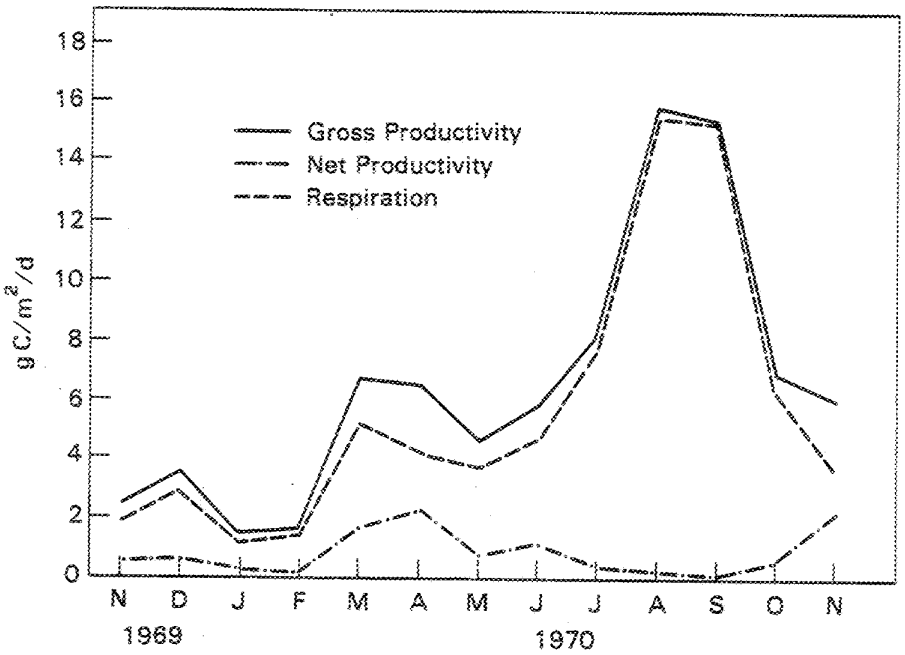

FIGURE 5.5. Seasonal Gross and Net Primary Productivity and Respiration Rates for Rattlesnake Springs (Cushing and Wolf 1984)

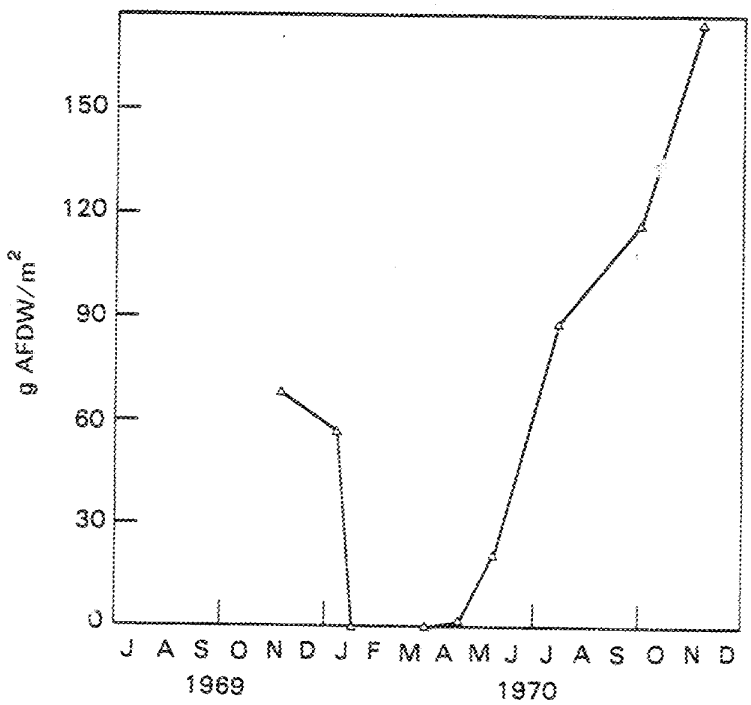

FIGURE 5.6. Watercress Standing Crop, Rattlesnake Springs (Cushing and Wolf 1984)

highest during the initial growth periods than for the entire growing season. Several workers have called attention to the underestimation of macrophyte productivity when data are expressed on a total stream basis rather than considering only the area occupied by the plants (Owens and Edwards 1961, Knight et al. 1962).

Light utilization efficiencies were calculated for periphyton P_n, watercress P_n (watercress-covered area and total stream area), and total P_n (Table 5.5). Periphyton net photosynthetic efficiency averaged about 0.22 percent for the study period and was highest in early spring prior to extensive watercress growth and in fall. Watercress net photosynthetic efficiency averaged about 0.07 percent expressed as either watercress- covered area or as total stream area. High spring, early summer, and fall efficiencies were found, with a marked mid-summer depression. Duffer and Dorris (1966) report that daily photosynthetic efficiency in the Blue River, Oklahoma, ranged from 0.1 to 2.7 percent; these generally exceeded the low values found in Rattlesnake Springs and are probably related to the constituents of the autotrophic community. No shading macrophytes are found in the Blue River.

A peak in community P_g occurred in spring and corresponded to the maximum periphyton standing crop. The highest level of activity, 16 $gC/m^2/d$, was measured in late summer. This increase corresponded to the exponential increase in the standing crop of watercress (Figures 5.5 and 5.6). Annual total gross primary productivity amounted to 2700 $gC/m^2/yr$ (Table 5.6) of which about 94 percent was attributed to periphyton and 6 percent to watercress. Community gross productivity averaged about 9.3 $gC/m^2/d$ (Table 5.4).

TABLE 5.5. Photosynthetic Efficiencies (%, P_n/Lt) by Sample Period [a, b] (Cushing and Wolf 1984)

Sample period	Periphyton	Watercress		Total
		Watercress covered	Total stream	
1 Nov 69 - 14 Jan 70	0.54	-	-	0.54
15 Jan - 25 Mar	0.35	-	-	0.35
26 Mar - 23 Apr	0.57	0.12	0.003	0.563
24 Apr - 22 May	0.23	0.29	0.01	0.24
23 May - 17 Jul	0.16	0.19	0.09	0.25
18 Jul - 25 Sep	0.06	0.12	0.07	0.13
26 Sep - 20 Nov	0.89	0.37	0.32	1.21
26 Mar - 20 Nov	0.22	0.07	0.07	0.29

(a) P_n data converted to calories using the factors in Duffer & Dorris (1966)
(b) Light measurements were recorded with an Epply pyrheliometer at a meteorology station ca 4 km east of the study site; the instrument recorded wavelengths from 300 to 5000 nm.

TABLE 5.6. Annual Metabolic Measurements, Rattlesnake Springs, $gC/m^2/yr$ (Cushing and Wolf 1984)

Gross primary productivity (P_g)	2526[a]	174[a]	2700[a]
Respiration (r)	2170[b]	87[c]	2257[d]
Net primary productivity (P_n)	356[e]	87[f]	443[e,f]

(a) Summation of P_n and R

(b) Measured from pH-CO_2 curves minus macrophyte instream R

(c) Assume 50% of P_g lost by respiration (Odum 1959; Westlake 1969)

(d) Measured from pH-CO_2 curves [does not include aerial respiration of watercress; includes invertebrate and microbial respiration, although this probably does not exceed 10% of total community R (Minshall 1978)]

(e) Measured from pH-CO_2 curves

(f) From biomass (AFDW) measurements

Community respiration (R) rates (Figure 5.5) closely paralleled the gross primary productivity rates. The late summer increase in respiration rates coincided with both the increase in watercress standing crop and an increase in invertebrate biomass. Since the diel curve method does not differentiate between autotrophic and heterotrophic respiration, both contributed to the measured rates. Average daily respiration rates ranged from 63 percent of P_g in November to essentially 100 percent of P_g in September; the average was about 86 percent for the study period. Lowest percentages occurred during months when periphytic activity was highest and watercress and invertebrate biomass were low. Annual community respiration amounted to 2257 $gC/m^2/yr$ (Table 5.6), of which about 96 percent was attributable to periphyton and 4 percent to watercress.

Net primary productivity was positive at all times of the year except during September when it was essentially zero (Figure 5.4). This indicates that Rattlesnake Springs is an autotrophic system that produces more organic matter than it consumes, at least in the reach studied for this time period. The P:R ratio (P_g:24 h R) for the system on an annual basis is 1.20. Net productivity rates peak in spring and fall (Figure 5.5). Annual net primary productivity amounted to about 443 $gC/m^2/yr$ (Table 5.6) of which 20 percent was from watercress and 80 percent from periphyton. Annual daily P_n averaged about 1.2 $gC/m^2/d$ (Table 5.4).

Data for annual community metabolism for several streams situated in either true deserts (Sycamore, Pinto, and Deep Creeks, Rattlesnake Springs) or in open arid regions (e.g. Great Plains) are shown in Table 5.7. Both annual gross productivity and respiration of Rattlesnake Springs are within the reported ranges of these streams. Net daily metabolism in Rattlesnake Springs is positive and supports the argument of Minshall (1978) that autotrophy is prevalent in low-order, arid streams, but contrary to the general contention that low-order streams are heterotrophic (Hynes 1969).

To be considered autotrophic, however, Busch and Fisher (1981) state that autotrophic streams must be net exporters of organic matter. Cushing and Wolf (1982) demonstrated that Rattlesnake Springs was a net importer of organic matter on an annual basis. This anomaly is related to the fact that desert streams are flushed periodically by flash floods (Busch and Fisher 1981); this occurred during our study when the entire standing crop of periphyton and watercress was scoured from the stream. Thus, Rattlesnake Springs appears to be a net importer of organic matter in a non-flood year, but becomes a net exporter during a year when a flash flood scours the

TABLE 5.7. Annual community metabolism in desert(a) streams, $gC/m^2/d$ (Cushing and Wolf 1984).

Stream	Gross Productivity	Respiration	Source
Blue River, Okla.(b)	0.99 - 4.12	2.51 - 6.99	Duffer & Dorris 1966
Skeleton Cr., Okla.(b)	4.45	10.96	Prophet & Ransom 1974
Honey Cr., Okla.(b)	0.87	-	Hornuff 1957
Cottonwood River, Kan.(b)	0.49 - 2.29	0.20 - 3.14	Prophet & Ransom 1974
Mountain Fork River, Okla.(b)	0.71	-	Hornuff 1957
Walnut River, Kan.(b)	1.67 - 1.87	2.36 - 3.93	Prophet & Ransom 1974
Lost Cr., Kan.(b,c)	0.27 - 0.40	0.18 - 0.62	Gelroth & Marzolf 1978
Sycamore Cr., Ariz.(b)	2.78	1.67	Busch & Fisher 1981
Pinto Cr., Ariz.(b,d)	1.73	1.41	Lewis & Gerking 1979
Cedar Cr., Okla.(b)	<1.0 -10.57	1.81 - 8.64	Prophet & Ransom 1974
Deep Cr., Id.(b)	0.80 - 3.14	-	Minshall 1978
Rattlesnake Spr., Wash.	7.4	6.2	Cushing & Wolf 1984

(a) Defined as occurring in true deserts or open prairie systems

(b) Original data converted from DO or kcal using a PQ = 1.2 (Strickland 1960), which is probably conservative (Bott et al. 1978, Gregory, pers. comm.).

(c) Natural section of stream

(d) Unpolluted reach of stream

system. The recurrence interval for these floods in Rattlesnake Springs is approximately 3.8 years (Cummins et al. 1983). Deep Creek, Idaho, also presents anomalies depending on station location.

It thus appears that streams in cold (Washington, Idaho) and hot (Arizona) deserts have several attributes in common, including dominance of autotrophic processes, flushing, or "re-setting", of the systems by flash floods, but differ as to whether they are net importers or exporters of organic matter on an annual basis. Unfortunately, the number of streams from each region that have been adequately studied are too few to draw definitive conclusions. It also appears that these systems need to be studied over time periods exceeding one annual cycle to fully understand their functioning in terms of organic matter budgets (see also Cummins et al. 1983).

ENERGY BUDGET STUDIES

Calculation of organic energy budgets has become a widely used method to compare lotic ecosystems and ecosystem functioning (c.f. Odum 1957, Teal 1957, Tilly 1968, Fisher 1977). Fisher and Likens (1973) included import and export of particulate organic matter (POM) with the parameters of production (P) and respiration (R), providing stream ecologists with an added refinement in characterizing the trophic basis of streams. Cummins (1974) also included import-export relationships in his characterization of streams, using this to describe them as either processors (net importers) or conduits (net exporters). Although they are essentially simple to determine, the interpretation of stream organic energy budgets is complicated and involves historical, geomorphological, spatial, and temporal considerations. Data collected during the primary productivity studies described above were used

to construct an organic energy budget for Rattlesnake Springs (Cushing and Wolf 1982). Comparable budgets have been published for cold temperate streams/springs in deciduous biomes (Fisher and Likens 1972, Fisher 1977, Teal 1957), warm-water spring-streams (Odum 1957, Hall 1972), a temperate midwestern spring (Tilly 1968), and a Pacific Coast coniferous stream (Sedell et al. 1974). Minshall (1978) published an energy budget for Deep Creek, Idaho, a cold desert stream, and these data are compared to Rattlesnake's. Minshall's data are the only published budget of arid desert streams that we are aware of, although Busch and Fisher (1981) recently published P:R data for an Arizona stream, Sycamore Creek.

In the Rattlesnake study, allochthonous input (>0.5 μm) was collected at irregular intervals in litter traps (12 traps, 0.05 m^2 each) placed flush with the ground along the stream equidistantly throughout the study reach. Transport POM (>0.5 μm) and dissolved organic matter (DOM, < 0.05 μm) were collected weekly by grab samples. Included in the export POM was the loss of standing crop of insects and watercress flushed out by a flood. Discharge data, necessary to adjust grab samples for annual volume, were obtained from recording Parshall flumes. Storage (sensu Fisher and Likens 1973) was not a consideration in the study since most of the organic matter in the stream bed was flushed from the system by a flood just prior to termination of the study. In a non-flood year, the standing crop of organic matter would need to be measured as storage. DOM, measured as oxygen consumed, was analyzed by the dichromate technique (Maciolek 1962), and converted to calories. The caloric content of POM was determined with a Parr oxygen bomb calorimeter.

Organic energy budgets for first order (Strahler 1957) Rattlesnake Springs and for second order Deep Creek, Idaho (Sta. 3, modified from Minshall 1978)

are shown in Table 5.8. The data indicate that Rattlesnake Springs was a net importer of organic matter in 1969-70. Since storage was essentially zero, the system consumed more organic matter than was produced. Thus, it would be classified as a heterotrophic system (based on the organic matter budget) despite the fact that the P:R ratio of 1.20 indicates autotrophy. Conversely, Deep Creek is a net exporter of organic matter and has a P:R ratio of 1.19; thus, both parameters indicate that Deep Creek is an autotrophic system. In terms of the definitions of Fisher and Likens (1973), Rattlesnake Springs would be an accretive (net importer) system [import (I) + gross photosynthesis (P_g) > ecosystem respiration (R) + export (E)], and Deep Creek would be a remissive (net exporter) system ($I + P_g < R + E$). Rattlesnake Springs ($I/E > 1$) would be classified as a net importer and Deep Creek ($I/E < 1$) as a net exporter, in the definitions of Cummins (1974). Thus, a situation exists in which Rattlesnake Springs is a net importing system and Deep Creek a net exporting system, and both have P:R ratios exceeding one. Busch and Fisher (1981) report that Sycamore Creek, a small unshaded desert stream, is autotrophic with a P:R ratio of 1.7; they emphasize that autotrophic streams must be net exporters.

Energy budgets must be interpreted carefully. Fisher (personal communication) points out that streams, especially desert streams which experience periodic flash flooding at varying intervals, can be net importers one year and net exporters another. This is apparently the case with Deep Creek. Station 3 on Deep Creek is located below a reservoir that

TABLE 5.8. Annual Energy Budgets for Rattlesnake Springs, Washington, and Deep Creek, Idaho[a] (Cushing and Wolf 1982)

	Rattlesnake Springs		Deep Creek	
	Kcal/m^2/yr	Percent	Kcal/m^2/yr	Percent
IMPORT				
Particulate organic matter	2728	8.6	142.7x10^3	46.6
Allochthonous	(1215)[b]	(3.8)	(12.2)	(tr)
Transport POM	(1513)	(4.8)	(142.7x10^3)	(46.6)
Dissolved organic matter	3699	11.6	149.1x10^3	48.7
Gross Primary Productivity	25380[c]	79.8	14.3x10^3	4.7
Total	31,807	10.0	306.1x10^3	100.0
EXPORT				
Particulate organic matter	2726	10.0	169.1x10^3	51.2
Watercress + benthos	(1213)	(4.5)		
Transport POM	(1513)	(5.5)	(169.1x10^3)	(51.2)
Dissolved organic matter	3201	11.8	149.1x10^3	45.2
Respiration	21216[c]	78.2	12.0x10^3	3.6
Total	27,143	100.0	330.2x10^3	100.0
STORAGE	0		0	
Total	27,143		330.2x10^3	
BALANCE (In-Out)	4,664		-24.1x10^3	

(a) After Minshall (1978)
(b) Figures in parentheses are subtotals
(c) Does not include aerial respiration of watercress

stabilizes the flow. The system has apparently been importing (accretive) for a number of years and is now exporting (remissive) simply because the system is "filled up" and experiences no scouring floods to reset the system (G. W. Minshall, personal communication). Rattlesnake Springs was a net importer over the year; the export event (flash flood) which scoured the system was not large enough to exceed the annual organic matter accumulation.

Low-order streams (1st to ca. 4th) usually are considered hetero- trophic, based on extensive shading and maximum input of allochthonous organic matter (Hynes 1969, Vannote et al. 1980). However, the data from Rattlesnake Springs, Deep Creek, and Sycamore Creek support the hypothesis of Minshall (1978) that low-order streams in semi-arid and arid regions of the West tend to be more open to insolation than eastern streams in deciduous regions. Thus, autochthonous production in low-order arid western streams frequently dominates in-stream community metabolism.

BIOENERGETIC STUDIES

In 1971, D.A. McCullough began detailed investigations of the bioenergetics of three aquatic insects in Rattlesnake Springs and Deep Creek, Idaho (McCullough et al. 1979a, b). These insects were the mayfly (*Tricorythodes minutus* Ephemeroptera:Tricorythidae), the caddisfly (*Hydropsyche occidentalis* Trichoptera:Hydropsychidae), and the blackfly (*Simulium* spp. Diptera:Simuliidae). These experiments resulted in an extensive data set too large to review in detail in this volume; hence, only a brief summary of the work is presented below. The interested reader is referred to the original publications (McCullough et al. 1979a, b) for further details and relevant literature.

The energy budget of the fine-particle collector organism T. minutus Traver was determined under conditions (flow, substratum, temperature) representative of its natural habitat. Digestion time (gut clearance) was rapid (30 minutes). Ingestion values ranged widely from 33 to 220 μg DW/mg DW/hr, depending on the type of food provided. Assimilation rates were lowest, about 2 μg ash-free DW/mg DW/hr, with mixed diatoms, intermediate with the blue-green alga Anabaena (about 23), and high with the blue-green Lyngbya (about 61) and with a pure culture of Nitzschia (about 62). Assimilation efficiencies showed a much narrower spread, being 33, 34, and 57 percent for mixed diatoms, blue-green algae, and Nitzschia. A mean respiration rate of 2.51 ml O_2/mg DW/hr was derived for T. minutus at 20°C. Growth, estimated from length-weight relationships, was 4.5 μg DW/mg DW/hr. The instantaneous growth rate for T. minutus (0.126) is higher than those reported for any other mayfly (0.034 to 0.060) except Tricorythodes atratus (0.153) (Hall 1975). Cast skins accounted for over 30 percent of the total production (G + Ex = 6.5 μg DW/mg DW/hr. Comparison with Stenonema pulchellum, the only other mayfly for which complete energy budget information is available (Trama 1972), showed respiration rates to be similar and assimilation and growth of Tricorythodes to be 2.9 and 5.3 times higher. However, the major distinction between the two was the high ingestion rate for Tricorythodes compared with that for Stenonema (7 μg Dw/mg DW/hr).

A second study was done to derive a set of bioenergetic parameters for the blackfly (Simulium spp.) and the caddisfly (Hydropsyche occidentalis) and to evaluate the impact of these filter feeders on the lotic environment.

In addition, comparisons were made between field- and laboratory-derived estimates of ingestion and between two methods of calculating assimilation rate.

Digestion (gut-clearance) time for Simulium ranged between 0.33 and 1.25 hours compared to 1.54 to 2.63 hours for Hydropsyche. Mean ingestion rate for Simulium in a series of experiments ranged from 1.36 to 54.74 μg DW/mg DW/hr. The mean assimilation efficiency for diatoms was about 55 percent as measured by the dual-label technique. Mean ingestion rates of diatoms for Hydropsyche in three experiments were 31.3, 31.0, and 29.2 μg DW/mg DW/hr, respectively; low values (3 μg DW/mg DW/hr) from a fourth experiment were associated with high concentrations of green algae. An assimilation rate for diatoms of 7.5 μg AFDW/mg DW/hr was derived for Hydropsyche. Measurements of growth rates of Hydropsyche under natural conditions were 3.6 to 4.4 μg DW/mg DW/hr. Respiration rate of Hydropsyche for water greater than about 62 percent O_2 saturation was about 2.3 μl O_2/mg DW/hr at 20°C.

The results of this research in combination with values derived from the literature, yielded the following mean energy budgets for Simulium and Hydropsyche, respectively (J/mg/hr): ingestion (C) 0.318, 0.393; respiration (R) 0.092, 0.042; growth (G) 0.092, 0.100; assimilation (A) (as C x AE) 0.182, 0.192; (as G + R) 0.184, 0.142 (values times 0.239 = cal/mg/hr).

The role of these filter feeders was evaluated in terms of their processing of suspended organic material and in directing energy to higher trophic levels. Simulium and Hydropsyche (with net growth efficiencies of 49.5 and 69.6 percent, respectively) are more comparable to bacteria in terms of metabolic removal of organic C from food sources. During the months in

which they were present, the mean biomass and density of Hydropsyche occidentalis in Deep Creek (station 2), Idaho, were 2.45 g DW/m^2 and 1786/m^2 and of Simulium were 0.22 g DW/m^2 and 1699/m^2. Based on all 12 monthly samples, Hydropsyche comprised 44 percent of the total invertebrate standing crop biomass of 4.84 g DW/m^2. From mean biomasses and numbers of invertebrates in riffles of Deep Creek and mean ingestion rates for Simulium and Hydropsyche (30.5 and 80 μg/mg/hr, respectively) it was calculated that the filter-feeders remove 0.01 percent of the seston flowing over them each day. The filter-feeders also are an important food for carnivorous insects and fish in Deep Creek.

DECOMPOSITION STUDIES

In 1978, a comparative study was undertaken to examine the processing rates of box elder (Acer negundo) leaves in a Rocky Mountain stream, Stewart's Creek, Utah, and a cold desert stream, Rattlesnake Springs (Barnes et al. 1986). In addition to examining processing rates of these leaf packs in the two streams, a replicate series of leaf packs was enclosed in 1-mm mesh cages to evaluate the effects of excluding large shredder organisms.

The processing of leaf litter in streams is mediated by an array of biological and physical factors. By excluding large shredders in the Rocky Mountain stream, the litter processing rates were significantly different ($k = -0.017$) from leaf packs in which the larger shredders were present ($k = -0.028$). In Rattlesnake Springs, k values were -0.021 for the exclusion packs and -0.042 for the open packs; the differences were statistically significant (Barnes et al. 1986). Processing rates were higher in Rattlesnake

Springs, probably because of the types of shredders present and the higher mean water temperature during the experimental period which increased microbial processing (Reice and Herbst 1982).

Section III. Radionuclides as Indicators of Aquatic Ecosystem Processes

In aquatic ecosystems, as in the vegetational communities dealt with in Chapter 6, radionuclides released to the environment as a consequence of Hanford nuclear production have shown a definite but limited usefulness for tracing ecosystem functional processes. Quantitative information is not well developed. There are several reasons for this difficulty. For example, 1) reaction velocities must be determined under well-bounded conditions of control, which is difficult to accomplish in the field; 2) the interactions among many concurrent processes in natural systems often confound the use of tracers to measure a particular process; and 3) processes can be discerned most readily by radioactive tracers only during a change in the tracer "injection" rate, e.g., during startup, shutdown or changed operation of a nuclear facility.(a)

The extensive radioecological literature chiefly documents physiological details of bioconcentration in fish and other organisms, tracer distributions among various ecosystem "compartments," and sometimes valuable data on chemical and physicochemical speciation of the radionuclides as they are found in the environment (Nelson 1971, Cushing 1976, Hanson 1980). Qualitatively, this literature has provided many valuable insights on ecosystem function, and it remains very important in the development of radiological monitoring practice (Vaughan et al. 1981).

(a) When radionuclide releases continue over very long periods of time at extremely low levels, they become diffused throughout aquatic and terrestrial ecosystems in such a way that little new information is provided beyond that provided by measuring elemental distributions.

At the Hanford Site, sediment transport rates and "scouring" of radionuclides from reactor effluents have been determined in the Columbia River (Perkins et al. 1965, Robertson et al. 1973, Robertson and Fix 1977), and comparative magnitudes of export from a plutonium-contaminated pond by biotic pathways have been determined as a function of seasonal biomass and trophic-level relationships (Emery et al. 1978). Relative to stream ecology, continuing studies on seasonal changes in radionuclides or metals associated with suspended particulate matter are providing important information on system handling of allochthonous mineral inputs.

Suspended particulate matter, for example, dramatically increased in the Columbia River during spring freshets, and it was shown to originate from terrestrial sources even under arid climate conditions characteristic of Hanford (Wildung et al. 1972). The material contained higher concentrations of colloidal particles with large surface areas, as well as minerals of high charge densities. This material was usually present in comparatively high concentration during the runoff periods, and it correlated with the spring peak in radioelement concentrations found in the river and in river organisms. Over 85 percent of the total particulate strontium exchange capacity measured in the spring was associated with the <2.0-micrometer clay size fraction.

In subsequent studies, suspended particulates were found to play a primary role in the distribution of mercury in the Columbia River and ultimately in its accumulation by fish (Garland et al. 1975). Mercury exhibited more complicated interactions with the river system than did radionuclides in cationic form. Based on later studies of the chemical speciation of mercury in waters and sediments, it appears that high levels of suspended particulates during the spring freshet are important in delivering mercury to bottom

sediments. Later, by chemical or biological means, the sediments release a significant part of the mercury to the overlying water as it reaches its temperature maximum; whereupon fish absorb chemically altered forms of the mercury (Garland et al. 1975, R. E. Wildung, personal communication). These studies point to the importance of studying biogeochemical events in determining how aquatic ecosystems process allochthonous inputs of minerals or other substances.

The Columbia River's size, complexity and enormous flow rate have placed severe constraints on suitable investigations at the ecosystem level. The importance of seasonal allochthonous inputs has, however, been demonstrated by investigation of the radiological and geological characteristics of suspended particulates that show seasonal periodicity. Similar seasonal phenomena have been found with other Columbia River ecosystem components such as periphyton, phytoplankton, macroinvertebrates and fish (Watson et al. 1970 and others).

Section IV. Summary

Although our knowledge of desert streams is far from complete, certain aspects of their structure and function are becoming apparent. Desert streams appear to be dominated by autotrophic processes, at least for the greater part of each year, but differ in their ability to be exporters or importers of organic matter. Many of the processes are keyed to the occurrence of flash floods which scour the stream beds and biota to varying degrees. These flash floods, which recur at varying and unpredictable intervals, reset many of the processes. This means that stability, if it occurs, is ephemeral and the communities are usually in various stages of succession; ecosystem resilience is high. Much remains to be learned about these unique ecosystems.

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CHAPTER 6. PLANT COMMUNITY CHARACTERISTICS AND RESPONSES

W. H. Rickard and B. E. Vaughan

Chapter 6. PLANT COMMUNITY CHARACTERISTICS AND RESPONSES

W. H. Rickard and B. E. Vaughan

The purpose of this chapter is to summarize and synthesize information gained over the past 20 years concerning responses of shrub-steppe plants and plant communities to seasonal fluctuations in the physical environment and also to human-induced disturbances. Perhaps the most practical use of the data base on plant productivity relates to water balance. Five consecutive years of data were obtained relating soil water and temperature to shoot productivity. These data were useful in developing water balance models and formulating a practical concept of biological barriers to prevent biotic contacts with buried radioactive wastes buried in the upper few meters of earth.

In this chapter, data are presented showing responses of plant communities to drought years, to experimental microclimatic manipulations, soil nutrients, fire, cattle grazing, and a severe soil disturbance (plowing). Because of continuing interest on the potential usefulness of radioactive tracers in determining fate and transport of hazardous materials, several examples are presented which provide insights on radionuclide behavior in a semi-arid region.

Section I. Characteristics of Contrasting Shrub-Steppe Plant Communities

In this section, we summarize the status of information and compare shoot production between native sagebrush-bunchgrass communities and cheatgrass communities comprised almost entirely of alien plant species. In particular, the documentation of "natural conditions" is a prerequisite for the interpretation of changes due to single or multiple disturbances perpetrated by human land use activities.

STANDING CROP AND SHOOT PRODUCTION IN A SAGEBRUSH-BUNCHGRASS COMMUNITY

In the years prior to 1800, plant communities in the semi-arid shrub-steppe region of interior Washington State consisted mainly of vast expanses of the sagebrush-bunchgrass (*Artemisia tridentata*/*Agropyron spicatum*) association (Daubenmire 1970). Following settlement in the mid-1800's by European peoples, much of the land was converted to dryland wheat and irrigated croplands. Today, the isolated remnants of these once- extensive communities are mostly confined to steep slopes or other places with extremely rocky soil, and even these are usually subjected to the impacts of chronic livestock grazing.

Most of the undisturbed, remnant sagebrush-bunchgrass communities in eastern Washington have been described in terms of their floristic composition, canopy cover, climate, topography and soil properties (Daubenmire 1970), but little information is available concerning standing crop or dynamics of organic matter production. The opportunities to study standing crops and natural variation dwindle with the passage of time as remnant communities become further modified by an ever increasing variety of human-induced land uses

(Coupland 1979). It is especially difficult to locate unperturbed sagebrush-bunchgrass communities growing on soil that is otherwise suitable for agricultural production. Only a few stands have escaped either cultivation or floristic changes induced by many years of continuous livestock grazing. The following text describes standing crop and shoot production in a relatively undisturbed sagebrush-bunchgrass community growing on deep, stone-free silt-loam soil on gentle topography.

The community chosen for study is located on the Arid Lands Ecology (ALE) Reserve, at an elevation of 380 meters above mean sea level. The community had been lightly grazed by livestock for about 50 years prior to government acquisition of the land in 1943. Since 1943 the community has had essentially no fugitive livestock grazing and no grazing at all since 1968. The scarcity of cheatgrass (Bromus tectorum), an aggressive alien, annual grass, was regarded as evidence of the relatively undisturbed status of the community (Daubenmire 1975). Wildfires were not known in the years between 1943 and 1972 or in earlier years; however, a part of the study community was burned by a wildfire in August 1973.

Sampling for shoot production and standing crop was conducted in the years 1971 to 1974 using the sampling procedures proposed by the U.S. International Biological Programme (Rickard et al. 1974, Rickard et al. 1975, Rickard et al. 1977, Uresk et al. 1980). The basic sampling unit consisted of 0.5 m^2 circular plots. Two plots were placed within eight 15 x 30-meter blocks that had been randomly located in each of four, contiguous 9-hectare plots. All above-ground vegetation (living and dead) was collected five times, at intervals between the beginning of the spring growing season in March until its end in late May or early June. The living plant (green) material

was separated from the dead. Root weights were measured by washing and sieving roots from soil cores, 1 decimeter deep, taken to a depth of 0.8 meters. Living and dead roots were not separated. Root, litter and grass crown data are presented as ash-free dry weight. Other values are presented as dry weights. A brief floristic description of the community follows.

Sagebrush shrubs of short stature (average height 0.5 meter) were widely spaced in an understory of herbaceous plants dominated by perennial bunchgrasses, especially bluebunch wheatgrass (Agropyron spicatum). Other perennial bunchgrass were Poa sandbergii, Poa cusickii and Stipa thurberiana. Semi-woody half-shrubs were important in the community, especially Erigeron filifolius, Phlox longifolia, and Antennaria dimorpha. Perennial forbs were represented by scattered individuals of Lomatium macrocarpum, Lupinus sulfureus, L. leucophyllus, Astragalus purshii, Brodiaea douglasii, Calochortus macrocarpus and others. Annual grasses and forbs, minor constituents of the community, were represented by Draba verna, Microsteris gracilis, Plantago patagonica, Vulpia octoflora, Descurainea pinnata and Bromus tectorum.

At the beginning of the spring growing season in each of 4 consecutive study years, the average dry weight of all live herbaceous species combined, ranged between 8 and 18 g/m^2 (Table 6.1). This amount represents fall and winter shoot production. Shoot production peaked in late May or early June, depending on the particular year, and ranged between 50 and 69 g/m^2 (Table 6.1). Perennial grasses dominated shoot production at all sampling times (Figure 6.1). Seventy-seven percent of the shoot production was contributed by perennial grasses. Half-shrubs contributed 16 percent, and perennial forbs contributed 5 percent. Annuals, mostly six weeks' fescue

TABLE 6.1. Mean Dry Weights of Green Herbaceous Shoots ($g/m^2 \pm SE$) in a Sagebrush-Bunchgrass Community, 1971-1974

1971	Mar 22	Apr 8	Apr 28	May 24	Jun 15
Perennial grasses	12 ± 1.0	20 ± 1.6	40 ± 1.6	46 ± 1.5	45 ± 6.5
Perennial forbs	0.37 ± 0.14	0.78 ± 0.21	1.2 ± 0.40	3.3 ± 1.3	2.1 ± 0.85
Annual grasses	0.03 ± 0.03	0.05 ± 0.03	0.43 ± 0.22	0.23 ± 0.07	0
Annual forbs	0	0.01 ± 0.01	0	0	0
Half-shrubs	3.6 ± 0.9	2.8 ± 0.91	6.1 ± 2.2	13 ± 4.1	8.0 ± 0.93
Total herbs	16 ± 1.7	24 ± 2.4	48 ± 5.0	63 ± 4.3	58 ± 5.7

1972	Mar 6	Mar 28	Apr 17	May 8	May 30
Perennial grasses	6.1 ± 0.57	21 ± 2.2	26 ± 2.8	28 ± 5.5	46 ± 7.4
Perennial forbs	0.16 ± 0.05	0.55 ± 0.15	1.1 ± 0.34	5.1 ± 1.7	4.9 ± 2.4
Annual grasses	0	Trace	0.17 ± 0.05	1.1 ± 0.21	0
Annual forbs	0	0.06 ± 0.03	Trace	Trace	Trace
Half-shrubs	2.6 ± 0.94	2.9 ± 0.64	4.2 ± 1.6	7.6 ± 2.6	14 ± 6.3
Total herbs	8.0 ± 0.97	25 ± 2.2	31 ± 3.4	42 ± 5.9	65 ± 3.6

1973	Mar 19	Apr 9	Apr 10	May 21	Jun 11
Perennial grasses	11 ± 1.3	27 ± 3.1	36 ± 4.5	28 ± 5.3	41 ± 6.0
Perennial forbs	1.1 ± 0.44	0.90 ± 0.87	4.1 ± 1.8	0.73 ± 0.02	Trace
Annual grasses	0	0.21 ± 0.10	0.32 ± 0.10	0	0
Annual forbs	Trace	0.07 ± 0.02	0.11 ± 0.10	0	0
Half-shrubs	6.2 ± 2.1	8.2 ± 2.3	11 ± 4.4	11 ± 4.4	8.8 ± 3.6
Total herbs	18 ± 1.8	36 ± 4.6	51 ± 7.2	41 ± 8.0	50 ± 5.2

1974	Feb 25	Mar 25	Apr 15	May 8	Jun 6
Perennial grasses	15 ± 2.2	21 ± 2.0	41 ± 4.1	54 ± 7.7	54 ± 11
Perennial forbs	0.15 ± 0.08	0.25 ± 0.06	1.6 ± 1.0	4.5 ± 3.6	2.1 ± 1.2
Annual grasses	Trace	0.09 ± 0.06	2.4 ± 0.40	4.8 ± 0.75	0
Annual forbs	0.16 ± 0.04	0.94 ± 0.25	2.1 ± 0.54	1.4 ± 0.09	0.94 ± 0.91
Half-shrubs	1.7 ± 0.86	4.1 ± 1.9	2.8 ± 1.4	4.2 ± 2.0	3.9 ± 2.2
Total herbs	17 ± 2.1	26 ± 2.1	50 ± 1.4	69 ± 9.3	61

(*Vulpia octoflora*), contributed less than 2 percent. These data illustrate the very small contribution to the undisturbed community made by annual plants.

The dry weight of grass crowns, standing dead herbaceous shoot material and the litter (dead shoots) showed no consistent increase or decrease from the beginning to end of the spring growing season (Table 6.2). Over the 4-year period, litter averaged 134 g/m^2; grass crowns, 84; and standing dead

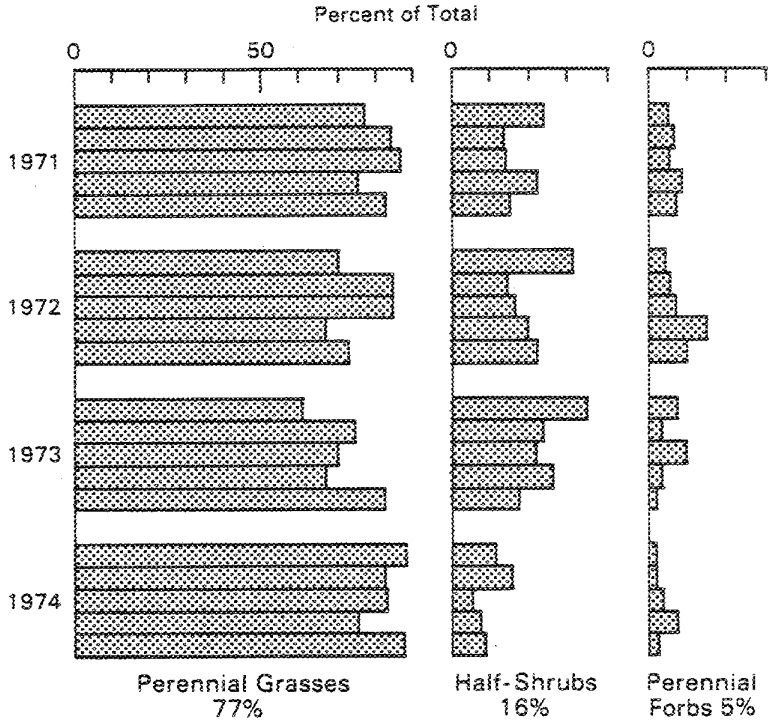


FIGURE 6.1. Percentages by Weight of Living Perennial Grasses, Half-Shrubs and Perennial Forbs in a Sagebrush-Bunchgrass Community at Five Harvest Periods distributed throughout the spring growing seasons of 1971, 1972, 1973 and 1974

herbage, 82. Sagebrush shrubs contributed 127 g/m^2 (Table 6.3). Dead sagebrush wood lying on the ground (wood litter) contributed 57 g/m^2.

Most of the dry weight of sagebrush was in the woody stems. Leaf weights averaged 10 g/m^2 per year. If leaf weight is used as an estimate of annual shrub production, then sagebrush provided 10 g/m^2 per year. If one-half of the crown weight of perennial grasses is considered as annual production, an additional 42 g/m^2 per year could be added to total shoot production.

TABLE 6.2. Mean Dry Weights (g/m^2 dry wt ± SE) of Grass Crowns, Standing Dead Plants and Litter in a Sagebrush-Bunchgrass Community, 1971-1974

1971	22 Mar	8 Apr	28 Apr	24 May	15 Jun	Avg.
Crowns	39±9.0	43±7.7	72±12	59±8.0	56±8.5	54
Standing dead	90±9.6	81±9.5	100±15	80±9.1	72±10	85
Litter	M	M	M	158±17	165±16	161
Total	---	---	---	297	293	300

1972	7 Mar	28 Mar	17 Apr	10 May	31 May	
Crowns	96±9.3	106±12	69±81	81±8.0	123±11	95
Standing dead	80±12	78±15	63±12	50±93	75±7.7	69
Litter	101±13	123±14	113±15	98±11	156±9.6	118
Total	277	307	245	229	354	282

1973	19 Mar	9 Apr	30 Apr	21 May	11 Jun	
Crowns	69±7.1	101±10	98±10	93±18	132±16	99
Standing dead	96±18	81±8.9	100±17	78±15	114±17	94
Litter	125±24	117±14	112±18	139±15	175±21	134
Total	290	299	310	310	421	327

1974	26 Feb	25 Mar	15 Apr	8 May	6 Jun	
Crowns	81±13	101±11	95±8.8	86±17	83±9.5	89
Standing dead	105±20	71±5.5	94±13	61±12	73±13	81
Litter	152±27	110±13	123±16	111±18	117±20	123
Total	338	282	312	258	273	293

M = missing datum

TABLE 6.3. Mean Dry Weights ($g/m^2 \pm SE$) of Sagebrush Shrubs in a Sagebrush-Bunchgrass Community, 1971-1973

1971	Mar 22	Apr 8	Apr 28	May 24	Jun 15	Avg.
Leaves	4.4±1.2	4.3±1.3	2.7±0.9	11±5.0	5.7±1.7	5.6
Live Wood	46±15	38±11	11±2	47±22	36±12	36
Dead Wood	50±17	18±6	35±7	57±17	60±15	44
Wood Litter	41±13	74±33	45±13	60±17	88±28	62
Total	141	134	94	175	190	148

1972	Mar 6	Mar 28	Apr 17	May 8	May 30	
Leaves	1.4±1.1	1.0±0.8	28±21	52±50	12±12	19
Live Wood	20±14	3.8±2.3	12±9.3	12±8.8	0.6±0.6	9.7
Dead Wood	36±25	0	22±12	0 0	12	
Wood Litter	68±25	97±32	23±5	48±18	52±20	58
Total	125	102	85	111	65	99

1973	Mar 19	Apr 9	Apr 30	May 21	Jun 11	
Leaves	5.8±3.0	1.5±1.4	3.9±3.0	8.1±3.0	5.4±5.4	4.9
Live Wood	113±94	2.4±2.3	9.3±6.8	33±17	47±47	41
Dead Wood	17±7.6	15±12	42±22	42±37	69±47	37
Wood Litter	35±16	97±39	47±21	36±16	30±9	49
Total	171	116	102	119	151	132

At the beginning of the spring growing season, root weights averaged 880 g/m^2, and at the end of the spring growing season they averaged 1150 g/m^2 (Table 6.4). About 25 percent of the total weight was concentrated in the surface decimeter and 41 percent was in the 2 surface decimeters of soil.

Total standing crop above ground averaged 490 g/m^2, with 1150 belowground (Table 6.5). Standing crop, above ground and below ground, amounted to 1600 g/m^2. Shoot production by all plants except sagebrush averaged 60 g/m^2 per year. Sagebrush contributed an additional 10 grams for a total of 70 grams.

TABLE 6.4. Mean Dry Weight of Roots ($g/m^2 \pm SE$) in a Sagebrush-Bunchgrass Community at the Beginning and End of the Spring Growing Season, 1972-1974

Soil Depth dm	1972 6 Mar	1973 19 Mar	1974 26 Feb	Avg.	%
0-1	155 ± 15	274 ± 31	297 ± 40	242	27
1-2	115 ± 28	117 ± 5	142 ± 17	125	14
2-3	101 ± 26	103 ± 2	95 ± 16	100	11
3-4	113 ± 21	108 ± 3	95 ± 10	105	12
4-5	101 ± 13	100 ± 4	81 ± 8	94	11
5-6	74 ± 12	95 ± 3	91 ± 7	87	10
6-7	57 ± 6	81 ± 3	69 ± 7	69	8
7-8	58 ± 7	66 ± 3	53 ± 6	59	7
Total	774	944	923	881	100

Soil Depth (dm)	1972 30 May	1973 11 Jun	1974 8 May	Avg.	%
0-1	282 ± 32	359 ± 85	216 ± 35	286	25
1-2	229 ± 25	193 ± 26	143 ± 17	188	16
2-3	167 ± 17	150 ± 20	98 ± 9	139	12
3-4	166 ± 22	135 ± 11	85 ± 4	127	11
4-5	170 ± 18	121 ± 10	87 ± 7	126	11
5-6	166 ± 16	108 ± 7	67 ± 7	114	10
6-7	126 ± 12	92 ± 8	58 ± 8	92	8
7-8	118 ± 14	68 ± 5	41 ± 6	76	7
Total	1424	1226	795	1147	100

TABLE 6.5. Summary of Major Standing Crop Components in a Relatively Undisturbed Sagebrush-Bunchgrass Community

Standing Crop Above and Below Ground ($1600\ g/m^2$)

Herb Component		Sagebrush Component	
Live shoots	62	10	Leaves
Standing dead	82	29	Live wood
Grass crowns	84	31	Dead wood
Litter	134	57	Wood litter
Total (g/m^2)	360	130	Total (g/m^2)

Below-Ground Component ($1150\ g/m^2$)

This value is at the low end of the scale of production as reported in the literature for other kinds of grass-dominated communities in semi-arid regions of western North America (Lauenroth 1979; also see Table 6.6). If 40 grams (50 percent of crown weight) is added as shoot production, the total is 110 g/m^2 per year.

It was expected that annual shoot production would show a direct relationship to the amount of growing season precipitation; that is, years with higher amounts of precipitation were expected to show higher shoot production, and low-precipitation years, lower shoot production. The relationship between peak shoot production and growing-season precipitation (October to May) during the years 1971-1974 is summarized below.

Measurement	1971	1972	1973	1974
Precipitation (cm)	21.4	17.4	12.9	36.2
Production (g/m^2)	63	65	50	69
Efficiency (g/m^2/ppt cm)	2.9	3.7	3.9	1.9

These data show that 1973, the year of lowest precipitation (12.9 centimeters), had the lowest shoot production, 50 g/m^2, and that 1974, the year of highest precipitation (36.2 centimeters), had the greatest shoot production, 69 g/m^2. The values were confined to a relatively narrow spread, i.e., 50-69 g/m^2. The precipitation values ranged between 12.9 and 36.2 centimeters. The conclusion is that the variation observed in shoot production in four growing seasons was not as great as was the variation in precipitation. The efficiency ratio (shoot production divided by growing season precipitation) was greatest during the 3 low-precipitation years (2.9-3.9) and least in the single

TABLE 6.6. Live Shoot Weights (g/m^2 dry wt.) in Steppe Communities[a] in the Western United States

<100g/m²		101-200g/m²		201-300g/m²		301-400g/m²		>400g/m²	
Albion, MT	42	SE Washington[b]	104	Bismarck, ND	203	Vermillion, SD	353	Paskuska, OK	567
Sundance, WY	76	SE Washington[b]	115	San Joaquin, CA	224	Cresco, IA	369	Columbia, MT	634
Ardmore, SD	86[b]	Las Cruces, NM	115	Dickinson, ND	224	Urbana, IL	373		
Richland, WA	82	Sydney, MT	122	Hopland, CA	228	Manhattan, KS	387		
Richland, WA	70[c]	Rexburg, ID[d]	123	St. Lanatius, MT	230				
		Newtown, ND	144	Hays, KS	234				
		Santa Rita, NM	144	Long Valley, SD	250				
		Nunn, CO	145	Amarillo, TX	257				
		San Jose, CA	166	Norman, OK	265				
				Throckmorton, TX	280				
				Cottonwood, SD	282				
				Boulder, CO	298				
Average	71		120		248		370		600

(a) Lauenroth 1979
(b) Daubenmire 1970
(c) This study
(d) Pearson 1965

high-precipitation year (1.9). This indicates that water losses by abiotic processes (i.e., runoff, infiltration, evaporation) are most pronounced during high-precipitation years and that such water is not used for plant production. The long-term role of sagebrush shrubs in sagebrush-bunchgrass communities is mostly one of conjecture, but there are some studies that lend insight to its possible role. Sagebrush is virtually the only nonaestivating plant in the community during the hot, dry summer months. It has a capacity to extract water from very dry soils with water potentials as low as -60 to -70 bars (Campbell and Harris 1977). However, sagebrush is physiologically most active during the spring months when soil water is most available (DePuit and Caldwell 1973, 1975).

Sagebrush shrubs participate in mineral cycling in a way that is not matched by its associated grasses and forbs. Mineral nutrients located deep in the soil may be brought to the soil surface by sagebrush roots, accumulate in sagebrush leaves and then be returned to the surface soil via leaf fall (Mack 1977, Mayland and Murray 1979). These sagebrush- incorporated nutrients are potentially available for use by shallow-rooted grasses and forbs following release from the dead sagebrush leaves that are dropped to the ground year after year and accumulate beneath the canopy spread of the widely spaced shrubs.

Sagebrush shrubs contribute to the characteristic appearance of sagebrush-bunchgrass communities, and they also provide nesting sites and shelter for small passerine birds, e.g., sage sparrows and Brewer sparrows. Without shrubs, these birds do not nest in the community (McAdoo and Klebenow 1979). Sagebrush leaves and twigs provide forage for jackrabbits, mule deer, and sage grouse. Sagebrush is usually not palatable to cattle and sheep, so

most rangeland research has been aimed at finding cost- effective ways of eradicating it from sagebrush-bunchgrass communities, and enhancing, thereby, the productivity of the livestock-palatable grasses (Britton and Ralphs 1979, Evans et al. 1979).

STANDING CROP AND SHOOT PRODUCTION IN A CHEATGRASS COMMUNITY

The initial plowing of sagebrush-bunchgrass communities effectively destroys all shrubs, grasses and forbs. Plowing is usually followed by planting, replowing and replanting. In only a few cases has cultivation ceased, providing opportunities to observe the self-revegetation process for 30 years or more. One of these places is the ALE Reserve.

Cheatgrass is an aggressive invader of cultivated ground. It has occupied abandoned dryland wheat fields on the Reserve for 40 years, and once established, it resists invasion by the native taxa (Rickard and Sauer 1982). Most of the ecological studies concerning cheatgrass have been directed towards understanding its autecology (Hulburt 1955, Harris 1967, Hinds 1975, and Mack 1981). Little research attention has been paid to cheatgrass as the dominant species in a kind of self-perpetuating plant community that is new to the region (Daubenmire 1975).

This study simultaneously compared shoot productivity in sagebrush-bunchgrass and cheatgrass communities growing on similar soils and altitudes without external interferences imposed by grazing livestock or by burning. At the time of this comparison, the sagebrush bunchgrass community had developed with the geological history of the Columbia Basin, and the cheatgrass community had occupied an abandoned dryland wheatfield for 30 years.

Shoot production in the cheatgrass community averaged 225 g/m^2/yr (Table 6.7). Shoot production of the herbaceous taxa in the sagebrush-bunchgrass community averaged 59 g/m^2/yr. Shoot production in the cheatgrass community showed an efficient use of precipitation. About 12 grams of dry shoot material was produced per centimeter of precipitation. This compares with only 2.7 g/cm in the sagebrush-bunchgrass community (Figure 6.2).

The shoot production curves for the cheatgrass community were similar during 1971, 1973 and 1974 growing seasons, but the shape of the curve was different in the 1972 season (Figure 6.3). In 1972, shoot production peaked

TABLE 6.7. Shoot Weights (g/m^2 Dry Weight ± SE) at Peak Yield, October-to-May Precipitation, and Efficiency in a Sagebrush-Bunchgrass and a Cheatgrass Community, 1971-1974

Year	Shoot Weight g/m^2	Precipitation cm	Efficiency[a]
	Sagebrush-Bunchgrass Community		
1971	63 ± 4.3	21.4	2.94
1972	42 ± 5.9	17.3	2.42
1973	50 ± 5.2	13.2	3.79
1974	69 ± 9.3	36.1	1.91
4-yr. ave.	59	22	2.7
	Cheatgrass Community		
1971	211 ± 11	17.3	12.2
1972	127 ± 5	17.4	7.3
1973	205 ± 14	11.7	17.5
1974	358 ± 25	31.5	11.4
4-yr. ave.	225	19.5	12.1

(a) Efficiency = grams of dry shoot/m^2 divided by the amount of growing season precipitation in centimeters.

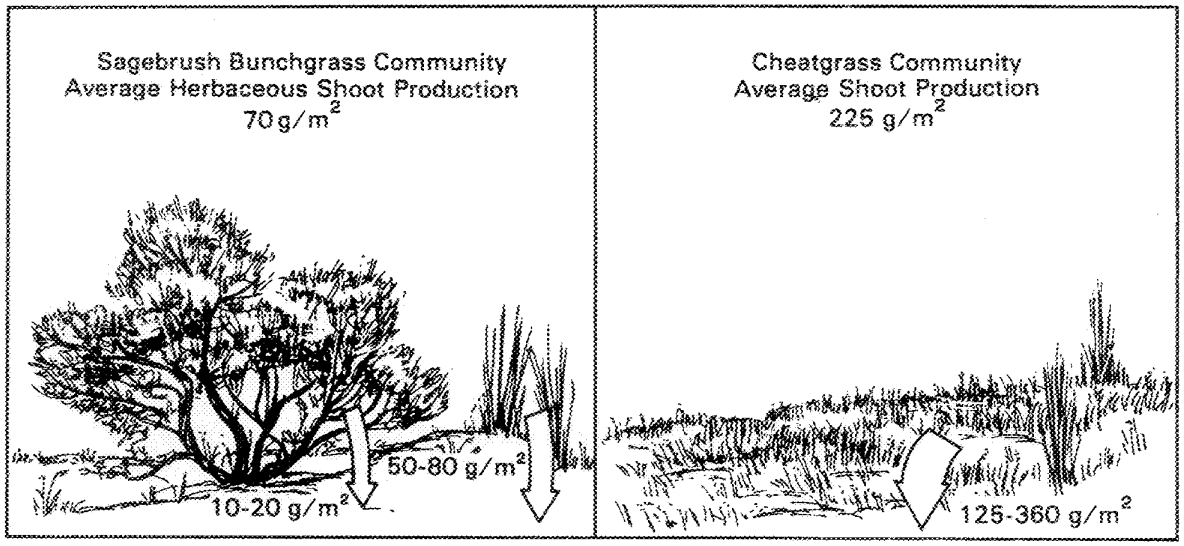


FIGURE 6.2. Comparison of Productivity in Sagebrush-Bunchgrass and Cheatgrass Communities

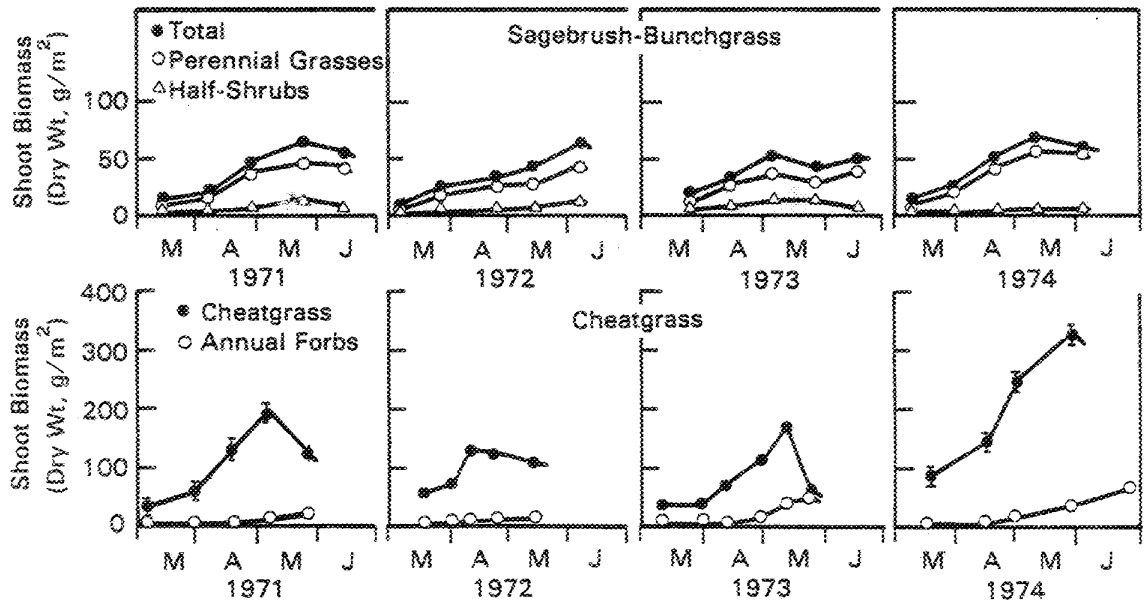


FIGURE 6.3. Changing Shoot Weights in Sagebrush-Bunchgrass and Cheatgrass Communities in the Spring Growing Seasons of 1971, 1972, 1973 and 1974 (Points are means ± SE)

in April rather than May. Shoot production was also the lowest, even though 1972 was not the year of lowest precipitation. The low-precipitation year, 1973, produced more shoot biomass than the 1972 season. This suggests that environmental factors other than the amount of growing-season precipitation contributed to diminished shoot production. Air temperatures in February were 3.7°F lower than any of the other years (Table 6.8). Colder temperatures may have accounted for the diminished productivity by damaging the tender cheatgrass seedlings to the point where they could not respond quickly enough to exploit the available soil water and soil nutrient resources. Shoot production in the sagebrush-bunchgrass community, as judged by the growth curves from 1971 to 1974, was not similarly affected by the same temperature regimen (Figure 6.3).

Total root weight in the sagebrush-bunchgrass community was greater than in the cheatgrass community (Figure 6.4). The root biomass in the cheatgrass community was heavily concentrated near the soil surface. On the average, 69 percent of the total cheatgrass root weight was concentrated in the surface decimeter of soil.

TABLE 6.8. Comparison of Average Monthly Air Temperatures (°F) at the Cheatgrass Community During the Growing Seasons of 1971, 1972, 1973 and 1974

Year	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
1970-71	50.9	39.7	30.8	35.8	39.1	40.7	52.0	64.0
1971-72	51.7	40.4	30.6	30.5	34.8	47.0	49.6	64.3
1972-73	52.3	39.9	27.3	29.1	38.5	47.4	53.6	63.1
1973-74	52.4	38.4	38.1	29.4	40.9	45.2	52.9	57.9

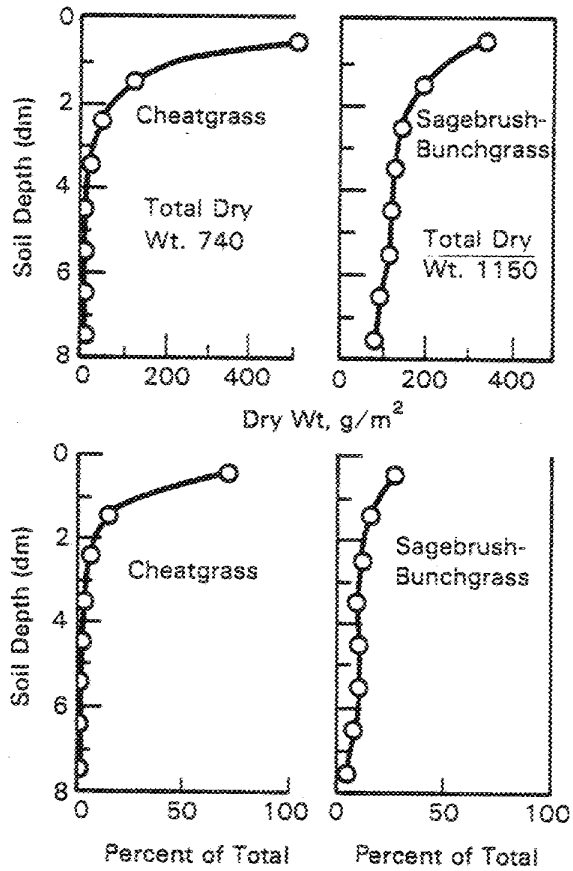


FIGURE 6.4. Dry Weights of Roots at 1-Decimeter Soil Depth Increments in Sagebrush-Bunchgrass and Cheatgrass Communities

Above-ground biomass did not differ greatly between the two kinds of communities, 465 g/m^2 and 426 g/m^2 in the cheatgrass and sagebrush- bunchgrass community, respectively (Table 6.9). However, litter weights were greater in the cheatgrass community, reflecting the greater shoot productivity.

The growing season of cheatgrass communities extends from October to May. By comparison, the growing season for the sagebrush-bunchgrass community is essentially year-long. The plants of the cheatgrass community tolerate the hot, dry summer months as seeds. Seeds are resistant to dessication.

TABLE 6.9. Comparison of Major Aboveground Biomass Categories of Cheatgrass and Sagebrush-Bunchgrass Communities, 1971-1974

Category	Cheatgrass Community	Sagebrush-Bunchgrass Community
Standing shoots	133	82
Litter	332	134
Wood litter	0	56
Grass crowns	0	84
Sagebrush		
leaves	0	10
wood	0	60
Total	465	426

In contrast, the perennial plants of the sagebrush-bunchgrass community are only quasi-dormant in summer. Energy is expended through respiration, although probably at a greatly reduced rate as compared to the spring months. This suggests that of the two, the cheatgrass communities are more energy conservative. The ecological strategy of cheatgrass communities is to allocate carbon resources (energy) to a multitude of viable seeds and none to long-lived vegetative tissues. The opposite strategy is practiced by sagebrush-bunchgrass communities, where carbon allocations to seeds are very small and allocations to long-lived tissue are comparatively large.

Figure 6.5 illustrates the efficiency of shoot production in the cheatgrass community as compared to that of other plant communities that were studied over the same timespan in the International Biological Programme. These data show that the sagebrush-bunchgrass community (Richland, Washington) is at the low end of the scale of shoot production. The efficiency ratios

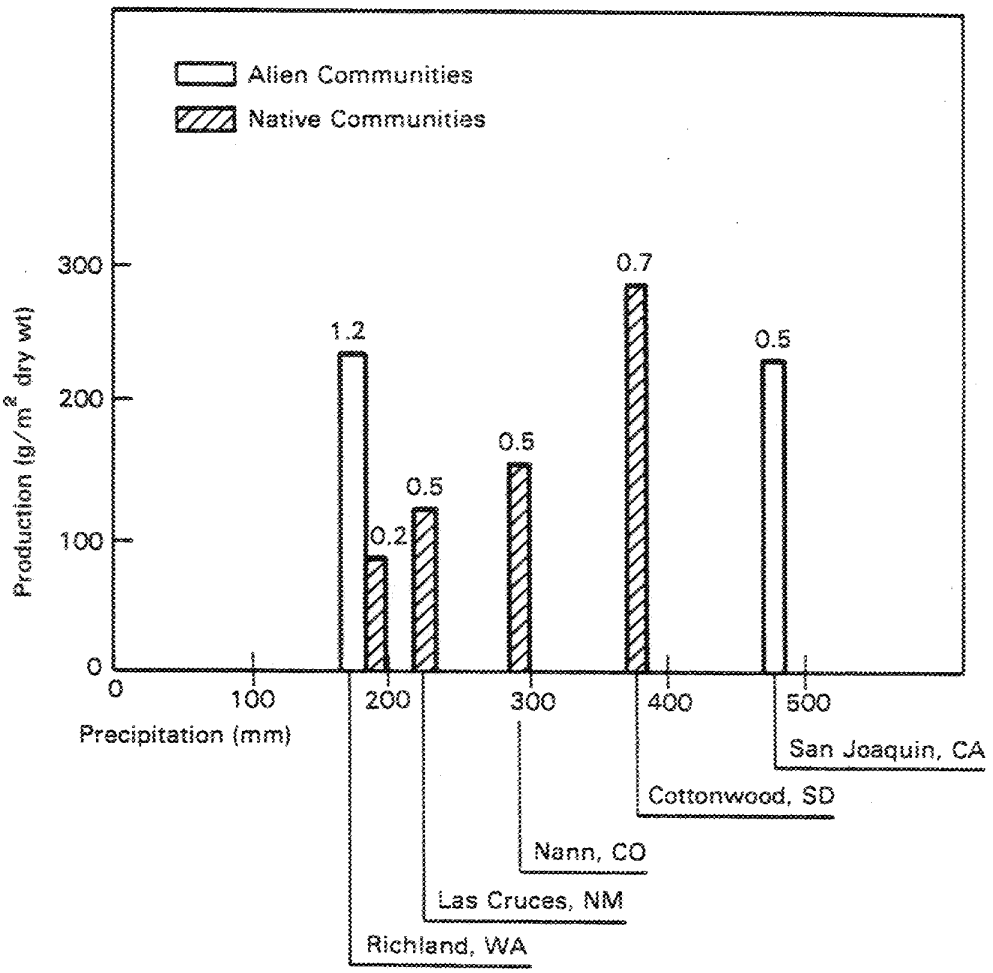


FIGURE 6.5. The Relationship Between Annual Shoot Production in Various Plant Communities in the Arid and Semi-Arid Regions of the Western United States and Cheatgrass and Sagebrush-Bunchgrass Communities at Richland, Washington (The number associated with each location is the grams of dry weight produced by plant shoots per millimeter of precipitation, or the efficiency ratio.)

of semi-arid perennial grass communities in Washington, New Mexico, Colorado and South Dakota are all less than 1.0, i.e, .28, .51, .46 and .72, respectively. The ratio was 0.46 for an annual grass community, the San Joaquin Valley of California. The ratio of 1.15 for the cheatgrass community (Richland, Washington) indicates the great efficiency of cheatgrass

communities. As far as is known, this is the most efficient wild plant community in the arid and semi-arid regions of the western United States.

PHENOLOGY OF SELECTED PLANT TAXA IN A SAGEBRUSH-BUNCHGRASS COMMUNITY

Phenology is the systematic documentation of the visual growth responses of plants to a continuously changing physical environment. Air and soil temperatures and soil water are examples of the environmental factors that vary in concert with the seasons and also from one year to another.

This section documents the phenological response of 12 plant taxa growing in a relatively undisturbed sagebrush-bunchgrass community during a normal year, 1973, and a wetter-than-normal year, 1974. Six phenological categories (phenophases) have been used to construct a comparative phenological chronicle (Sauer and Uresk 1976).

Phenophases

1)	new growth begins	4)	flowering terminates
2)	floral buds appear	5)	ripe seeds ready for disposal (end reproduction phase)
3)	flowering begins	6)	growth terminates or slows (aestivation)

The spring flush of sagebrush growth commenced in April, floral buds appeared in June, and flowering occurred in September (Figure 6.6). Growth terminated in late October, but seeds remained attached to the flowering branches until late November. Sagebrush shrubs failed to flower in 1973. The perennial bunchgrasses, *Agropyron spicatum* and *Stipa thurberiana*, had relatively long growing seasons with closely similar phenophases. Other

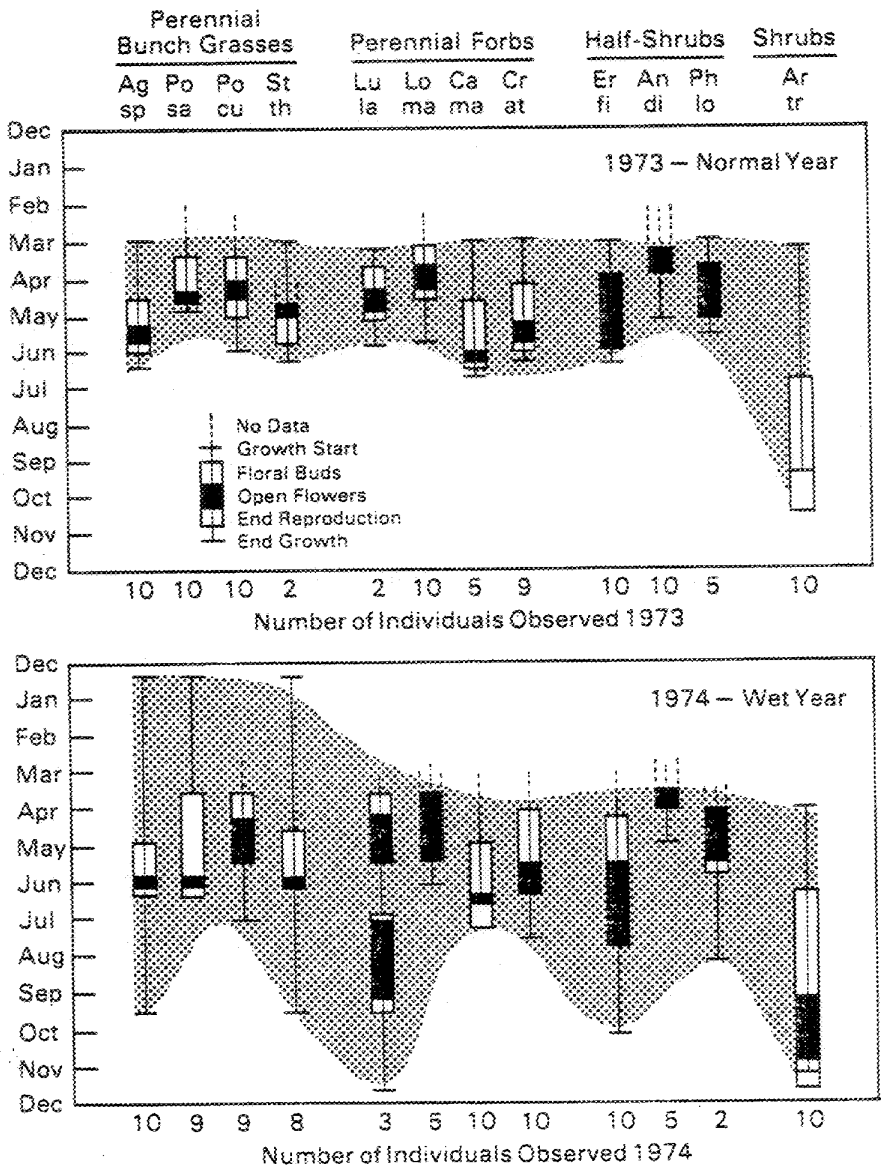


FIGURE 6.6. A Graphic Representation of the Phenological Stages of 12 Plant Taxa in a Sagebrush-Bunchgrass Community in 1973 and 1974

Ag sp =	*Agropyron spicatum*	Ca ma =	*Calochortus macrocarpus*
Po sa =	*Poa sandbergii*	Cr at =	*Crepis atrabarba*
Po cu =	*Poa cusickii*	Er fi =	*Erigeron filifolius*
St th =	*Stipa thurberiana*	An di =	*Antennaria dimorpha*
Lu la =	*Lupinus leucophyllus*	Ph lo =	*Phlox longifolia*
Lo ma =	*Lomatium macrocarpum*	Ar tr =	*Artemisia tridentata*

perennial grasses, Poa sandbergii and P. cusickii, had shorter growing seasons. P. cusickii flowered earlier than did P. sandbergii.

Of the four perennial forbs, Lupinus laxiflorus exhibited a second flowering in 1974, and its growth period in that year extended into November. The earliest flowering forb was Lomatium macrocarpum, followed by Crepis atrabarba and finally Calochortus macrocarpus. Of the various taxa of half-shrubs, Erigeron filifolius had the most extended flowering period, May to July. Antennaria dimorpha flowered in late March; its flowers were open for only a brief time. Phlox longifolia was intermediate between the other half-shrubs in terms of its phenological phases.

The 1974 growing season was characterized by above-normal precipitation, and this was reflected in stored soil water (Figure 6.7). The greater amount of soil water storage contributed to the extended spring growth period. Even in July there was still some available water in the soil profile.

The difficulty of visually detecting leaf fall in evergreen sagebrush shrubs prompted a need to explore some other kind of methodology that could be used for documenting the periodicity of leaf fall. The utility of using leaf collecting trays as a way to document the periodicity and magnitude of annual leaf-fall in sagebrush shrubs was explored.

Two sagebrush-bunchgrass communities were selected. One was located at 870 meters above mean sea level (high) and the other at 360 meters (low). Five to seven shrubs were used during the years 1976-1980 (Figure 6.8) (Rickard and Warren 1981a). The data show that leaf-fall in sagebrush shrubs is a year-round process, most pronounced during the hot, dry summer months. The

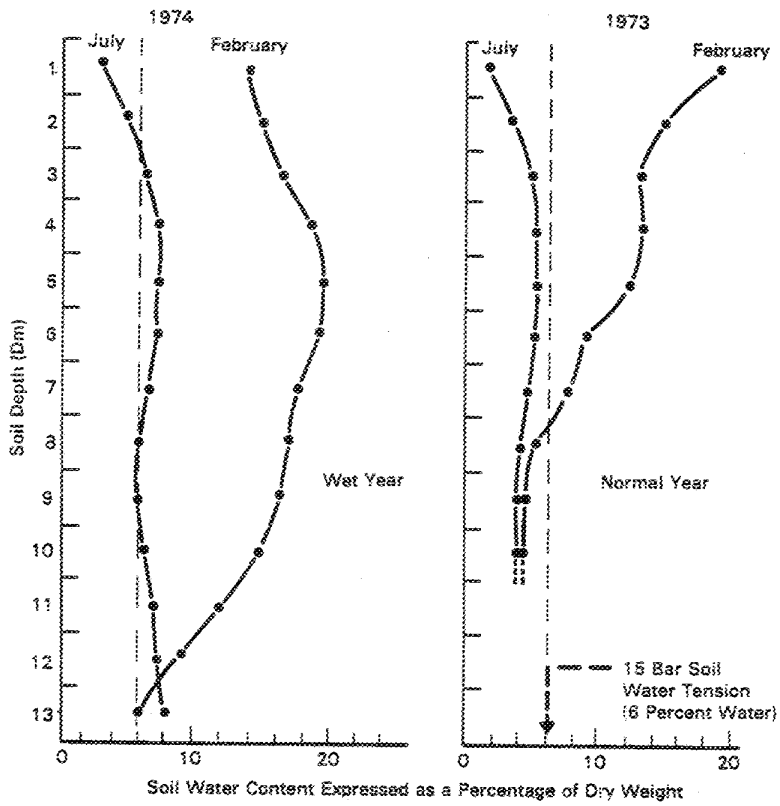


FIGURE 6.7. Soil Water in the Upper Meter of Soil Profile of a Sagebrush-Bunchgrass Community at the Beginning (February) and End (July) of the Spring Growing Season in 1973 and 1974 (The 1974 season was wetter than normal.)

shrubs at the lower elevation exhibited a low amount of litterfall during the 1976-1977 growing season, a year of extreme drought (Figure 6.8). The data also show that sagebrush shrubs responded to a normal precipitation regimen during the following growing season by restoring leaf-fall to pre-drought values. The capacity of sagebrush to quickly restore leaf production following a year of severe drought--and the utility of leaf fall collections in documenting the periodicity of leaf fall in desert shrubs--are demonstrated.

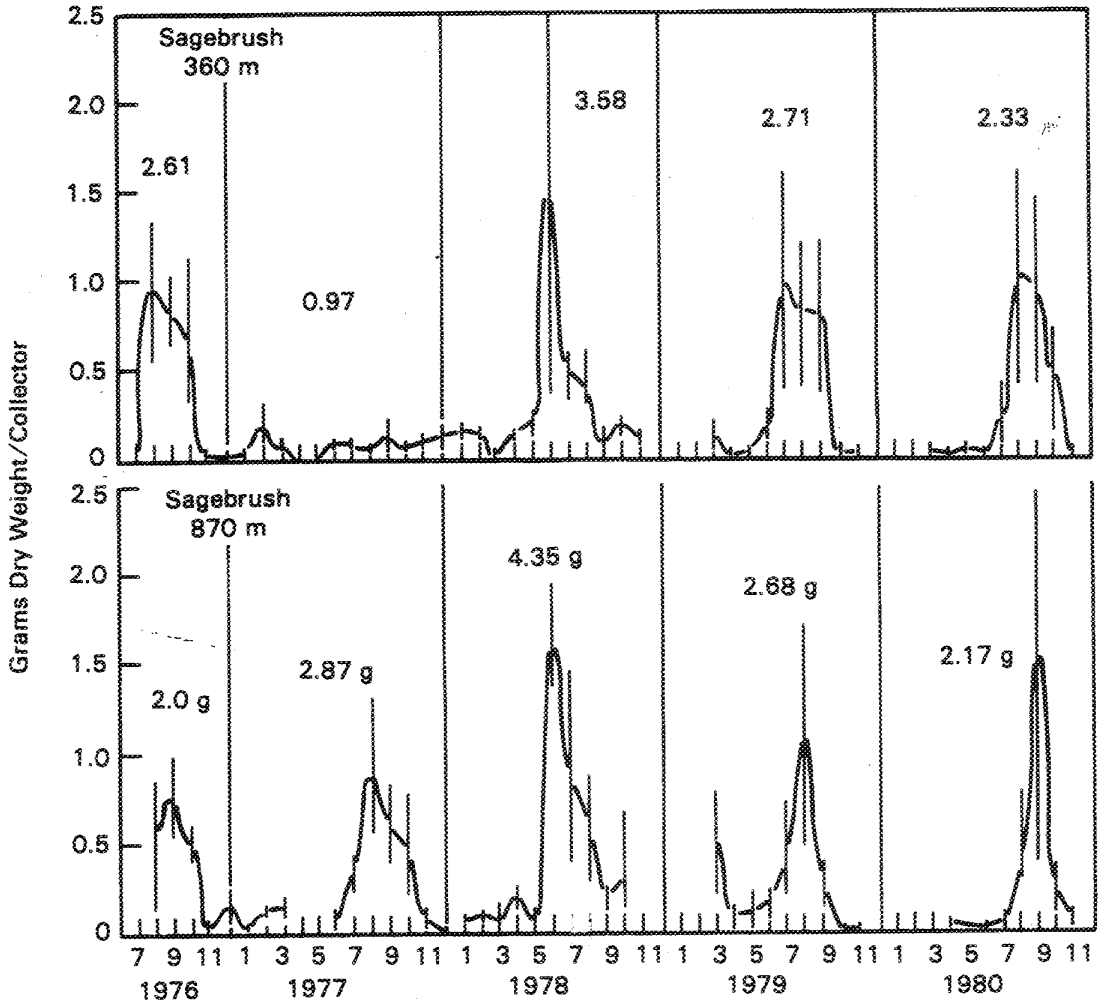


FIGURE 6.8. Monthly Leaf Fall of Sagebrush Shrubs at Different Elevations, 1976-1980 (The vertical bars represent the extreme values for 5-7 shrubs; the grams represent the average leaf fall per collecting tray for each year; the months are designated by numbers, Number 1 = January; 1977 was a year of extreme drought.)

It is tempting to speculate that the earliest growing perennial taxa in the sagebrush-bunchgrass community (e.g., Poa spp.) have, through time and evolutionary change, developed a different set of survival strategies than those of the late flowering taxa such as Agropyron and Stipa. In late winter and early spring, air and soil temperatures are at yearly lows, but the upper few decimeters of soil are at yearly high soil water content, and this water is located within the rooting depth of even the most shallowly rooted plant taxa. This pattern suggests that the early-growing (cool season) taxa can exploit shallowly stored soil water, which is most plentiful during late fall, winter and early spring months, even in the years of scantiest rainfall. However, these early-growing taxa are also the first to flower and the first to enter summer dormancy. Once this dormant stage is reached, the plants are probably not capable of exploiting soil water that has penetrated more deeply into the soil. Any rewetting of the soil surface that might occur in summer is also probably not available for use by these kinds of plants. Taxa with deep root systems and the capacity to extend their growth into early summer could take advantage of years with above-average precipitation, allowing soil water to penetrate more deeply into the soil, or those years with late-season precipitation that re-wets dry surface soil. Several consecutive years of above-average precipitation would tend to favor the late-growing taxa. On the other hand, a series of drought years would likely favor the early-growing taxa.

The taxa of the sagebrush-bunchgrass community behave somewhat like those that comprise the shortgrass prairie communities located on the high-elevation plains at the eastern edge of the Rocky Mountains in Colorado (Lauenroth 1979). There, the climate is characterized by well-defined periods

of winter and summer precipitation, and the warm- and cool-season grasses have overlapping growth periods. However, the differences are more subtle among the various taxa that comprise the sagebrush-bunchgrass community, which is attuned to a fall-winter precipitation pattern rather than a winter-summer pattern.

The phenological chronicle of sagebrush contrasts strongly with that of its associated grasses and forbs. Sagebrush experiences autumnal rather than vernal flowering. However, there are no data to indicate that autumnal flowering has any competitive advantages over vernal flowering.

NITROGEN AND PHOSPHORUS

The long-term self maintenance of natural plant communities on nutrient-poor soils depends in part on their ability to efficiently use and conserve scarce essential mineral nutrients (Chapin et al. 1980). The growing season changes in concentrations of nitrogen (N) and phosphorus (P) in the shoot component of cheatgrass communities and a sagebrush-bunchgrass community are compared in this section.

Two cheatgrass communities were studied. They were located at different elevations (Figure 6.9). On the average, soil concentrations of organic matter, nitrogen (N), potassium (K), and calcium (Ca) were greater in the surface soil at the low elevation (Table 6.10). However, there was considerable variation in these soil properties from place to place within each 0.1-hectare study plot, as indicated by the ranges of values.

Forb shoots generally had greater concentrations of N, P, K, and Ca than cheatgrass (Figure 6.10). Concentrations of N, P, and K also tended to

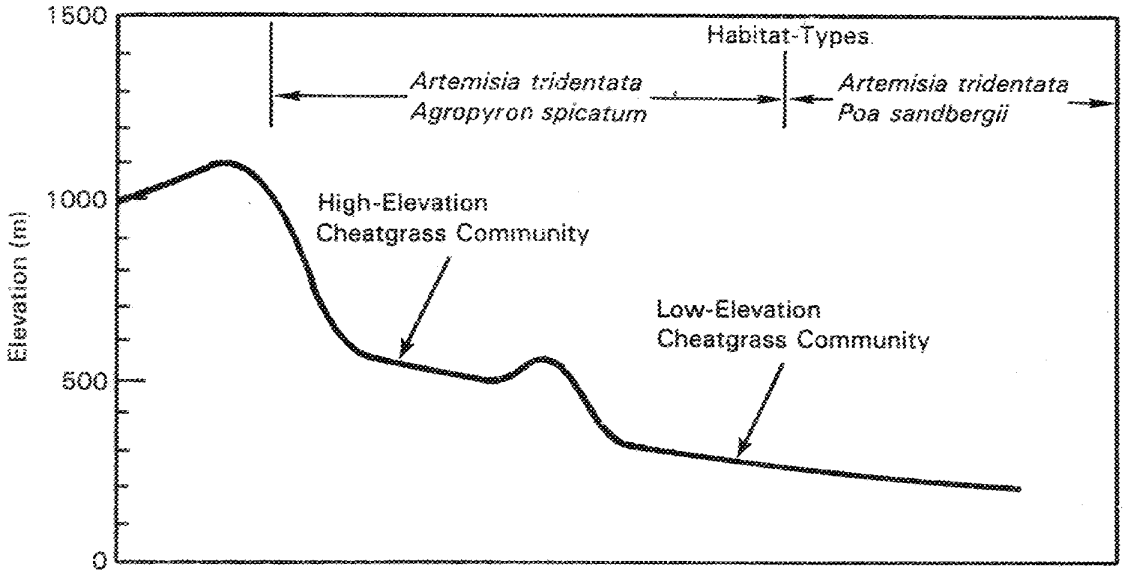


FIGURE 6.9. The Topographic Positions of Two Cheatgrass Communities in Southcentral Washington

TABLE 6.10. Soil Properties, Means and Ranges of Values (n=5), Obtained for Samples of Surface Soil from Cheatgrass Communities at High and Low Elevations on the ALE Reserve

Soil Properties	High Elevation (520 m)		Low Elevation (320 m)	
Organic Matter %	1.6	(1.5-1.8)	2.0	(1.6-3.5)
Nitrogen %	.073	(.064-.086)	.094	(.072-.112)
Phosphorus µg/g	34	(32-38)	32	(24-46)
Potassium µg/g	1100	(940-1210)	1400	(1080-1630)
Calcium µg/g	2600	(2500-2900)	3200	(2900-3700)
Soil pH		(6.4-6.9)		(7.0-7.3)
Bases meq/100g	10.6	(10-11.4)	12.5	(11.6-13.6)

decline in forb shoots as the season progressed, but Ca tended to increase. Concentrations of N, P, K and Ca in cheatgrass shoots declined as the growing season progressed.

Nitrogen and P concentrations were greater in the ripened culms of cheatgrass than in the attendant foliage, but the foliage had greater concentrations of Ca (Table 6.11). Concentrations of K were greater in foliage

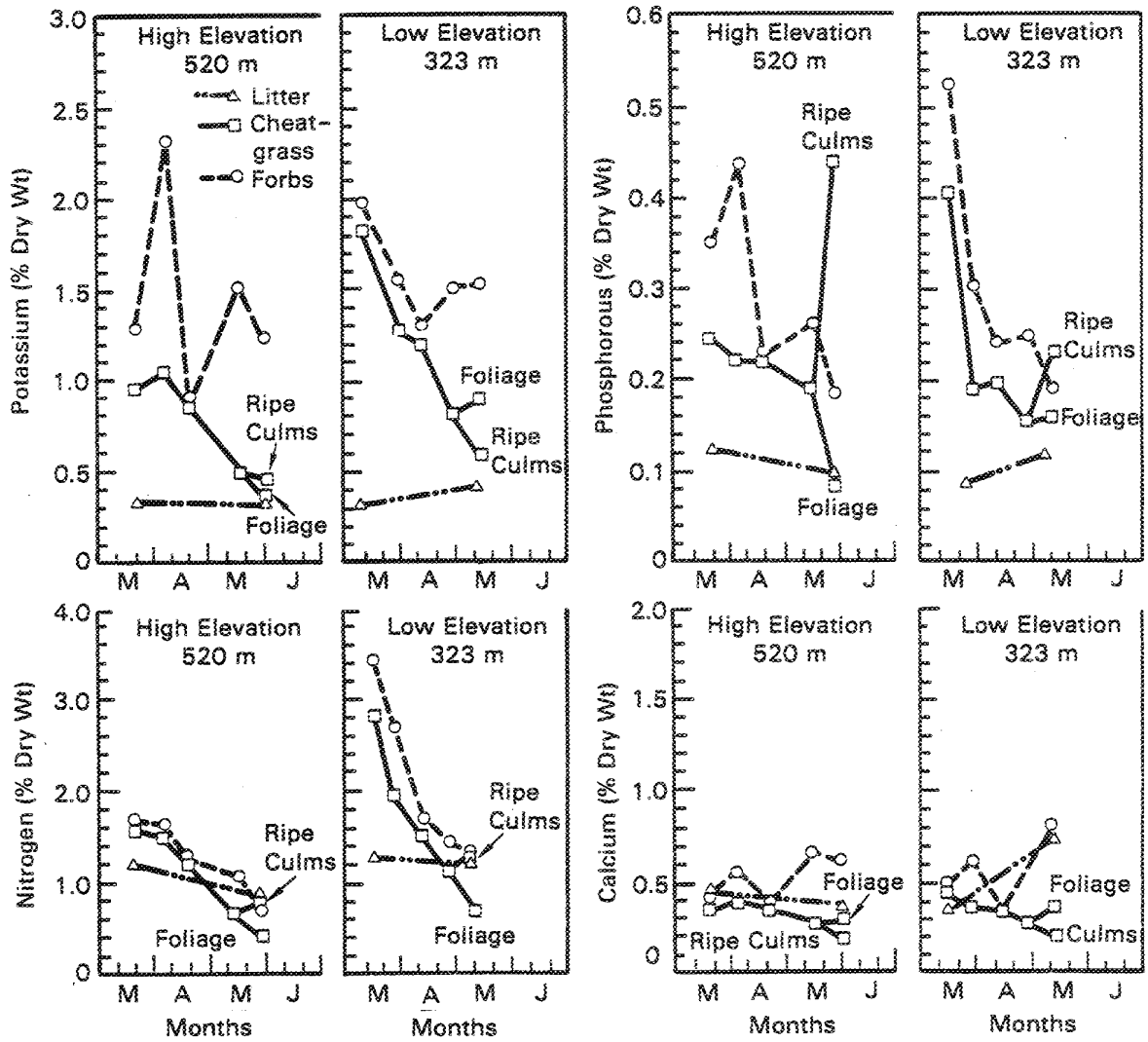


FIGURE 6.10. Nitrogen, Phosphorus, Potassium and Calcium Concentrations in Cheatgrass and Forbs in Cheatgrass Communities at Elevations of 323 and 520 Meters

than in ripened culms at the low elevation; but at the high elevation, the K concentration was greatest in culms. Litter had lower concentrations of K and P than did the shoots, but greater concentrations of N and Ca. This indicates that P and K are not strongly retained in dead plants, and that N

TABLE 6.11. Mean Concentrations (Percentages of Dry Weight ± SE) of Nitrogen, Phosphorus, Potassium and Calcium in Cheatgrass Foliage, Ripe Culms, Forb Shoots and Litter in Cheatgrass Communities at High and Low Elevations

Elevation	Cheatgrass	Culms	Forbs	Litter
		Nitrogen		
High	0.38±.01	0.82±.08	0.70±.03	0.78±.09
Low	0.65±.08	1.38±.09	1.36±.08	1.22±.05
		Phosphorus		
High	0.08	0.44±.02	0.18±.009	0.10±.004
Low	0.16±.03	0.23±.01	0.19±.01	0.12±.03
		Potassium		
High	0.35±.01	0.44±.02	1.20±.13	0.32±.005
Low	0.88±.14	0.57±.03	1.50±.09	0.42±.04
		Calcium		
High	0.29±.01	0.20±.01	0.66±.04	0.39±.01
Low	0.37±.05	0.21±.01	0.80±.03	0.77±.02

and Ca tend to be retained. Apparently, Ca is not as readily mobilized from litter by leaching and decay processes as are P and K. The enriched concentrations of N in the litter as compared to mature foliage suggests an external source of N, perhaps dry and wet deposition from the atmosphere or else a retention of N in living cells of microorganisms that use dead plants as a carbon source (Woodmansee 1979).

The plant:soil ratio (concentration of elements in dry plant tissue to concentration in dry soil) is one way of expressing the capacity of plants to absorb mineral nutrients from their rooting substrates. The highest plant/soil ratios were obtained for P, with lesser values for N > K > Ca

(Table 6.12). Plant:soil ratios for P in forbs from the high and low fields were 53 and 59, respectively, 23 and 50 for cheatgrass foliage and 29 and 37 for litter. This difference suggests that plants growing at the low study site had a greater capacity to obtain P from their rooting substrate. The plant/soil ratios for P were greatest for cheatgrass culms, suggesting that cheatgrass shoots have some capacity to allocate P from foliage to culms and that this concentration process was most efficient in cheatgrass at the high elevation.

The plant:soil ratios for N in the three categories (cheatgrass foliage, ripened culms and litter) ranged between 5.2 and 11 on the high field and between 6.9 and 15 on the low field. The ratios for K ranged between 2.9 and 11 on the high field and between 3 and 11 on the low field (Table 6.12). The Ca ratios ranged between 0.77 and 2.5 on the high field and between 0.66 and 2.5 on the low field. These ratios indicate that K and Ca were about equally available for shoot assimilation on both fields. The low field was more efficient for N assimilation as judged by the higher plant:soil ratio.

Once mineral nutrients are assimilated into cheatgrass shoots, they can be re-allocated to different parts of the shoot. In the early stages of cheatgrass growth, mineral nutrients are allocated exclusively to vegetative tissues. As the growing season advances, nutrients are re-allocated from the stems and foliage to the flowering culms and especially to seeds. Some of the N and P assimilated into seeds can be passed directly to the next generation of plants upon seed germination. Although the amount is very small in terms of a single seed, it is more impressive when the total seed produced is considered as a community component. About 30 percent of the

TABLE 6.12. Plant:Soil Ratios for Nitrogen, Phosphorus, Potassium and Calcium in Cheatgrass Foliage, Ripe Culms, Forb Shoots and Litter from Cheatgrass Communities at High and Low Elevations

Elevation	Cheatgrass	Culms	Forbs	Litter
		Nitrogen		
High	5.2	11	16	11
Low	6.9	15	14	13
		Phosphorus		
High	23	129	53	29
Low	50	72	59	37
		Potassum		
High	3.2	4.0	11	2.9
Low	6.3	4.1	11	3.0
		Calcium		
High	1.1	0.77	2.5	1.5
Low	1.2	0.66	2.5	2.4

shoot biomass of a mature cheatgrass plant is allocated to ripened culms. The N and P concentrations in ripened culms are greater than those of foliage (rigure 6.10). Not all of the N and P assimilated in seeds can be passed to the seedlings. Some seeds are eaten by animals. Others are destroyed by fungal infestations, and others simply do not germinate. Some of the seedlings die, and their tissues become incorporated into the litter pool. In this way litter serves as an accumulation site for plant- assimilated nutrients. The N, P and other nutrients are transferred from the litter to the underlying minerals where they are potentially available for re-assimilation by living plants (Jones and Woodmansee 1979, Woodmansee and Duncan 1980).

A schematic diagram showing major components of a cheatgrass community and the routes of mineral nutrient flow is illustrated in Figure 6.11. Nitrogen is ordinarily the soil nutrient that limits shoot productivity. In

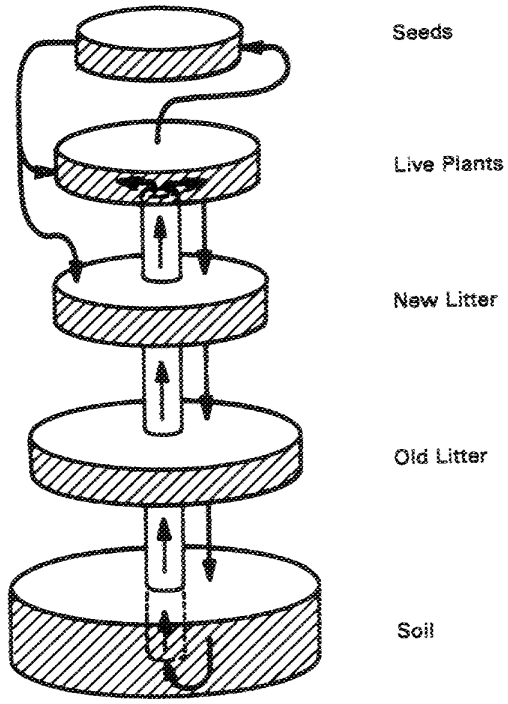


FIGURE 6.11. A Schematic Diagram Showing Major Components and Pathways for Mineral Nutrient Cycling in Cheatgrass Communities (Rates of release from each component are not accurately known.)

order to exploit the available soil water and soil nitrogen to the fullest each year, cheatgrass communities depend upon the return to the root zone of at least a portion of the pool of nutrients that are bound in dead plants. The rates of releases of N from dead plant litter are not known for cheatgrass communities, but a range from 30 to 48 %/yr can be estimated from soil decomposition studies in Chapter 3. The stable isotope ^{15}N has been used to determine the rates of N transfers between the various components of plant communities (Clark 1977, Van Cleve and White 1980), and it could be useful for determining the rate of release of N from litter to the soil as illustrated in Figure 6.11.

A comparison of N and P in shoot and litter components of cheatgrass communities and California annual grass communities is made in Table 6.13. Only 24 percent of the total above ground N was in the litter component of a California annual grass community, compared to 43 and 62 percent for the cheatgrass communities. The litter component of cheatgrass communities also contained a greater percentage of the total above ground P.

Only in a few cases can the data from the cheatgrass communities be compared with other communities dominated by low-production herbs. The above ground component of cheatgrass communities contained 1.56-2.60 percent of the total community N and 8-9 percent of the P. By comparison, Arctic wet meadow and tussock communities contained less than one percent of the

TABLE 6.13. Comparison of Nitrogen and Phosphorus in Shoot Biomass and Litter (g/m^2) in Annual Grass Communities in Washington and California (Figures in parentheses indicate percent of total biomass.)

Category	Washington	Washington	California	California
		Nitrogen		
Grass	1.12 (23)	1.65 (25)	1.29 (16)	3.60 (63)
Forb	0.71 (15)	2.04 (31)	4.71 (60)	0.72 (13)
Total Shoot	1.83 (38)	3.69 (57)	6.00 (76)	4.32 (75)
Litter	2.96 (62)	2.86 (44)	1.92 (24)	1.40 (24)
Total	4.79	6.55	7.92	5.72
		Phosphorus		
Grass	0.42 (43)	0.24 (30)	0.36 (29)	0.25 (40)
Forb	0.17 (17)	0.28 (35)	0.65 (52)	0.20 (32)
Total Shoot	0.59 (61)	0.52 (65)	1.01 (81)	0.45 (72)
Litter	0.38 (39)	0.28 (35)	0.24 (19)	0.17 (27)
Total	0.97	0.80	1.25	0.62

community N and only 0.3-1.3 percent of the P (Table 6.14). The relatively large allocation of aboveground P in the cheatgrass communities is attributable to the relatively high P concentrations in the ripened culms of cheatgrass and the relatively large amount of ripe seed attached to the culms.

A shortgrass prairie community in eastern Colorado contained about the same total amount of N as did the cheatgrass communities, but it also had a greater percentage of its N allocated to aboveground biomass (Table 6.14). This discrepancy reflects the relatively large amount of biomass in the living crowns of the sod-forming perennial grasses that dominate the shortgrass prairie community.

How similar are communities of similar life forms that grow on different parts of the landscape? This question is often asked of ecological investigators. The existence of two cheatgrass communities with very similar histories but growing in slightly different microclimates and rooting substrates provided an opportunity to determine whether different landscape positions had a measurable influence on the shoot assimilation of nitrogen and phosphorus by cheatgrass. The N and P concentrations in cheatgrass shoots

TABLE 6.14. Comparison of Nitrogen and Phosphorus (g/m^2) in Shoots and the Upper 2 Decimeters of Soil in Five Plant Communities

Community	Location	$g\ N/m^2$	%	$g\ P/m^2$	%
Cheatgrass	Washington	195	1.5	10.8	8.9
Cheatgrass	Washington	250	2.6	10.0	8.0
Shortgrass[a]	Colorado	273	3.2	---	---
Wet Meadow[a]	Alaska	960	0.9	63.2	1.3
Tussock Meadow[a]	Alaska	964	0.9	48.7	0.3

(a) Data from Chapin et al. (1980)

were greatest in the early spring (Figure 6.12), followed by a predictable decline as the growing season advanced. At the end of the growing season, cheatgrass shoots had 4.0-5.3 times lower concentrations of N than they did at the beginning of the season. The scattering of the data points obtained

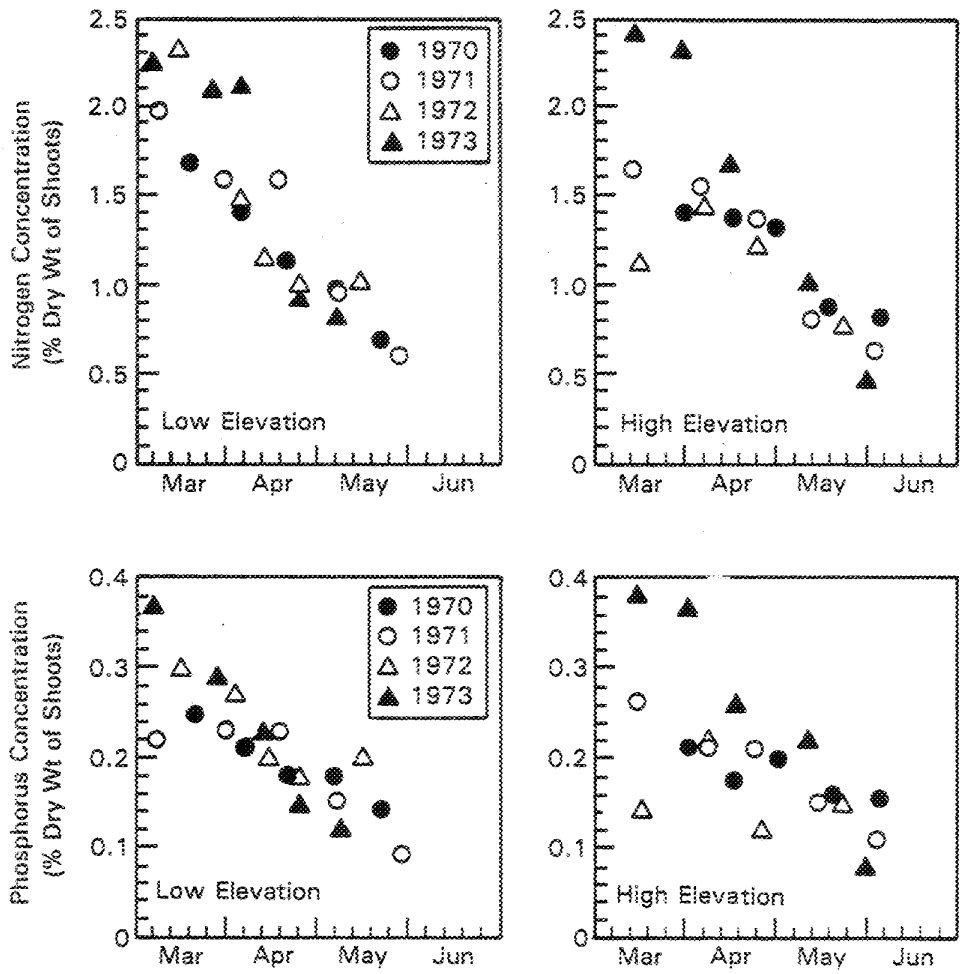


FIGURE 6.12. Nitrogen and Phosphorus Concentrations in Living Shoots of Cheatgrass in Cheatgrass Communities at Different Elevations, during the Spring Growing Seasons of 1970, 1971, 1972 and 1973

over the 4-year study period was somewhat wider at the higher elevation than at the lower elevation, indicating greater variability. The litter had greater concentrations of N and P than the standing dead plants; but levels also varied between years (Table 6.15).

Analyses of variance were performed on the data set using the methods described by Johnson and Leone (1976). A two-way analysis of variance indicated that only the litter component of the cheatgrass communities was statistically different in both N and P (Table 6.16). The N concentration, however, was significantly different in the standing dead plants. According to Ostle (1963), regression statistics for cheatgrass shoots showed a high correlation between N and P in plant tissues ($\alpha = 0.05$) during the spring growing season (Table 6.17). Between the low and high communities, the correlation between N and P for cheatgrass shoots showed little if any difference, and regressions were significant at the 5 percent level. For standing dead plants, at low elevation, the correlation between N and P was significantly less than at high elevation (Table 6.18).

Bluebunch wheatgrass is the native counterpart to cheatgrass. It differs from cheatgrass by its perenniality, the presence of long-lived crowns, and relatively low seed productivity. Shoots of bluebunch wheatgrass ranged from a high of 3.4 percent N at the beginning of the spring growing season in mid-March to a low of 1.0 percent in mid-June (Figure 6.13). Phosphorus concentrations ranged from a high of .35 in mid-March a low of 0.14 in mid-June. At the end of the growing season, approximately seven times more N than P had been assimilated in the shoots. The concentrations of N and P in crown tissues did not change from the beginning to the end of the spring growing season; 0.90 and .096 percent respectively. Standing dead grass had

TABLE 6.15. Mean Concentrations of Nitrogen and Phosphorus and Coefficient of Variation in Cheatgrass Shoots, Standing Dead and Litter in Cheatgrass Communities at Low and High Elevations (CV = coefficient of variation)

	Shoots		Standing Dead		Litter	
Year	X	CV	X	CV	X	CV
			Low Elevation, Nitrogen			
1970	1.17	.33	.46	.084	1.32	.084
1971	1.34	.42	.81	.29	1.14	.073
1972	1.39	.39	.90	.092	1.09	.079
1973	1.64	.44	.88	.14	--	--
	1.38	.39	.76	.15	1.18	.079
			High Elevation, Nitrogen			
1970	1.17	.25	.56	.056	1.01	.17
1971	1.21	.38	.72	.17	.97	.62
1972	1.12	.29	.68	.083	.83	.20
1973	1.60	.54	.77	.11	--	--
	1.27	.36	.68	.10	.94	.33
			Low Elevation, Phosphorus			
1970	.19	.21	.070	.25	.17	.13
1971	.19	.37	.084	.27	.13	.063
1972	.23	.23	.098	.38	.14	.22
1973	.23	.44	.10	.14	--	--
	.21	.39	.088	.26	.15	.14
			High Elevation, Phosphorus			
1970	.18	.13	.070	.10	.15	.20
1971	.19	.31	.094	.22	.12	.071
1972	.16	.28	.094	.05	.10	.056
1973	.23	.57	.11	.18	--	--
	.19	.32	.092	.14	.12	.11

TABLE 6.16. Analysis of Variance Between Nitrogen and Phosphorus Concentrations in Cheatgrass Community Components at High and Low Elevations

Component	N	F value	d.f.	P	F value	d.f.
Shoots	NS	0.34	1,31	NS	0.71	1,31
Standing Dead	*	5.23	1,32	NS	0.09	1,31
Litter	**	28.37	1,21	**	9.44	1,21

NS = Not significant
* Significant at .05 level
** Significant at .01 level

TABLE 6.17. Correlation Between Nitrogen and Phosphorus for Cheatgrass Shoots in Communities at Low and High Elevations (r = correlation coefficient)

Statistic	Low Elevation	High Elevation
n	20	19
Slope	0.1105	0.1326
Error	0.1739E-3	0.1446E-3
Intercept	0.0548	0.0216
Error	0.3832E-3	0.2769E-3
r	0.8921	0.9367

TABLE 6.18. Correlation Between Nitrogen and Phosphorus for Standing Dead Plants in Communities at Low and High Elevations

Statistic	Low Elevation	High Elevation
n	20	19
Slope	0.0689	0.1546
Error	0.4506E-3	0.3190E-3
Intercept	0.0356	-0.0154
Error	0.2879E-3	0.1537E-3
r	0.5970	0.9028

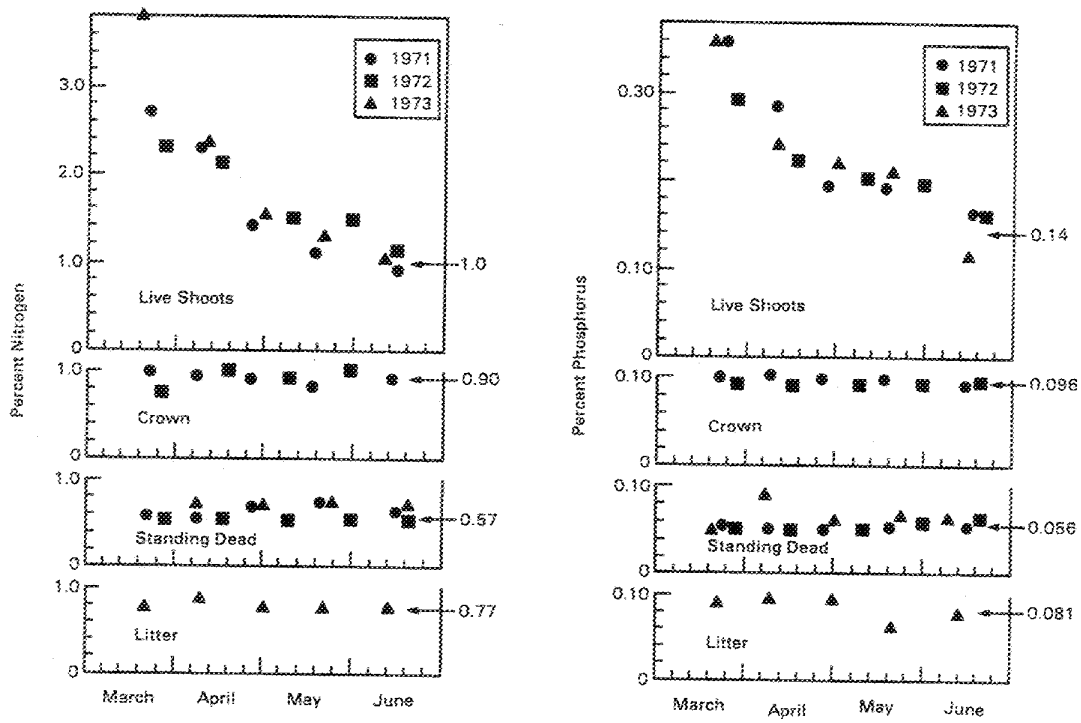


FIGURE 6.13. Nitrogen and Phosphorus Concentrations (percent dry wt.) in Components of a Sagebrush-Bunchgrass Community, 1971-1973

an average N concentration of 0.57 percent and a P concentration of .056 percent (Figure 6.13). Litter averaged 0.77 percent N and .081 percent P. The N:P ratios were 7.1 for shoots, 9.4 for crowns, 10 for standing dead and 9.5 for litter. These data indicate that in comparison to N, P is richest in the shoots and poorest in the standing dead.

At the peak of herbaceous shoot production in June, about .62 g/m^2 of N and .083 g/m^2 of P were present in the sagebrush-bunchgrass community. Sagebrush leaves contained about .18 g/m^2 of N and .02 g/m^2 of P. The greatest inventory of N and P was in the standing dead grass and litter components at 2.24 and 0.22 g/m^2, respectively (Table 6.19). There was at least 3 g/m^2 of

N and .32 g/m^2 of P in the aboveground components of the sagebrush-bunchgrass community; this compared with 6.5 g/m^2 N and 0.80 g/m^2 P in a cheatgrass community. However, the amount of N and P in the wood component of the sagebrush-bunchgrass community was not determined.

In the sagebrush-bunchgrass community, the N and P in above-ground components is allocated to a relatively rich mixture of plant taxa. By

TABLE 6.19. Concentrations of Nitrogen and Phosphorus (percent dry wt.) and Inventory (g/m^2) in Major Above-ground Components of a Sagebrush-Bunchgrass Community in June

Community Components	Dry Wt.	N		P	
	g/m^2	%	g/m^2	%	g/m^2
Shoots					
Perennial grass	45	1.0	.45	.14	.063
Half-shrubs	10	1.1	.11	.16	.016
Forbs	5	1.3	.06	.23	.011
	60		.62		.090
Standing dead					
Perennial grass	82	.57	.47	.056	.041
Crowns	84	.90	.76	.096	.081
Litter	134	.77	1.03	.081	.11
	300		2.26		.23
	Sagebrush				
Leaves	10	1.8	.18	.27	.03
Wood	60	M	M	M	M
Total	370		3.06		0.35

M = Missing data.

comparison, the cheatgrass community supports only a few taxa. The wood component in the sagebrush-bunchgrass community immobilizes a fraction of the community pool of N and P and retains it for a relatively long period of time because wood decay is much slower (but unquantified) than it is for herbaceous tissues. The quickest natural way to release wood-bound N and other minerals is by burning.

Cheatgrass is most efficient at extracting soil water and assimilating nitrogen from the upper layers of soil. Shoot production depends upon a number of variables, but the availability of water and N in the months of March and April is crucial to shoot production. The apparent failure of the cheatgrass community at the high elevation to show more shoot production than the low community suggests that essential mineral nutrients were limited (Cline and Rickard 1972a).

Sagebrush-bunchgrass communities differ from cheatgrass communities by having a thin soil crust comprised of crustose lichens, soil algae and small-statured mosses that generally covers the ground between the grass clumps. This crust is absent in cheatgrass communities where the ground is completely shaded year-round by stems of standing dead plants and a complete ground cover of protrated cheatgrass stems is usually present. Although it is suspected that the cryptogamic crust plays a role in N and P cycling in sagebrush-bunchgrass communities, there have been no studies to demonstrate that the presence of a well-developed cryptogamic crust has any positive or negative benefits for the associated vascular plants.

If the cheatgrass community at the low elevation really is more efficient at assimilating N from the soil than the higher-elevation community, it

suggests that seedlings of any invading perennial taxa will face the most severe competition for soil nutrients at the low elevation. The ability of cheatgrass to assimilate N from soil promptly as it becomes available through microbial decomposition and other processes may, at least in part, account for the lack of success of perennial taxa to re-colonize the low-elevation cheatgrass community, even after 40 years. Mycorrhizae are known to influence the availability of mineral nutrients to higher plants, and there may be differences in mycorrhizal components of the high and low communities: this specialized aspect of mineral nutrition was not investigated but is worthy of future study.

MINERAL ELEMENTS IN SHRUB LEAVES

Desert shrubs usually dominate the natural vegetation mosaics of the arid and semi-arid intermountain valleys between the Rocky and the Sierra/Cascade Mountains; however, only a few studies have investigated the mineral cycling behavior of desert shrubs in the northern valleys (Mack 1977, Murray 1975, Rickard 1965, Rickard and Keough 1968, Cline and Rickard 1974). In recent years, considerable attention has been paid to the dispersal and accumulation potential of trace elements released into the air from coal-fired power plants (Connor et al. 1976).

Accumulations of airborne trace metals in surface soils and selective uptake by forage plants has some potential to create a chronic toxicity hazard to rangeland wildlife and domestic stock. Molybdenosis and selenium toxicity in cattle have been observed at the endogenous concentrations that can be attained in range forage plants (Allaway 1975).

Historically, eastern Washington has been relatively free from air pollution of coal-burning power plants. Electrical power has been largely provided by hydro-electric dams on the Snake and Columbia rivers or by nuclear power plants located on the Hanford Site. However, most of the sites for hydro-electric dams have been filled, and coal-fired power plants are expected to be power sources of the near future.

In view of a perceived need to establish baseline data before the creation of a future generation of coal-fired power plants in eastern Washington, the mineral element compositions of four of the most common shrub taxa were determined. The leaves of sagebrush, bitterbrush, spiny hopsage and greasewood were collected in trays placed beneath individual shrubs (Rickard and Warren 1981b). The air-dry leaves, collected during peak leaf fall months, were dissolved by refluxing them in a nitric/ perchloric acid mixture (4:1). Argon-inductive coupled plasma spectroscopy was used to simultaneously analyze for aluminum (Al), barium (Ba), boron (B), calcium (Ca), copper (Cu), iron (Fe), manganese (Mn), magnesium (Mg), phosphorus (P), potassium (K), sodium (Na), strontium (Sr), and zinc (Zn). Antimony (Sb), chromium (Cr), cobalt (Co), lead (Pb), molybdenum (Mo), nickel (Ni), and vanadium (V) were analyzed by means of graphite furnace atomic absorption spectroscopy. Bromine (Br) and chlorine (Cl) were determined by neutron activation and subsequent gamma spectroscopy. Arsenic (As) and selenium (Se) were determined by atomic absorption spectroscopy of the separated hydrides. All tissue samples were analyzed in duplicate and run concurrently with National Bureau of Standards reference biological standards (Rickard and Garland 1983).

The leaves of halophilic shrubs (spiny hopsage and greasewood) were characterized by comparatively high levels of K, Cl, Br, Mn and Na (Table 6.20). Sagebrush had comparatively high levels of Ca, and bitterbrush and spiny hopsage had comparatively high concentrations of Mg. Greasewood was comparatively low in Fe and Al. The trace element concentrations of leaves of the different shrub taxa were not greatly different. However; Zn concentrations were comparatively low in greasewood leaves, and As and Cr were comparatively high in bitterbrush leaves.

A broad spectrum of trace metals found in coal is released into the air through the stacks at large coal combustion steam electric plants, even when pollutant suppression devices are operational (Vaughan et al. 1975, Connor et al. 1976, Turner and Strojan 1978, Van Voris et al. 1984). After many years of coal burning, several of these trace elements have been found to show at least some level of enhancement in soils, especially those near the power plants (Van Voris et al. 1984). The potential exists for these trace elements to appear in shrub leaves as the elements are moved downward into the soil by

TABLE 6.20. Concentrations of Mineral Elements in Leaves of Southeastern Washington Desert Shrubs, 1978 (ppm dry wt.)

Taxa	Ca	K	PO_4	Mg	Cl	Fe	Al	SO_2	Na	Mn	Ti
Sagebrush	16,700	12,200	6,820	2,450	1,510	1,420	990	300	250	180	120
Sagebrush	17,500	10,800	3,680	1,460	1,770	1,250	950	290	140	90	140
Bitterbrush	11,500	10,700	1,970	7,100	4,830	1,300	880	450	170	93	121
Hopsage	9,100	27,500	5,500	7,850	9,500	1,200	850	390	1,190	147	90
Greasewood	11,800	9,610	2,420	1,490	14,400	695	505	350	950,000	202	75

Taxa	B	Sr	Ba	Zn	Cu	Br	Pb	Mo	V	Ni	Cr	As	Co	Sb	Se
Sagebrush	73	61	34	27	15	15	5.0	2.0	2.0	1.2	1.1	0.91	0.40	0.12	0.11
Sagebrush	74	45	17	14	11	9	8.9	2.0	2.0	1.4	0.90	0.42	0.30	0.13	0.05
Bitterbrush	77	54	28	14	10	46	12	2.4	2.5	22	12	8.3	0.30	0.45	0.10
Hopsage	40	27	18	14	5.9	120	3.1	6.0	2.0	2.0	1.8	1.4	0.30	0.08	0.50
Greasewood	59	38	13	4.1	8.3	555	3.9	1.9	1.0	1.4	0.70	0.20	0.40	0.05	0.55

leaching, freezing, thawing and other physical processes over long periods of time. Once in the root zone, it is expected that some of the water-soluble trace elements would be absorbed by roots and transported to leaves, where they would be ingested by deer, elk and rabbits, as well as domestic livestock.

Although it is technologically possible to measure and model the atmospheric deposition patterns of trace elements from a coal-fired power plant with reasonable accuracy, the uptake of these elements from the soil by desert shrubs is mostly unknown. Most experimental studies of trace elements related to coal combustion have been designed to determine uptake from agricultural soils by crop plants (Elseewi et al. 1978). Such experiments are usually of short duration (weeks) and have been aimed at providing data useful for designing disposal sites for coal-ash rather than providing information pertinent to stack releases and low-level chronic deposition.

To be able to detect small increases in trace metal concentrations, desert shrubs need to be sampled year after year over a long period of years. Natural leaf fall collection serves as a nondestructive sampling method as well as providing data on the periodicity and magnitude of leaf fall.

To obtain information on the uptake of B, Cu, Mn, Mo, and Zn by sagebrush, 100 sagebrush shrubs in a study plot on the ALE Reserve were tagged. The various treatment concentrations were randomly distributed among this population (Rickard and Van Scoyoc 1984). Analyzed reagent-grade chemical compounds were mixed in 1 liter of distilled water. Four concentrated solutions were used (0., 0.5, 5 and 20 grams) for each of five compounds: boric acid (H_3BO_3), cupric chloride ($CuCl_2 \cdot 2H_2O$), manganous chloride ($MnCl_2 \cdot 4H_2O$), molybdenum trioxide (Mo(VI) oxide) and zinc chloride ($ZnCl_2$).

These compounds were applied to the ground beneath the canopy of individual shrubs after the dead plant debris covering the soil was scraped away to expose the mineral soil. The wetted ground was approximately 0.5 m^2 in area. The treatments were made in March 1979 and applied to five shrubs for each experimental concentration. In May 1981, newly emerged leaves were hand picked from individual shrubs, oven dried, dissolved in nitric acid and analyzed using inductively coupled plasma spectroscopy. Of the five elements added to soil, only Mo was incorporated into sagebrush leaves in enhanced concentrations (Figure 6.14). The amount of Mo assimilated in the leaves generally increased with increasing amounts of Mo added to soil. The greatest leaf concentration was measured in the shrubs growing in soil treated with the greatest amount of molybdenum trioxide. The difference in leaf concentrations of Mo between the controls and the treated plants was statistically significant ($P < 0.05$). These data indicate that Mo is present in very low concentrations in sagebrush leaves when growing in soil with background levels of Mo and that it is readily available to sagebrush when applied to surface soil. This supports the premise that Mo is likely to be among the most biologically available trace elements when deposited on land via stack releases from coal-fired power plants (Vaughan et al. 1975).

Concentrations of B, Cu, Mn and Zn showed considerable overlap in the range of values between the control and the treated shrubs. These elements were either not available for root uptake or had not penetrated deeply enough into the soil to contact the functional roots of sagebrush. It is also

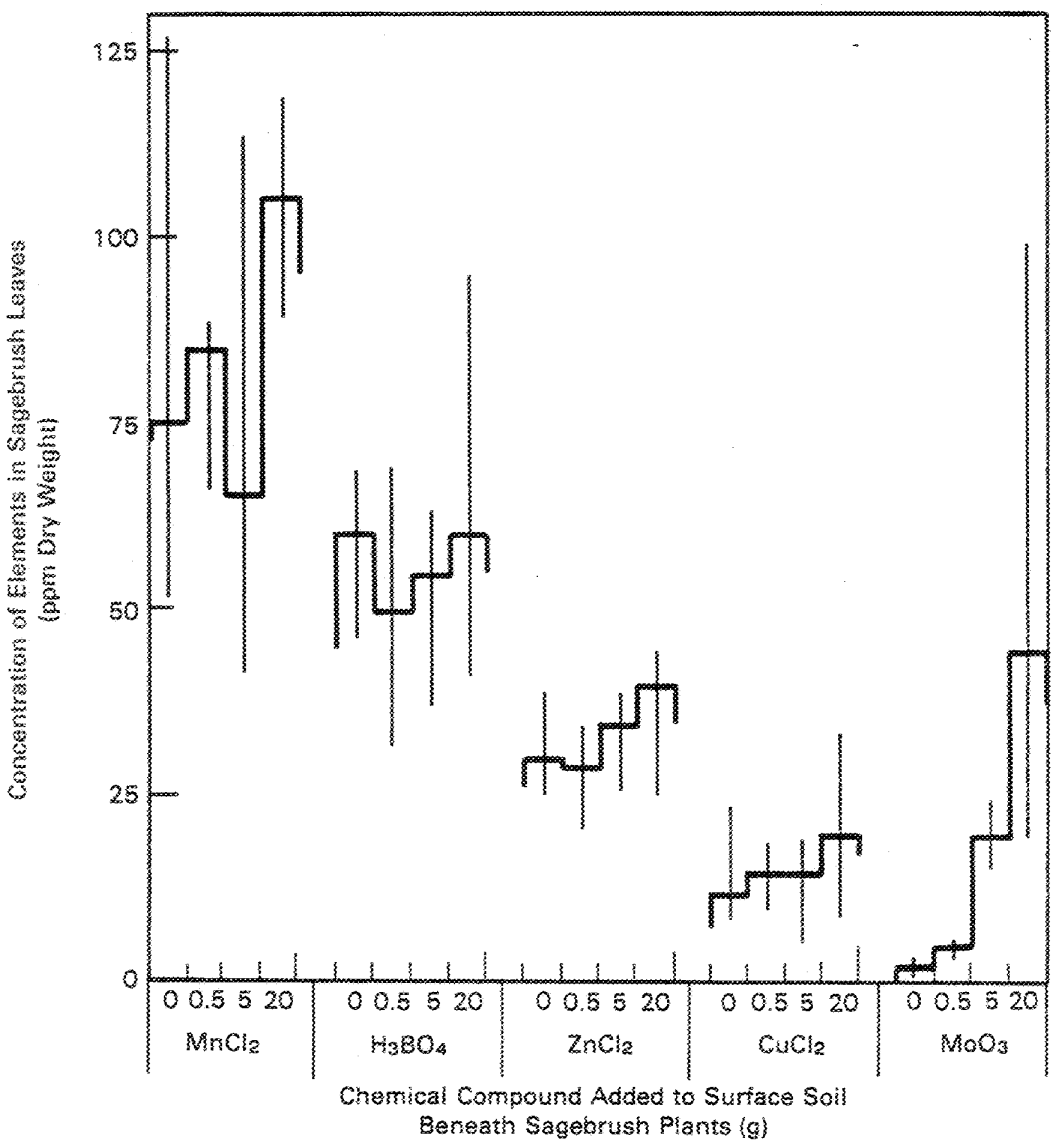


FIGURE 6.14. Manganese, Boron, Zinc, Copper and Molybdenum Concentrations in Sagebrush Leaves with Different Amounts of Elements Added to the Ground Beneath Shrubs (Vertical lines represent the extreme values of five shrubs and the bars represent mean values.)

possible that these elements may have entered the roots but were not moved from the roots to leaves by stem transport processes.

Although Mo added to soil was assimilated into sagebrush leaves, B added as boric acid was not. Boric acid is believed to be in a chemical form available for plant uptake (Clarkson and Hanson 1980). This suggests that factors other than chemical form per se are involved in B uptake by sagebrush shrubs in the field. Perhaps mycorrhizae and/or other kinds of micro-organisms are involved in organo-metal complexations, or else sagebrush has some physiological mechanism to exclude B.

This field experiment was designed for a period of 10 years or more; however, it was inadvertently terminated on August 13, 1981, when a wildfire burned through the study site and destroyed all the sagebrush shrubs. The frequency of wildfire needs to be considered in the design of long-term studies involving elemental uptake from soils by plants in habitats that support desert shrubs.

WEIGHT LOSS OF DEAD PLANTS IN A CHEATGRASS COMMUNITY

The decomposition of dead plants is an important ecological process in natural plant communities because it releases plant-bound mineral nutrients to the underlying soil where they are placed in a favorable position to be absorbed by roots. The decomposition process consists of interacting weathering (abiotic) and biotic factors. Weathering includes the wetting and drying of dead plants, leaching of water-soluble materials to the underlying soil, and the physical breakdown of plant tissues by the abrasive actions of wind and repetitive wetting and drying processes. Biological processes include ingestion and shredding by insects and other small invertebrate animals and degradation of plant tissues by bacteria and fungi that use the organic carbon compounds of dead plants as an energy source.

Weight losses of dead cheatgrass shoots were compared over a 1-year period (October to September) in two cheatgrass communities at different elevations. Standing dead plants, mostly culms of cheatgrass produced in the 1968-69 growing season, were harvested in September from 0.093-m^2 plots. The dead plants were arranged in a layer and confined inside mesh bags the same size as the harvested plots. The holes in the mesh were circular, about 3 millimeters in diameter, and were believed to be large enough to allow access to the contained litter by most of the detritivorous invertebrates and also to assure wetting of the litter by rainfall and snow melt.

The average weight of dry litter placed in the bags was 213 g/m^2 at the low elevation community as compared to 137 g/m^2 for the high community (Table 6.21). The bags were set out in early October 1969, and the first retrieval was made in March 1970. At this time 80 percent of the dead plant material remained. There was no detectable weight loss in the period from March 1970 to October 1970. Total weight losses (expressed as a percentage of the initial weight) were about the same in both communities. However, the low community lost more weight, i.e., 46 g/m^2 as compared to 36 g/m^2.

Assuming that weight loss of dead plants amounts to 20 percent per year over several consecutive years, total loss would be expected in 4 to 5 years. This appears to be a much slower rate of litter weight loss than that described for annual grass communities in California, where Woodmansee and Duncan (1980) reported that the disappearance of the previous spring's plant production was essentially completed over one growing season.

TABLE 6.21. Dry Weight of Dead Plant (g/m^2) in Mesh Bags After Field Exposure in Cheatgrass Communities at High and Low Elevation [( ) = percent of dead plant material remaining in mesh bags]

Wt. in Bags Oct. 1969		Wt. Mar. 1970	Wt. June 1970	Wt. Oct. 1970
		Low Elevation (520 m)		
Mean	Range	Mean	Mean	Mean
216	171-284 (n=5)	166 (77)	--	--
199	134-269 (n=5)	--	161 (81)	--
225	191-254 (n=5)	--	--	174 (77)
213				
		High Elevation (320 M)		
139	100-208 (n=5)	110 (79)	--	--
114	89-160 (n=5)	--	91 (80)	--
158	79-210 (n=5)	--	--	121 (77)
137				

( ) = percent of dead plant material remaining in mesh bags

Although the mesh bag methodology i. simple to practice, there are some constraints to its use in cheatgrass communities. Seeds that are located between the bag and soil germinate, and seedlings grow through the mesh. These new plants must be segregated from the dead plants in order to obtain a reliable estimate of weight loss for the dead plants. It seems likely that a reliable estimate would only be possible by the mesh bag methodology for the first year. Other techniques for determining weight losses from dead plants need to be devised to quantify the rate of decomposition in cheatgrass communities. One likely method is the use of radioactive ^{14}C as a tracer element. It has considerable potential for monitoring litter disappearance (Dahlman and Kucera 1968, Wieder and Carrel 1979).

The rate of release of mineral nutrients to the underlying soil from dead plants is an important consideration if shoot production is to be sustained over extended periods of time. Dead plants can withhold a sizable fraction of the community inventory of plant-assimilated N. This N needs to be returned to the soil in a chemical form available for plant uptake. It seems likely that the return of N and other nutrients to the soil from dead plants would be slowest during the dry, hot, summer months. Release rates would likely be accelerated in early autumn following the onset of autumn rains; then, rates would likely be slowed by the onset of below-freezing temperatures in winter. The most accelerated rates of decomposition are likely to occur in early spring as moist soils are subjected to warming air temperatures and microbial activity at the soil-litter interface becomes enhanced. If this is true, then the timing of mineral nutrient releases from dead plants to soil is synchronized with the spring flush of cheatgrass growth.

Mineral nutrient behavior in litter is an important consideration of community productivity, but the physical presence of dead plants also creates special microhabitats for seeds and seedlings. Dead plants help to diminish wind speeds and retard evaporation loss. In this way, dead plants aid in the germination of cheatgrass seeds (Young et al. 1971). Apparently, dead cheatgrass has no chemical phytotoxins that inhibit the germination of its own seeds.

INFLUENCE OF GREASEWOOD ON SOIL CHEMISTRY AND GROWTH OF CHEATGRASS

Greasewood (*Sarcobatus vermiculatus*) is a desert shrub with a broad geographic distribution in the semi-arid western United States. It accumulates

sodium in its leaves throughout the leaf-bearing season which extends from April to November (Rickard and Keough 1968).

It is reasonable to expect that leaf-fall and leaf decay, when performed over many years, would influence the chemical composition of the surface soil beneath the canopy of greasewood shrubs. Both beneficial and deleterious effects on nearby herbaceous plants have been perceived from leaf fall of greasewood shrubs. The concentration of N in the soil beneath shrubs is enhanced, compared to adjacent open ground. However, greasewood shrubs also increase the Na concentration of the soil (Table 6.22). Most plants accumulate only small amounts of Na in their leaves and high concentrations of Na, especially as sodium chloride, are deleterious to the growth of most plants. On the other hand, N is an essential nutrient that is in scarce supply in

TABLE 6.22. Chemical Analyses of Soil Samples Collected Beneath Greasewood Shrubs and Adjacent Inter-shrub (Open) Areas

Soil Properties	Beneath Greasewood	Open Ground
Nitrogen %	.13 ± .02	0.059 ± .002
Phosphorus (μg/g)	23 ± 4	15 ± 1
Potassium (μg/g)	1480 ± 38	1033 ± 67
Calcium (meq/100g)	12.0 ± 1.5	9.3 ± 1.0
Manganese (meq/100g)	2.3 ± 0.4	3.0 ± 0.5
Sodium (meq/100g)	4.7 ± 2.7	0.3 ± 0.1
Total bases (meq/100g)	18.1 ± 1.9	14.9 ± 9.9
pH	8.9 ± 0.1	7.7 ± 0.3

Data are $\bar{X}$ ± S.E. (n=3).

semi-arid-zone soils, and it is avidly taken up by plants when in an appropriate chemical form.

When cheatgrass was grown in pots filled with greasewood-affected soil it produced 0.343 ± .09 g dry wt./pot as compared to only 0.146 ± .01 g/pot for pots filled with adjacent intershrub soil (Rickard et al. 1973). Greasewood-affected soil also produced cheatgrass shoots with comparatively high N concentrations, 6.1 ± 0.13 percent as compared to 2.7 ± 0.19 for cheatgrass shoots grown in the inter-shrub soil. Clearly, greasewood-affected soil not only increased shoot yields, it also increased the N concentrations of cheatgrass shoots.

In another experiment, ammonium nitrate (NH_4NO_3) was added to the two kinds of soils at a concentration of 500 μg/g dry weight (0.5 g/pot). The average yield of cheatgrass grown in the greasewood-affected soil with added N was 1.39 g/pot, compared to only 0.78 g/pot for those pots without the added N. The yield of cheatgrass grown in the inter-shrub soil without added N averaged only 0.34 g/pot. When N was added, the yield was increased fourfold to 1.44 g/pot. Following soil additions of N, shoot yields were equivalent in the two kinds of soil, 1.39 and 1.44 g/pot. This provided evidence that the more vigorous growth observed for cheatgrass growing near greasewood shrubs is a response to a more favorable supply of N in the soil. No yield-suppressing effects of elevated Na concentrations were seen. However, cheatgrass was not grown to maturity, so the effects on seed production and seed viability are not known.

To determine the influence of the greasewood-affected soil on plant uptake of other kinds of mineral elements, the radioactive isotopes ^{45}Ca, ^{32}P, ^{65}Zn

and ^{35}S were added to 1-kilogram aliquots of soil at a concentration of 100 μCi/kg of dry soil (Cline and Rickard 1974). The yield of barley shoots was not statistically different when grown in the nitrogen- fertilized, greasewood-affected or the intershrub soil, respectively, i.e., 0.31 ± .02 and 0.32 ± .01 g/pot. However, there were differences in the plant uptake of isotopes. The order of isotope uptake was $^{35}S > ^{65}Zn > ^{32}P > ^{45}Ca$, regardless of the soil source. Uptakes of ^{45}Ca, ^{32}P and ^{35}S were greatest in the plants grown in the inter-shrub soil. However, the plant uptake of ^{65}Zn was most enhanced in the greasewood-affected soil (Table 6.23). These data indicate that soil chemistry affected by the presence of greasewood shrubs does influence the ability of barley shoots to accumulate isotopes of P, S, Ca and Zn.

TABLE 6.23. Concentrations of Radioactive Isotopes (nCi/g dry wt. ± SE) of Barley Shoots Grown in Shrub-Affected and Open Soil

Soil Type	^{45}Ca	^{65}Zn	^{32}P	^{35}S
Greasewood soil	.89 ± .11	95 ± 4	42 ± 1	3,700 ± 380
Open soil	7.7 ± .7	22 ± 6	210 ± 9	37,000 ± 1,200

n=4

Greasewood and other terrestrial halophytes have a special ability to accumulate Na in their leaves without apparent harm. Halophytes are not simply plants that lack the ability to physiologically exclude Na ions; Na accumulation appears to have a role in water uptake and osmo-regulatory functions (Flowers et al. 1977, Waisel 1972).

Saline-sodic soil is only one of many factors in the environment of terrestrial plants; nevertheless, excessive soil salinity is regarded as a

serious societal problem because of its deleterious effect upon the yields of crop plants. Crop plants attract much research attention because of their great importance in providing food for people and livestock, and finding new ways to improve crop yields is a practical aim of applied research. Another research approach worthy of attention is to examine the mineral and water behavior of non-crop plants. The study of Na tolerance in wild populations of halophilic plants is an appropriate research subject because it is fundamental to discovering ways of developing new varieties of Na-tolerant plants, as well as providing insight as to mechanisms of Na accumulation and osmo-regulation.

Halophilic taxa are especially well represented in the family Chenopodiaceae, but halophytes are also represented in other plant families. This suggests that the genetic basis for Na^+ uptake and salt tolerance in various plant taxa involves relatively few genetic units. It has been demonstrated that natural and artificial genetic selections can produce "adapted" plants in a relatively short time. Examples are the increases in toxicity tolerance of grasses to heavy metals when growing on heavily contaminated mine spoils (Woolhouse 1983) and the increased tolerance of barley to salinities at concentrations as great as that of sea water (Epstein and Norlyn 1977).

It might be expected that cheatgrass growing in the presence of greasewood shrubs over long periods of time would produce ecotypes that are especially suited to grow in greasewood-affected soil. The present-day cheatgrass plants growing in the greasewood community probably represent about 100 generations of cheatgrass since its introduction to the shrub-steppe region from Europe in the late 1800's.

CATIONS IN HALOPHYTES AND GLYCOPHYTES

The southern latitudes of the intermountain western United States are characteristically dominated by creosotebush (*Larrea tridentata*) and the northerly latitudes by big sagebrush (*Artemisia tridentata*). These plants tolerate several months of very dry soil each year and are ecologically classified as "xerophytes." However, other shrubs often grow in association with big sagebrush and creosotebush. Some of these have a special capacity to accumulate comparatively large amounts of Na and/or K in their leaves. These plants are ecologically classified as "halophytes." Examples are the various species of *Atriplex*, *Sarcobatus* and *Grayia*. Plants that do not have a special capacity to assimilate sodium salts from soil are classified as "glycophytes," i.e., creosotebush and sagebrush.

In a study of the two halophilic shrubs growing side by side, greasewood differed from hopsage by assimilating large amounts of Na in its leaves (Rickard and Keough 1968). Hopsage assimilated K and only small amounts of Na. Hopsage leaves from Idaho had greater concentrations of Ca than those from Nevada and Washington, but Na concentrations in greasewood leaves were similar (Figure 6.15). Among the glycophytes, Ca dominated the cations of sagebrush leaves in Washington and Idaho, but K dominated leaves from Nevada. Bitterbrush leaves were available only from Washington and Idaho. Like sagebrush leaves, the leaves of bitterbrush were dominated by Ca. Creosotebush does not grow in Washington or Idaho. However, its cation concentrations were similar to those of big sagebrush.

On a local scale, desert shrubs may occur in pure of nearly pure stands or in mixed stands. A relatively rich mixture of desert shrub taxa occurring in Rock Valley in southern Nevada (Wallace et al. 1980) provided an opportunity

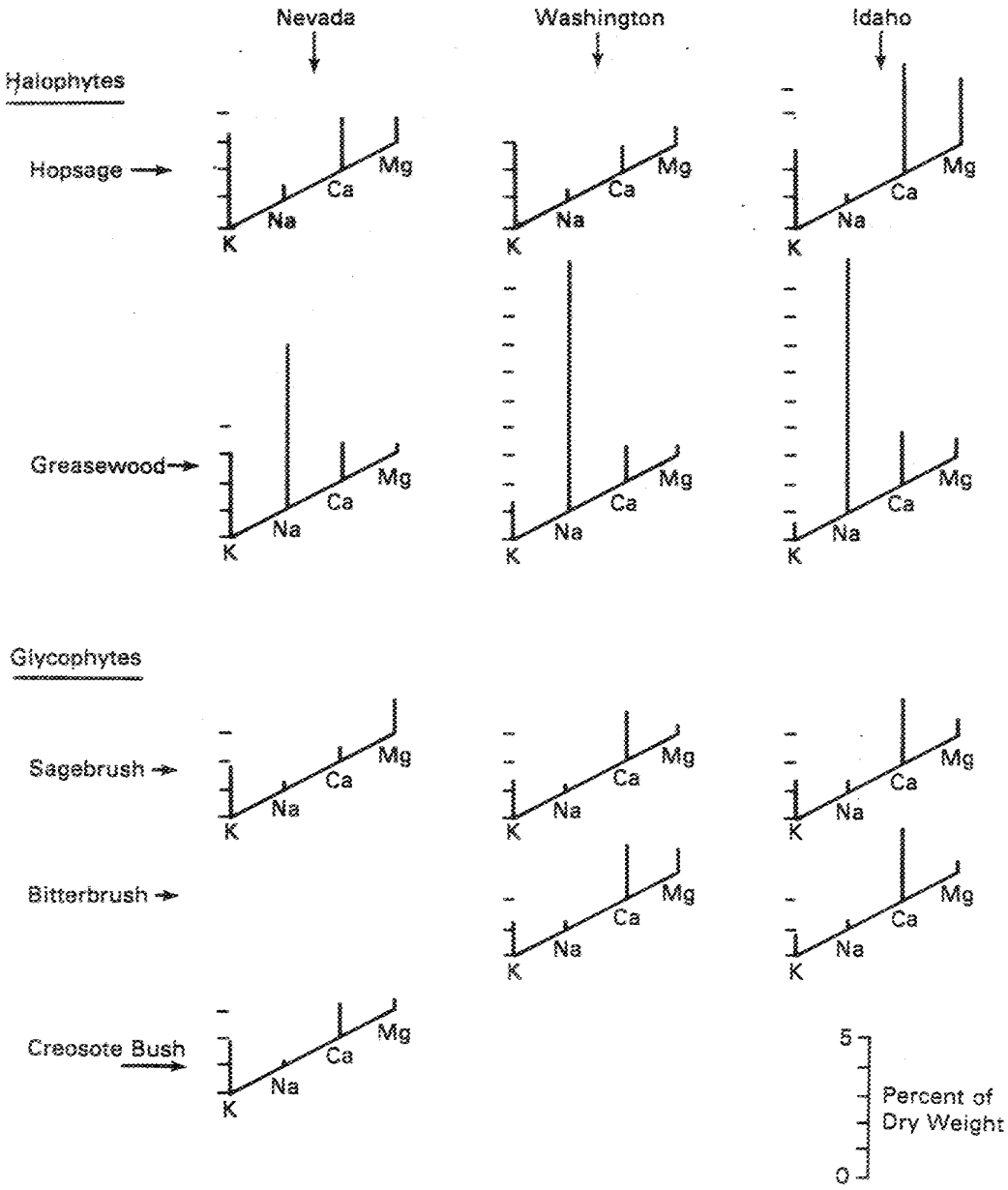


FIGURE 6.15. Cation Concentrations (Percentage of dry weight) in Six Common Shrub Taxa Growing in Nevada, Washington and Idaho

to measure the cation concentrations of leaves from different plant taxa rooted in a common soil (Figure 6.16). Calcium dominated the cation content of leaves of desert thorn (Lycium andersonii). Potassium dominated the cations in creosotebush, rattany (Krameria parvifolia), Bursage (Ambrosia dumosa), winterfat (Eurotia lanata), and hopsage. Magnesium concentrations were greatest in hopsage and desert thorn and lowest in bursage. These data show that the cation composition and concentrations in the leaves of desert shrubs depends upon the particular taxon rather than the chemical composition of the rooting substrate.

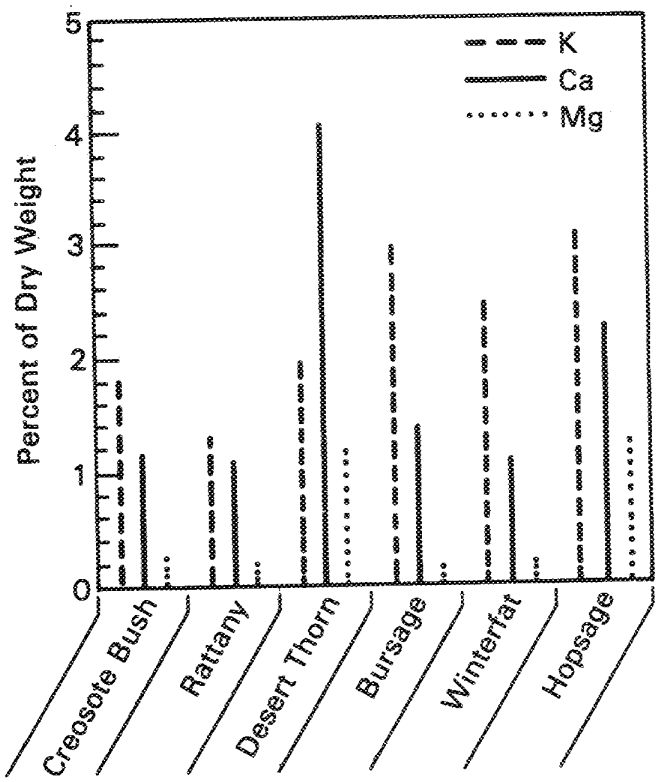


FIGURE 6.16. Cation Content in Leaves of Six Shrub Species Growing in a Mixed Plant Community at Rock Valley, Nevada (Wallace et al. 1980)

Although desert shrubs in the western U.S. have attracted the attention of plant scientists for a century or more, relatively little progress has been made in developing theories or understanding of the physiological and biochemical mechanisms of ion and water uptake, or of the genetic factors that control them.

Section II. Responses of Plants and Plant Communities to Disturbances

In this section, we summarize and synthesize the status of our information concerning the response of shrub-steppe plant communities to natural and human-induced perturbations. The studies focus on three general kinds of responses, to fire, to experimental cattle grazing, and to long-term abandonment of previously plowed land. One study involved the experimental modification of microclimate and measurement of plant productivity and evapotranspiration. Water loss through evapotranspiration is believed to be important to water balance in semi-arid regions. Therefore, plants play important roles in returning soil water to the atmosphere, and different kinds of plant communities occupy different places on the land. A more complete discussion of the surface and subsurface hydrology and plant interrelationships is treated in other chapters.

EXPERIMENTAL CATTLE GRAZING

Cattle grazing is the most economically important renewable-resource use of sagebrush-bunchgrass communities, and it is the most widespread human-induced stress throughout the shrub-steppe region. Cattle grazing has been practiced in eastern Washington since the mid-1800's (Galbraith and Anderson 1971), but there is a paucity of experimental data that can be used to document the impacts of controlled grazing on sagebrush-bunchgrass communities. Over-grazing of sagebrush-bunchgrass communities can lead to the demise of the native perennial grasses and encourage the invasion by cheatgrass (Mack 1981). However, the community impacts of moderate grazing in a relatively undisturbed community had not been documented prior to the investigation

described below. To fill this gap in knowledge, an experiment was conducted to determine the short-term impact of moderately intensive spring grazing by cattle on a relatively undisturbed portion of the sagebrush-bunchgrass community previously characterized in this chapter. To accomplish this goal, two 9-hectare pastures (plots) were subjected to spring grazing by steers for 3 consecutive years (Rickard 1985). The pastures were provided with a shared 500-gallon water trough and a block of salt. Adjacent pastures of the same size served as ungrazed treatments (controls). Fifteen head of 400-500 pound yearling hereford steers were rotated at weekly intervals between the two "grazed" pastures in 1971 and also in 1972 (Rickard et al. 1975, Uresk and Rickard 1976). In 1973, only one of the pastures was grazed, by seven steers. At the termination of grazing, the steers were removed from the pastures, held in a pen without food or water for one day and then weighed. The grazing design yielded 3 consecutive years of grazing on one 9-hectare pasture. In 1974, this pasture was rested from grazing and shoot weight measurements were made to record changes in shoot production and standing crop that had been induced by 3 consecutive years of spring grazing.

When the steers were introduced to the pastures in April, they selectively grazed the clumps of Cusick's bluegrass. In the first week, virtually every clump was grazed; some were grazed to crown level while others were only partially eaten. Clumps growing beneath the canopy spread of sagebrush shrubs tended to be protected by its branches. These clumps generally escaped being eaten; they also tended to produce flowering culms while the grazed clumps did not. The palatability of Cusick's bluegrass to cattle has been noted by Rickard et al. (1977) and by Uresk and Rickard (1976). In contrast, Sandberg's bluegrass was seldom grazed, and it produced flowering culms each year. The

most sought-out forb was hawk's beard. At flowering time, its large, yellow blossoms were conspicuously distributed throughout the adjacent ungrazed pastures, but flowers were noticeably absent in the grazed pastures. Bluebunch wheatgrass was grazed only after the green shoots of Cusick's bluegrass became depleted. Sagebrush, long-leaf phlox and fleabane were seldom, if ever, eaten by cattle.

In 1974, after the experimental pasture had been "grazed" for 3 years and rested for one season, shoot production was compared with that of the adjacent ungrazed "control" pasture (Table 6.24). Shoot production at peak harvest in 1974 averaged 69 g/m^2 in the control pasture and 64 g/m^2 in the grazed pasture (Figure 6.17). These means were not statistically different, indicating that cattle grazing did not greatly affect the capacity of grasses to maintain near-normal shoot production after 3 consecutive years of spring grazing. Perennial grasses provided 78 percent of the total live shoot biomass on the control pasture and only 72 percent on the grazed pasture (Table 6.23). Annual forbs were sparsely represented in both pastures. The most abundant annual grass in both pastures was six weeks' fescue. The conclusion was that 3 consecutive years of spring grazing did not measurably diminish shoot production; shoot production recovered appreciably in the first season after grazing was stopped. However, spring grazing did deleteriously affect the grasses in other ways; i.e., their capacity to produce flowering culms was diminished (Rickard et al. 1977). Also, below-ground biomass, as estimated by CO_2 evolution, was severely depressed during the years of cattle grazing (see Chapter 3, Section III).

During spring grazing, cattle removed one-half to two-thirds of the annual shoot production, which diminished the amount of standing dead grass

TABLE 6.24. Mean Dry Weight of Live Shoots at Peak Yields Grouped by Botanical Categories in Control and Grazed Sagebrush-Bunchgrass Pastures in 1974 (n=16)

Botanical Categories	Control Pasture	% of Total	Pasture with 3 Years of Grazing[a]	% of Total
Perennial grasses[b]	54.0 ± 7.7	78	46.0 ± 5.3	72
Perennial forbs[c]	4.5 ± 3.6	7	4.3 ± 1.2	7
Half-shrubs[d]	4.2 ± 2.0	6	4.7 ± 1.4	7
Annual grasses[e][f]	4.8 ± .70	7	5.7 ± 1.2	9
Annual forbs[g]	1.4 ± .09	2	3.0 ± .73	5
Total shoot phytomass	69		64	

(a) Pasture not grazed in 1974
(b) Perennial grasses: Agropyron spicatum, Poa sandbergii, Poa cusickii, Stipa thurberiana.
(c) Perennial forbs: Crepis atrabarba, Astragalus purshii, Lupinus sulfureous, L. leucophyllous Brodiaea douglasii, Calochortus macrocarpus, Lomatium macrocarpum and others.
(d) Half-shrubs: Phlox longifolia, Erigeron filifolius, Antennaria dimorpha.
(e) Mostly Vulpia octoflora
(f) Annual grasses: Bromus tectorum, Vulpia octoflora.
(g) Annual forbs: Draba verna, Microsteris gracilis, Descurainea pinnata, Plantago purshii.

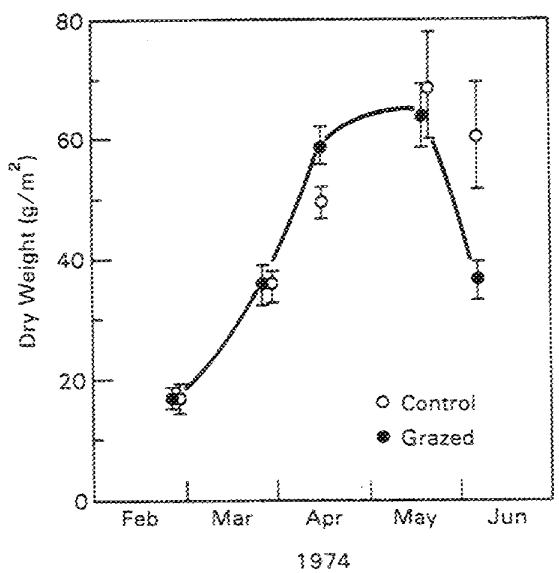


FIGURE 6.17. Comparison of Herbaceous Shoot Production in Grazed and Ungrazed Pastures from Beginning to End of the 1974 Growing Season (Data points are means ± SE.)

(Figure 6.18). Crown weights also averaged less on the grazed pasture than on the control pasture, but the total amount of litter showed no consistent-decline under the imposed grazing use (Figure 6.19). Most of the plant materials that had been ingested by the steers remained in the form of manure. Manure pats were concentrated near the water trough and in fence corners. In this way, grazing cattle created a different form and spatial distribution of dead plant materials that could, over long periods of grazing, alter the spatial patterns of plant decomposition.

At places where steers tended to congregate (e.g., gate entries, water trough locations and fence corners), plants were trampled. Some were killed, and the soil was bared in places. These bare places were later invaded by annual plants, especially cheatgrass and tumble mustard (Sisymbrium altissimum). Trampling tended to break up the soil crust of lichens, algae and mosses throughout all parts of the grazed pasture, but the extent of the damage was not quantified.

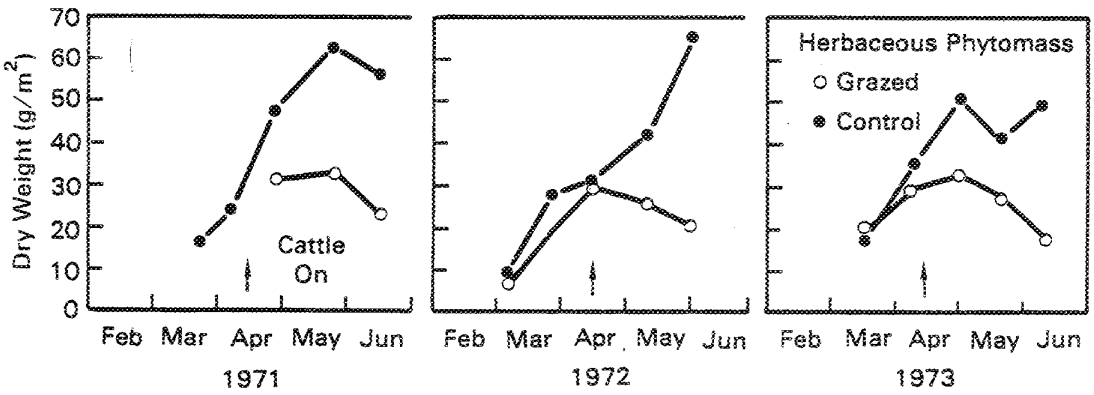


FIGURE 6.18. Comparisons of Dry Weights of Herbaceous Shoot Production in Pastures Actively Being Grazed by Steers and Adjacent Ungrazed Pastures

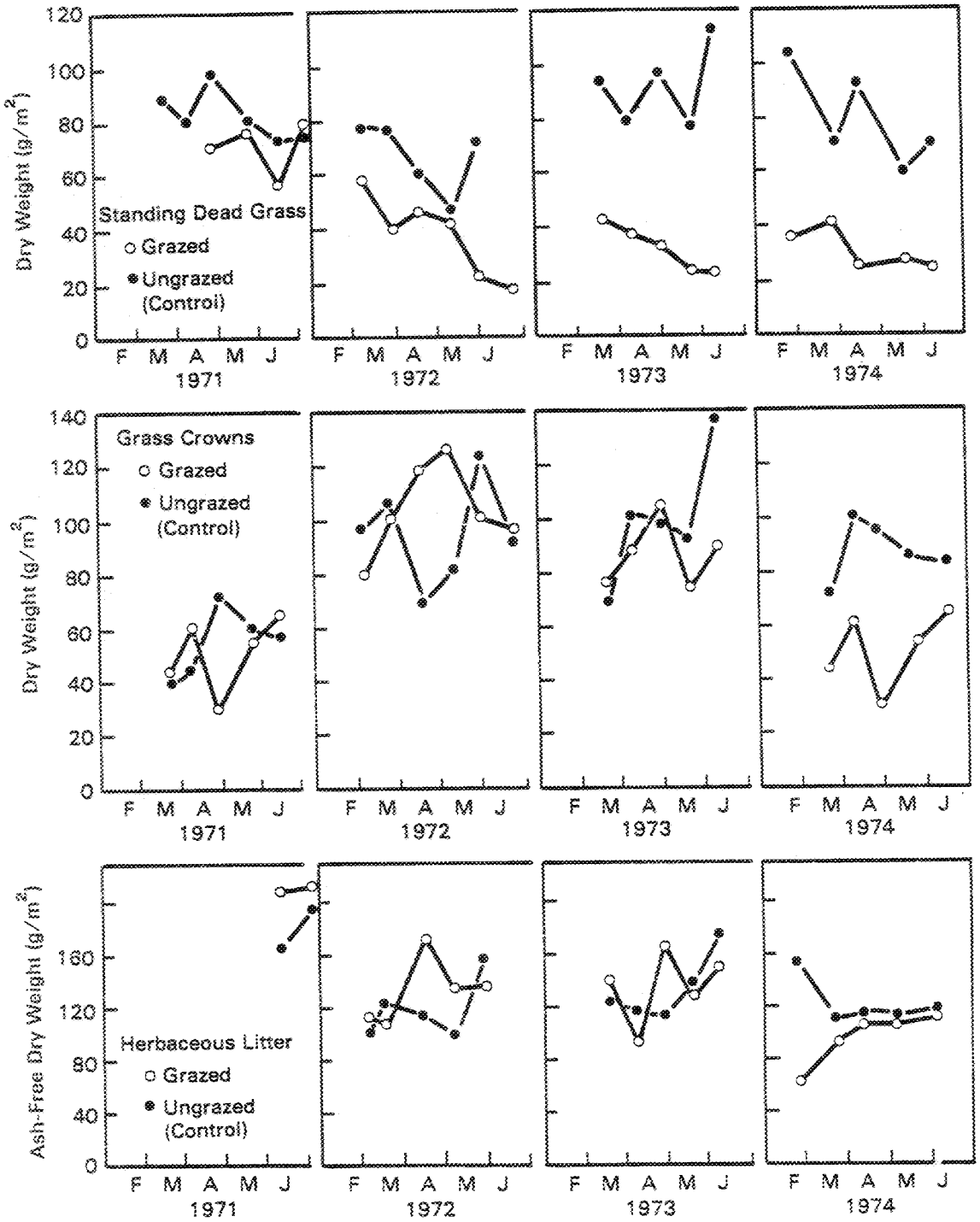


FIGURE 6.19. Comparisons of Dry Weights of Standing Dead Shoots, Grass Crowns and Herbaceous Litter in Grazed and Ungrazed Pastures

The average live weight gain of steers was 213 kg/9-ha/yr (Table 6.25). This amounted to a weight gain of 24 kg/ha. The average rate of live weight increase per steer was 0.63 kg/grazing day.

Cattle weight gains provide a basis for judging the economic potential of native sagebrush-bunchgrass communities as a cattle-grazing resource. Weight gains can also be compared with those obtained by grazing plant communities that have been botanically modified by years of grazing use, i.e., cheatgrass-dominated communities or those comprised of exotic perennial bunchgrasses such as Agropyron cristatum and/or A. desertorum. For example, a recent grazing study in A. cristatum communities in Wyoming showed steer weight gains of 0.85 to 1.20 kg/day of grazing use (Hart et al. 1983). This weight gain is greater than that obtained in the sagebrush-bunchgrass community of this investigation.

Historically, the native plants of the Columbia Basin region of eastern Washington had not been subjected to centuries of grazing use by large mammals (Mack and Thompson 1982). This virtual absence of herds of large grazing mammals suggests that sagebrush-bunchgrass communities may be inherently more vulnerable to livestock grazing than other kinds of grass-dominated

TABLE 6.25. Weight Gains of Yearling Steers During Spring Grazing in a Sagebrush-Bunchgrass Community in 1971, 1972, 1973 and 1974

Year	Days of Grazing	Animal Days Per Pasture	Total Wt. Gain (kg)	Wt. Gain per Animal per Day (kg)
1971	58	435	308	0.78
1972	41	307	193	0.63
1973	49	343	156	0.45
1974	57	285	194	0.68
Average	51	342	213	0.63

North American plant communities (e.g., shortgrass prairies) that have developed over long periods of time under grazing imposed by large populations of bison.

Worldwide, livestock grazing is one of the most important human uses of semi-arid lands, especially those lands that are neither suitable for dryland wheat farming nor favorably located near water supplies that can be used to sustain irrigated agriculture. Even so, grazing research on semi-arid lands, even in the most technologically developed countries of the world, has been minimal. An inadequate data base has tended to encourage the use of casual observations and untested theories in land management practices involving livestock grazing (Valentine 1979).

Sagebrush-bunchgrass communities as important habitats for wildlife are attracting increased attention, especially on the vast acreages of federally owned lands (McAdoo and Klebenow 1979). In the future, land areas, such as the Hanford Site, that have a history of abstinence from livestock grazing will become especially useful baseline cases. Quantitative and qualitative ecological comparisons can then be made with those plant communities that have had long histories of livestock grazing.

EXPERIMENTAL PLOWING, RECOVERY OF CHEATGRASS COMMUNITIES

The rates at which various kinds of plant communities recover from human imposed and natural perturbations are of scientific and practical interest. For example, community recovery following plowing is usually a process that requires several decades of time in humid regions, and it is much slower in arid and semi-arid regions. Community recovery as a long-term process is

not amenable to experimentation on a short-term basis nor is it amenable to very small plots or to pot experimentation.

For the purposes of this small-scale outdoor experiment, two small plots, 10 x 20 meters each, were plowed in the autumn of 1974 in cheatgrass communities located at different elevations. There was little growth on the plowed plots in the spring of 1975, and weight measurements were not made. Shoot weights were made in the spring of 1976. The plowed plots at the high elevation produced 302 g/m^2 of shoot weight as compared to 85 for the adjacent unplowed control plots (Table 6.26). At the low elevation, the plowed plots produced 160 g/m^2 of shoot weight as compared to 290 g/m^2 on the adjacent control plots. Plowing enhanced shoot production at the high elevation, and it decreased shoot production at the low elevation. Plowing favored the establishment of tansy mustard at the low elevation, but not at the high elevation (Table 6.27).

TABLE 6.26. Shoot and Litter Weights (g/.032 m^2) on Plowed and Unplowed Plots in Cheatgrass Communities at High and Low Elevations the Second Year After Experimental Plowing

	Shoot Weight		Litter Weight	
Treatment	High Elevation	Low Elevation	High Elevation	Low Elevation
Plowed	9.68 ± 4.7 (302)	5.28 ± .23 (160)	1.27 ± 1.9 (40)	1.40 ± 1.5 (44)
Unplowed	2.73 ± 1.3 (85)	9.42 ± 1.9 (290)	12.6 ± 5.8 (390)	11.5 ± 1.7 (360)

( ) = g/m^2

TABLE 6.27. Canopy Cover (Percent) Provided by Various Plant Taxa Self-Established on Plowed and Unplowed Plots in Cheatgrass Communities at High and Low Elevations, the Second Year After Experimental Plowing

Taxa	Unplowed		Plowed	
	Low Elevation	High Elevation	Low Elevation	High Elevation
Cheatgrass	97	80	58	80
Tumble mustard	0	<1	6	8
Tansy mustard	0	0	30	4
Jagged chickweed	2	3	2	0
Wild lettuce	0	6	0	2
Lanceleaf microseris	0	8	0	6
Yellow salsify	2	1	0	0
Sandberg's bluegrass	2	0	0	0

The litter weights were about nine times less on the plowed plots than on the unplowed controls (Table 6.26), which indicates the capacity of cheatgrass communities to accumulate dead plant material and shows that the decomposition of dead plants in cheatgrass communities is a relatively slow process.

Cheatgrass communities exhibited a capacity to recover quickly (two growing seasons) from a severe human-induced perturbation (plowing) that has few, if any, counterparts in nature. The inadvertent introduction of cheatgrass and other alien annuals to eastern Washington, coincident with the advent of agriculture more than a century ago, has created an ecological scenario that was not foreseen in the classical conception of secondary plant succession. In the classical sense, succession is viewed as an orderly temporal process with a predictable end product, i.e., a plant community that is functionally more productive than its predecessor communities, with the assumption that the terminal community is comprised of regional taxa and

that these are mostly perennials. The role of cheatgrass in secondary plant succession in the western United States needs to be clearly understood, especially for land uses that depend upon the prompt establishment of a vegetative cover to retard erosion of the soil by wind and water. Some examples where revegetation is required by law are surface-mined land and low-level radioactive waste burial sites. In some cases, a purposefully planted, self-sustaining cheatgrass community can play an important role in the early weeks, months, and even years of surface soil stabilization. In other cases, a self-sustaining cheatgrass community could be the aim of revegetation, especially in time frames of 100 years or less.

The aggressiveness of cheatgrass as an invading taxon also requires an extrapolation of what the future might hold for the few remnant stands of native plant communities that still persist in eastern Washington. Experience has shown that once the native communities are destroyed or damaged, the native taxa are very slow to re-establish themselves. The aggressiveness of the alien taxa suggests that the stands of native sagebrush-bunchgrass communities will continue to accept influxes of these aliens. Unless offered some form of protection from human disturbances, communities in the native floristic (i.e., "pure") condition will disappear from the land. On the other hand, cheatgrass communities can be expected to become even more important as more ground is disturbed by livestock grazing and human activities. The conscious conservation of representative sagebrush-bunchgrass communities in undisturbed (native) condition needs to be based upon an awareness that such communities are vulnerable to human activities. At the same time, aggressive alien annuals can play important roles in soil conservation in the early years following human-induced soil perturbations.

The relatively limited geographic extent of annual grass communities in North America (compared to a broad distribution in western Eurasia) is of interest concerning the evolutionary origin of the world's plant communities. It has been postulated that three general survival strategies have evolved in annual plants - stress tolerance, ruderal ability and competitiveness (Grime and Hunt 1975). In eastern Washington, cheatgrass grows on the steepest south-facing slopes having the most extreme microclimates (Sauer and Rickard 1979, Hinds 1975, Rickard and Warren 1981a). In this respect, it is a stress-tolerant taxon. Cheatgrass is regarded by dryland wheat farmers as a noxious weed. It competes with winter wheat for soil water and mineral nutrients. In this respect cheatgrass is a ruderal taxon. Rangelands, especially those that have experienced years of livestock to the point where the native grasses and forbs have been weakened or killed, are readily invaded by cheatgrass (Daubenmire 1970). Once cheatgrass becomes established on range lands, it persists for decades and interferes with the reinvasion by the native perennial plants even when native taxa seed sources are adjacent (Daubenmire 1975, Rickard and Sauer 1982). From this point of view, cheatgrass is a competitive taxon. The success of cheatgrass in eastern Washington over the past 100 years is attributable to its inherent genetic capacity to be stress tolerant, competitive and ruderal, depending on the particular site.

RESPONSES TO WILDFIRE: SAGEBRUSH-BUNCHGRASS AND CHEATGRASS COMMUNITIES

Over the past few decades, a considerable body of information has been compiled concerning the effects of burning upon forest and grassland plant communities (Daubenmire 1968, Kozlowski and Ahlgren 1974). The effects of

burning upon different kinds of plant communities have been recently reviewed by Rundel (1981). Daubenmire (1975) examined the role of fire in sagebrush-bunchgrass communities in eastern Washington, and the responses of perennial bunchgrasses characteristic of sagebrush-bunchgrass communities to burning have been described by Uresk et al. (1976) and McShane (1981). Burning has received special scrutiny as a management practice for increasing the yields of forage plants for livestock usage on semi-arid rangelands (Blaisdell 1953, Britton and Ralphs 1979, Wright and Bailey 1982).

A wildfire in August 1973 burned a portion of a sagebrush-bunchgrass community that had been measured for standing crop and shoot production in the spring seasons of 1971, 1972 and 1973. Prior to burning, the aboveground weight of sagebrush shrubs on the 9-hectare study plot averaged 132 g/m^2. Live wood and attached dead wood and leaves averaged 83 g/m^2; also, 49 g/m^2 of detached sagebrush wood lay on the ground (Table 6.28). Burning killed all the sagebrush shrubs and burned all of the standing dead herbaceous plant material. Shoot production in the spring of 1974, as measured in the first growing season after burning, indicated that about one-half of the litter was lost (Figure 6.20). There was also less grass crown material on the burned portion of the community during the March sampling period; but at the end of the spring growing season, crown material closely matched that of the unburned portion. Shoot production by herbs in the first year post-burning appeared not to be greatly impaired by summer burning, if at all.

TABLE 6.28. Sagebrush Categories (g/m^2 Dry Weight ± SE) in a Sagebrush-Bunchgrass Community at Five Sampling Periods in the 1973 Spring Growing Season (This community burned in August 1973.)

Category	6 Feb	5 Mar	3 Apr	6 May	6 Jun	Average
Leaves	5.8±3.0	1.5±1.4	3.9±3.0	8.1±3.0	5.4±5.4	5
Live Wood	113±94	2.4±2.3	9.3±6.8	33±17	47±47	41
Attached Dead Wood	17±7.6	15±12	42±22	42±37	69±47	37
Unattached Wood	35±16	97±39	47±21	36±16	30±9	49
Total	171	116	102	119	151	132

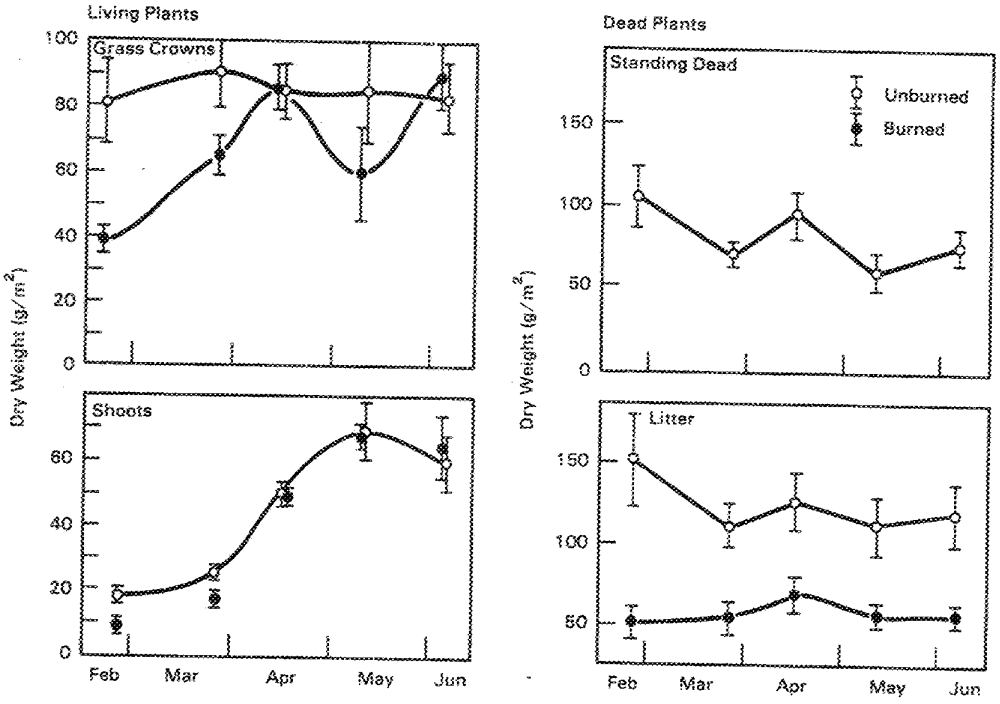


FIGURE 6.20. Dry Weight (Means ± SE) of Grass Crowns, Shoots, Standing Dead and Litter in Burned and Unburned Portions of a Sagebrush-Bunchgrass Community During the First Growing Season After August Wildfire

Over a 3-year post-burning period, 1974, 1975 and 1976, herbaceous shoot production averaged 79 g/m^2 in the burned portion of the community as compared to only 59 g/m^2 in the unburned portion (Table 6.29). Shoot production on the burned area was especially enhanced during the second growing season; 98 g/m^2 was produced, compared to only 59 g/m^2 in the unburned area. Perennial grasses provided 78 percent of the shoot weight in the burned portion of the community, compared to only 69 percent in the unburned portion. These data suggest that summer burning favors the perennial grasses at the expense of the perennial forbs and half-shrubs (Table 6.29). Summer burning also increased the average number of flowering culms produced by individual clumps of bluebunch wheatgrass (Uresk et al. 1976, McShane 1981), but it tended to shorten the leaves and to lengthen the flowering culms. However, this stimulation effect was diminished by the onset of the third growing season.

Cheatgrass communities are vulnerable to summer wildfires because dry, dead plants provide a form of readily combustible fuel. If summer burning damaged or destroyed the cheatgrass seeds, cheatgrass communities would be expected to show a very weak recovery response in the next growing season, especially if there were no unburned portions of the community to provide a source of seeds.

A wildfire in August 1981 destroyed all the standing dead plants and some of the litter in two cheatgrass communities (Table 6.30). With the onset of autumn rains, seeds that have survived the burning germinated and produced seedlings. By the end of the winter, these seedlings provided canopy coverages of 53 and 66 percent for the high and low elevation communities, respectively (Table 6.30). Most of the canopy cover was provided by only two taxa, cheatgrass and tumble mustard. Less than 10 percent of the vegetative cover

TABLE 6.29. Herbaceous Shoot Weights (Grams per m^2) in Burned and Unburned Portions of a Sagebrush-Bunchgrass Community on the ALE Site in Three Growing Seasons Following a Summer Wildfire (Figures in parentheses indicate percentage of total shoot biomass.)

Year	Perennial Grasses	Annual Grasses	Perennial Forbs	Annual Forbs	Half-Shrubs	Total[a] Shoot
			Burned			
1974	62 (81)	6.0 (7.8)	1.9 (2.5)	5.7 (7.4)	1.1 (1.4)	77
1975	82 (84)	11 (11)	1.9 (1.9)	0.4 (<1)	2.5 (2.5)5)	98
1976	43 (67)	13 (20)	3.7 (5.8)	0.05 (<1)	4.7 (7.3)	64
Average	62 (78)	10 (13)	2.5 (3.2)	2.0 (2.5)	2.8 (3.5)	79
			Unburned			
1974	54 (77)	4.8 (6.9)	4.5 (6.4)	2.1 (3.0)	4.2 (6.0)	70
1975	37 (63)	5.4 (9.1)	9.2 (16)	0.2 (<1)	6.8 (12))	59
1976	31 (65)	7.0 (15)	0.9 (1.9)	0.13 (<1)	8.6 (18))	48
Average	41 (69)	5.7 (10)	4.9 (6.9)	0.81 (1.4)	6.5 (11)	59

(a) Shoot biomass for each category represents peak yields during the spring growing season. Total shoot yields represent the sums of the peaks.

was provided by all other taxa. Sandberg's bluegrass and squirreltail, both fire-insensitive, were the only perennial grasses on the study plots. The perennial forbs, lance-leaf microseris and cluster lily, did not grow at the low elevation before or after the fire.

Live shoot weights averaged 530 and 270 g/m^2 on the low and high communities, respectively (Table 6.30). The difference in shoot weights was statistically significant at the 0.01 level. At the low elevation, forbs provided 20 percent of the shoot weight as compared to only 11 percent for the high community. The dry weight of litter averaged 530 and 320 g/m^2 at

TABLE 6.30. Percent Canopy Cover in Two Cheatgrass Communities on March 23, 1982, After a Wildfire in August 1981 (The letters represent averages of 10-meter segments along one 50-meter line.)

	Low Elevation 320 m						High Elevation 520 m					
Taxa	A	B	C	D	E	Avg.	A	B	C	D	E	Avg.
Bromus tectorum[a] Cheatgrass	38	29	24	39	16	29	22	33	53	44	38	38
Sisymbrium altissimum[a] Tumble mustard	25	29	21	40	23	28	6	20	5	3	3	7
Erodium cicutarium[a] Filaree	0	7	1	5	9	4	0	0	0	0	0	0
Amsinckia lycopsoides Fiddleneck tarweed	1	1	0	4	1	1	0	6	5	2	+	3
Poa sandbergii[b] Sandberg bluegrass	1	1	3	0	2	1	0	0	+	0	0	+
Chorispora tenella[a] Purple mustard	1	0	0	0	0	+	0	0	0	0	0	0
Descurainea spp. Tansy mustard	0	0	0	1	5	1	+	3	0	1	7	2
Sitanion hystrix[b] Squirreltail grass	0	0	0	0	1	+	0	0	0	0	0	0
Holosteum umbellatum[a] Jagged chickweed	+	0	0	0	0	+	0	0	0	0	0	0
Microseris lanciniata[b] Lanceleaf microseris	0	0	0	0	0	0	+	2	2	8	1	3
Tragopogon dubius[a] Yellow salsify	0	0	0	0	0	0	1	0	0	1	0	+
Brodiaea douglasii[b] Cluster lily	0	0	0	0	0	0	+	0	0	0	0	+
Total canopy %	66	67	49	89	57	66	28	64	65	59	49	53
Number of taxa	6	5	4	5	7	9	6	5	5	6	5	8

(a) alien taxon
(b) perennial taxon
+ = < .05 percent cover

the low and high elevations, respectively. The difference was statistically significant at the 0.05 level. The 13-year average of shoot production was 260 and 226 g/m^2 for the low and high elevation, respectively. Shoot

production in 1982 the growing season following burning was 200 percent higher than that of the 13-year average at the low elevation; at the high elevation it was 20 percent greater.

Although summer burning undoubtedly destroyed many cheatgrass seeds that were on the ground or lodged in the litter, many survived, germinated and produced plants that developed ripe seeds. Clearly, the occurrence of a summer wildfire did not destroy the capacity for cheatgrass communities to restore shoot productivity during the next growing season. The capacity of the cheatgrass community to respond to severe drought and summer burning is illustrated in Figure 6.21. The cheatgrass community responded to these natural perturbations with better-than-average shoot productivity the following year.

Cheatgrass has dominated the vegetation of abandoned agricultural fields for 40 years, even without periodic human-induced perturbations, e.g., livestock grazing or cultivation. Summer burning helps cheatgrass to dominate because fire kills sagebrush shrubs while having little impact on the survivability of cheatgrass. Because cheatgrass seeds survive burning and germinate, they can compete with the native perennial grasses and forbs, which produce fewer seeds.

Summer burning of sagebrush-bunchgrass communities that had only trace amounts of cheatgrass in them before burning did not promote a dramatic increase in cheatgrass. This indicates that summer burning alone is insufficient to encourage cheatgrass invasion in these kinds of communities. The features of the pristine sagebrush-bunchgrass community that permit it to resist invasion by cheatgrass are subjects for future study. Allopathy,

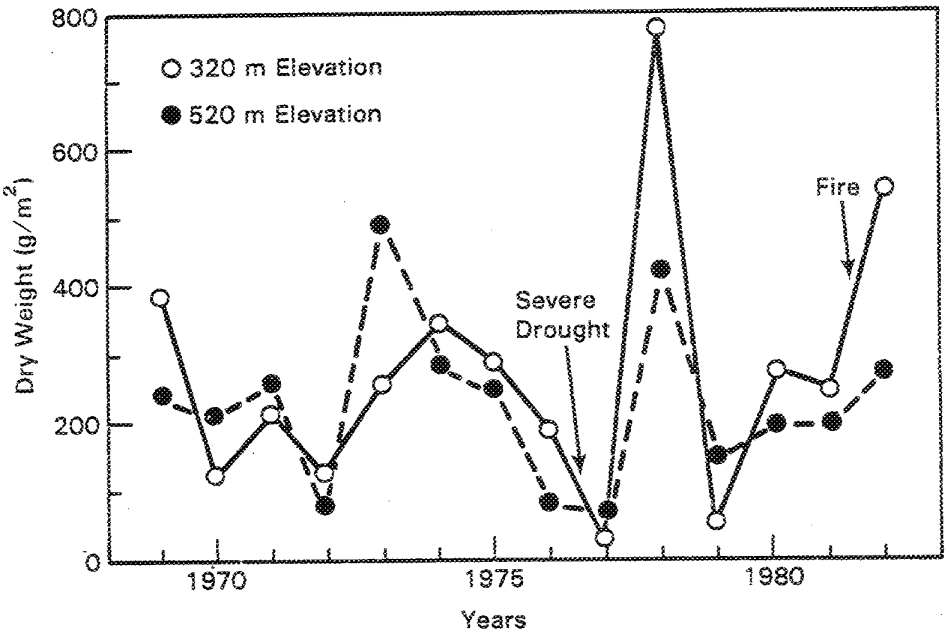


FIGURE 6.21. Dry Weight of Shoots in Cheatgrass Communities at Peak Production for 13 Consecutive Years, 1969-1981 (Years of severe drought, 1977, and summer wildfire 1981, are indicated by arrows.)

or perhaps some other kind of biotic mechanism, may play a key role in the ability of sagebrush-bunchgrass communities to resist cheatgrass invasion in the long-term absence of human-induced perturbations.

RESPONSE TO WILDFIRE: GREASEWOOD AND SPINY HOPSAGE

Two of the most abundant desert shrubs in eastern Washington are big sagebrush and antelope bitterbrush. These shrubs do not usually sprout after wildfire (Daubenmire 1970). Rabbitbrush, greasewood and spiny hopsage are less abundant than either sagebrush and bitterbrush, but these shrubs have been observed to sprout after burning. Humphrey (1974) has extensively reviewed the literature of range fires, but makes no mention of the response of spiny hopsage to burning.

The response of shrubs in a greasewood-spiny hopsage community to a summer wildfire is described in the following text. The fire history of the community in the years before 1943 is unknown. The community is known to have been grazed by stray livestock in the years 1943-1963 and for many years prior to 1943. The attraction was a nearby permanent water supply (Rattlesnake Springs). In 1963, a part of the community and 800 acres of surrounding land were fenced to exclude livestock. The community has not since been grazed by livestock, and the riparian vegetation along the spring stream has responded by showing a great amount of tree growth over a 15-year time span (Rickard and Cushing 1982).

In 1965, a 30 x 30-meter study plot was established in the greasewood-hopsage community and permanently marked by steel fence posts. The only known human perturbations since its establishment have been one-day visits by field ecology classes made in mid-April on alternate years.

The study plot and its immediate vicinity are known to have supported three shrub taxa in the past 20 years: greasewood, spiny hopsage, and sagebrush (Rickard 1964). A few living sagebrush plants were present in the community 20 years ago, although they were not rooted within the boundaries of the study plot. The dead, standing stems of sagebrush were more numerous than were the living plants. The absence of charcoal and burn scars on the standing dead sagebrush stems in 1965 indicated that the demise of sagebrush shrubs was probably not due to burning. The causal factors are not known, but the decline in sagebrush shrubs may have been promoted by soil erosion after many years of livestock grazing had weakened the herbaceous understory plants and trampled the surface soil (Rickard 1964).

In late July 1981, a wildfire burned through the study plot and the surrounding vegetation. Burning destroyed the shrubs and the standing dead portions of herbaceous plants. The plot was revisited in 1983. Canopy cover and shrub density were determined at the same time and in the same way as in previous years (Rickard and McShane 1984). The results showed that burning had killed all of the spiny hopsage shrubs; their demise in this particular community would probably have gone undetected were it not for the establishment of the study plot. Greasewood shrubs had not only survived but had produced substantial amounts of new shoot growth (Table 6.31). Canopy cover of greasewood shrubs was restored to 47 percent of its preburn value, but only 31 percent of total pre-burn shrub canopy was restored. The density of greasewood shrubs in 1981 was 185 shrubs. After burning there were 210 greasewood shrubs on the study plot. Burning apparently stimulated the sprouting of new greasewood clumps. The dominant herbaceous species, Sandberg's bluegrass and cheatgrass, appeared to be unaffected by summer burning. Although in 1957, 1973, and 1981, wildfires occured in the vegetation that surrounds the community, 1981 was the first time that the study community itself burned-after a 17-year respite from livestock grazing. The years of protection from grazing probably contributed to the spread of fire by allowing dead grass to buildup and act as a full supply.

Wildfires in eastern Washington usually occur in the hot, dry months of July and August. Hopsage is dormant and leafless at this time, and was thought to be resistant to fire damage. The failure of spiny hopsage to sprout after burning on this particular habitat suggests that the shrubs may have been

TABLE 6.31. Canopy Cover (Percentage) and Density of Greasewood and Spiny Hopsage Shrubs on a 30 x 30-Meter Study Plot, April 1981 and April 1983

Shrub Taxa	Number of Shrubs	% Canopy Cover 1	2	Average of 1 and 2
		Pre-Burn Measurements, 1981		
Greasewood	185	10.7	12.2	11.4
Spiny hopsage	43	6.4	5.6	6.0
Total	228	17.1	17.8	17.4
		Post-Burn Measurements, 1983		
Greasewood	210	4.8	5.9	5.4
Spiny hopsage	0	0	0	0
Total	210	4.8	5.9	5.4

1) Average of seven east-west lines
2) Average of seven north-south lines

growing under less-than-optimal environmental conditions and were more sensitive to burn damage than if they had been growing in a more favorable habitat.

Spiny hopsage is reported to be susceptible to the chemical herbicides used to kill weeds in agricultural fields (Daubenmire 1970). However, thedemise of spiny hopsage in the study community was likely not caused by herbicides. The community is remote from agricultural fields, and roadside spraying of chemicals for weed suppression has not been practiced.

An important contribution of future ecological research would be to develop the capability to distinguish between plant populations that are "stressed" and those that are not. Many plant populations that appear "normal" by visual inspection react unexpectedly to external perturbations such as burning, chemical herbicides, sulfur dioxide, fluoride, ozone and other air

pollutants. Research is needed to develop ways of identifying plant populations that are sensitive to human-induced stresses before irreversible damage is sustained.

EXPERIMENTAL MANIPULATION OF MICROCLIMATE AND THE RESPONSE OF PLANTS

In the shrub-steppe region of the western United States, the amount of plant cover and its taxonomic composition vary according to the physical and chemical properties of the rooting substrate and to the variations in microclimates as influenced by the topographic features of the land, especially steep slopes. Manipulation of the plant root zone (soil) has been practiced by agriculturalists for hundreds of years. In arid and semi-arid regions, fertilization, irrigation, seed bed preparation, weed suppression and genetic selection have all contributed to increased crop yields. However, manipulation of microclimates rather than rooting substrate has seldom been attempted in the shrub-steppe.

An earth mound was built to create contrasting phytoclimates on north and south slopes while maintaining a common rooting substrate (Hinds 1975). The long axis of the mound extended in an east-west direction to form steep (40°) slopes facing north and south. Cheatgrass was selected as the experimental plant. Water loss was measured with weighing microlysimeters (Hinds 1973). Shoot production was not found to be greatly different between slopes, but the north-facing slope produced more seed and more root biomass (Table 6.32). All terms in the radiation balances (shown in Figure 6.22) were significantly greater on the south exposure, as was sensible heat flux to the atmosphere.

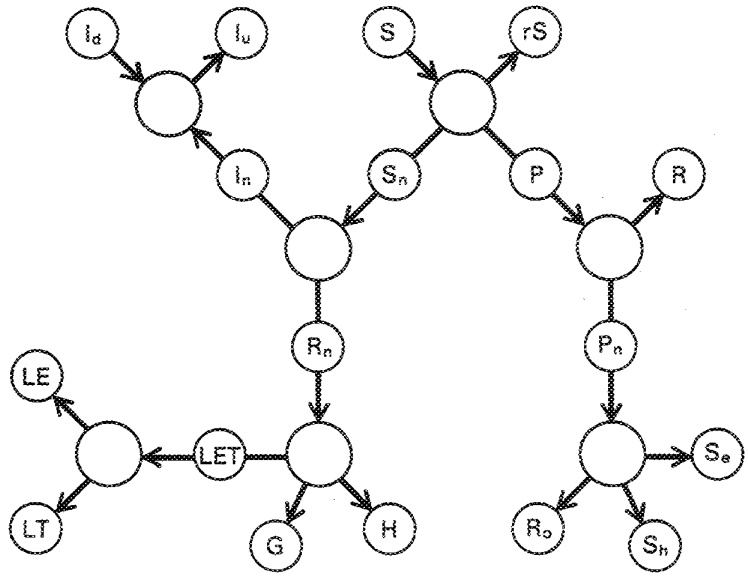
TABLE 6.32. Biomass production (g/m^2 ash-free) of Cheatgrass Grown in Small Lysimeters on North- and South-Facing Slopes Between March 31 and May 31, 1972 (Hinds 1975)

Part	Exposure	31 Mar	n(a)	31 May	n	Net Production
Root	North	18 ± 2(c)	16	139 ± 11	13	121 ± 13
	South	18 ± 2	16	112 ± 8	13	94 ± 10
	p(b)			.009		.04
Shoot	North	136 ± 9	15	350 ± 19	13	214 ± 34
	South	136 ± 9	15	364 ± 16	13	228 ± 31
	p			.4		.50
Seeds	North	---	--	119 ± 7	13	119 ± 7
	South	---	--	88 ± 7	13	88 ± 7
	p			10		10
Total	North	154 ± 11	--	608 ± 37	13	454 ± 54
	South	154 ± 11	--	564 ± 31	13	410 ± 48
	p			.2		.1

(a) n = sample size
(b) p = probability of the difference occurring by chance
(c) Standard error

A follow-up experiment was made to determine species composition and shoot production on the contrasting slopes of the mound after seeding with cheatgrass. Four years later (1978), the plant species composition, canopy cover and shoot and litter weights were determined.

After 4 years, cheatgrass and tumble mustard were the most abundant plants on the slopes (Rickard and Warren 1981a). Other self-established taxa were Russian thistle, spring draba, tansy mustard, willow herb, bluebunch wheatgrass, Sandberg's bluegrass, Cusick's bluegrass, hawks' beard, yellow salsify, fleabane, and big sagebrush. The plants on the north slope provided more canopy cover than those on the south slope (Table 6.33). Cheatgrass



G Heat Flux to the Soil
H Heat Flux to the Atmosphere
I_d Longwave Radiation from the Atmosphere
I_n Net Longwave Radiation
I_u Longwave Radiation from Plant and Soil Surfaces
LE Evaporation from Soil Surface
LET Total of Evaporation and Transpiration
LT Transpiration from Leaves
P Gross Photosynthesis
P_n Net Photosynthesis
rS Reflected Shortwave Radiation
R Respiration
R_n Net All-Wave Radiation
R_o Root Biomass
S Shortwave Radiation
S_e Seed Biomass
S_h Shoot Biomass
S_n Net Shortwave Radiation

FIGURE 6.22. Energy Flows in a Plant Community and Its Environment, Showing Terms Used for Determining Radiation Balance (from Hinds 1975)

was the major contributor to the canopy cover on the north slope, and cheatgrass and tumble mustard provided most of the canopy cover on the south slope. This particular year was also wetter than average. The autumn-to-winter shoot production on the north slope was about six times that of the south slope, 120 vs. 22 g/m^2 dry weight, respectively (Table 6.34). At the end of the spring growing season, the north slope had produced 830 g/m^2 of shoot weight, as compared to only 163 grams for the south slope.

TABLE 6.33. Canopy Cover Provided by Plant Taxa Growing on Contrasting Slopes of an Experimentally Shaped Earth Mound in the Spring of 1978

Taxa	North-Facing Slope (% Cover)		South-Facing Slope (% Cover)	
	Mar 10	Apr 17	Mar 12	Apr 17
Annual Grasses				
Cheatgrass	63	84	24	30
Annual Forbs				
Tumble mustard	12	26	22	65
Tansy mustard	1	1	1	1
Willow herb	0	1	0	0
Spring draba	0	1	0	0
Russian thistle(a)	0	0	0	1
Total Annual Cover	76	113	47	97
Perennial Grasses				
Bluebunch wheatgrass	1	1	0	0
Sandberg bluegrass	0	1	0	0
Cusick bluegrass	0	1	0	0
Perennial Forbs				
Hawks' beard	0	1	0	0
Fleabane	0	0	0	1
Yellow salsify	0	1	0	0
Shrubs				
Big sagebrush(a)	0	0	0	1
Total Perennial Cover	1	5	0	2
Total Canopy Cover %	77	118	47	99
Total Taxa	4	10	3	6

(a) seedlings

The experimental mound also provided a way to observe the influence of contrasting microclimates on litter accumulation and decomposition, but those processes were beyond the scope of the investigations reported here.

TABLE 6.34. Mean Litter and Shoot Weights ($g/m^2 \pm SE$) on Contrasting Slopes of an Earth Mound During the Spring of 1978

Slope Exposure	Feb 22	Mar 24	Apr 18	May 17
		Shoot Weight		
North-Facing	120 ± 28	115 ± 32	133 ± 22	830 ± 43
South-Facing	22 ± 10	30 ± 7	163 ± 30	(a)
		Litter Weight		
North-Facing	244 ± 77	243 ± 45	216 ± 50	124 ± 52
South-Facing	335 ± 84	114 ± 43	182 ± 82	

(a) peak growth was attained in April on the south-facing slope.

After 4 years, the north slope of the experimental mound supported more self-established plant taxa than the south slope. Similar observations have been made on the slopes of aged railroad embankments (Dillon 1967), on artificially formed earth mounds (Rickard et al. 1975), and also on the natural north and south slopes of ancient gullied bluffs (Sauer and Rickard 1979).

Hinds' study (1975) focused on the autecology of cheatgrass, its energy and carbon balances. The results show that differences in slope microclimates played the major role in determining the amount of seed production in cheatgrass, but that total shoot production was not different. Rickard and Warren (1981a) measured a marked increase in shoot production on the north facing slope. It is not clear whether the weather conditions during the time of Hinds' study explains the responses he observed in cheatgrass shoot production.

Nevertheless, both studies confirm the importance of microclimate as a factor in community growth and performance. As shown in Hinds' study, cheatgrass on the north slope was able to convert available sunlight, soil, water and mineral nutrients into dry matter more efficiently than cheatgrass

on the south slope. Plant physiological factors (Hinds 1975) and the extended growth period on the north slopes accounted for this higher efficiency.

Manipulations of microtopography through slope angles and exposures provide a way to obtain information concerning the behavior of mixed plant populations that is not obtainable by conventional experimental designs using glasshouses, growth chambers or agricultural field plots located on level ground. Artificial mounds also can provide an experimental basis for determining mineral uptake by plants as influenced by microclimates and wind and water erosion of surface soil.

Section III. Radionuclides as Indicators of Biological Fate and Transport of Materials

Questions frequently arise as to the usefulness of controlled releases of radionuclides for detecting the biological fate and transport of materials. Interest centers on industrial sites such as Hanford, where releases of low levels of radioactive materials to the surface environment have been a steady feature for 40 years. In different situations, as during the era of above-ground nuclear weapons testing, the pattern of large-scale pulsatile injections of radionuclides into the atmosphere allowed several food chain pathways to be identified and modeled. Russell (1965) accomplished this for agricultural systems, and Eberhardt and Hanson (1969) modeled wild systems. This same approach is not generally applicable at industrial production sites, where releases are regulated at very low levels and extend over several decades (Price et al. 1985, Cline et al. 1985). The field use of environmental monitoring data to discern fate and transport needs more critical assessment. In this section, we examine the behavior of radionuclides that have provided useful information about fate and transport mechanisms at the Hanford Site.

RADIOACTIVE STRONTIUM AND CESIUM IN THE SOIL PROFILE

Strontium-90 and Cesium-137 are moderately long-lived (≈30 year half life) radionuclides that are produced in the nuclear fission process. They are of ecological concern because they have been introduced into soils on a global scale as depositions of airborne fallout from nuclear weapons testing (Francis 1978). Strontium-90 is only moderately sorbed to soil colloids, and

when present in the root zone, it is readily available for uptake by plants. It accumulates in the bone and bone marrow of vertebrate herbivores following ingestion of contaminated forage. Deleterious health effects in humans can be induced with increased body burdens of ^{90}Sr (Francis 1978). Cesium-137 is strongly absorbed by soil, and it is not as readily available to plants through root uptake as ^{90}Sr (Dahlman et al. 1975). In this respect, ^{137}Cs can be regarded as less of a long-term human health hazard than ^{90}Sr.

Field observations were carried out over a period of 26 years to determine the ability of cheatgrass to extract radioactive Sr from soils after an initial soil application of ^{137}Cs and ^{90}Sr. A crop experiment was established in 1954 (Cline and Rickard 1972b). The study site consisted of 12 plots, each 1.2 x 3 meters (4 x 10 feet), separated from one another by a 1.2-meter (4-foot) buffer zone. In 1954, ^{90}Sr was added to six of the plots at a concentration of 1470 $\mu Ci/m^2$ and to six other plots at 270 $\mu Ci/m^2$ ("high-treatment" and "low-treatment") plots. The ^{90}Sr was mixed into the upper soil by plowing to approximately 12.5 centimeters, and no further disturbance of the soil has occurred during the ensuing 30 years.

In 1965, irrigation was terminated. The plots were abandoned and were promptly colonized by cheatgrass and a few annual forbs, especially tansy mustard (Descurainea sp.). In the spring of 1970, samples of cheatgrass and tansy mustard shoots were clipped 2 to 3 centimeters above the ground in early, mid and late growing season and were radiochemically analyzed for ^{90}Sr and ^{137}Cs. At the peak of shoot growth, plots 1 meter square were clipped of all new shoot growth to obtain an estimate of annual shoot production. Almost all of the yield was cheatgrass. Shoot production averaged 228 g/m^2 on the plots treated with high amounts of ^{90}Sr and 176 g/m^2 in the plots treated

with low amounts of ^{90}Sr. Both values are within the expected range of normal productivity for cheatgrass. Radionuclide concentrations generally decreased from the beginning to the end of the spring growing season. Tansy mustard had greater concentrations of ^{90}Sr than did cheatgrass (Figure 6.23), and generally the ^{90}Sr concentrations in plants were highest when rooted in plots that had the highest soil concentrations, i.e., 1470 $\mu Ci/m^2$, and the lowest ^{90}Sr concentrations were in those plots with low soil concentrations. About 0.03 and 0.02 percent of the ^{90}Sr added to the soil was assimilated in the shoots of the high-treatment and low-treatment plots, respectively.

Uptake of ^{137}Cs was also determined. The fraction assimilated by the shoots relative to ^{137}Cs added to soil was 1/100 lower than that for ^{90}Sr (Cline and Rickard 1972b).

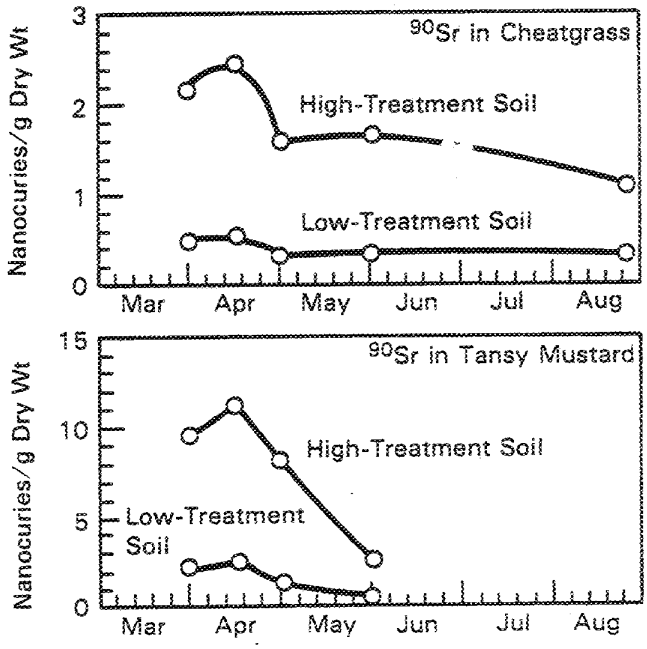


FIGURE 6.23. Uptake of ^{90}Sr by Cheatgrass and Tansy Mustard from Experimental Plots Contaminated 16 Years Earlier

Under the influence of irrigation, ^{90}Sr was redistributed to a depth of approximately 6 cm after 10 years. The results are shown in Figure 6.24; the distinct peak of ^{90}Sr distribution was interpreted to be the ionic front mobilized largely as a consequence of irrigation. Once irrigation ceased, there was a further downward migration of the front, which appears to have stabilized during this 10-year period.

This stabilization might be expected since the most obvious mechanisms for transport of strontium ions in agricultural soil, plowing and irrigation, had ceased. A closer examination of Figure 6.24 shows that in 1980, ^{90}Sr had spread above and below the peaks shown in 1970 and 1980, with the 1980

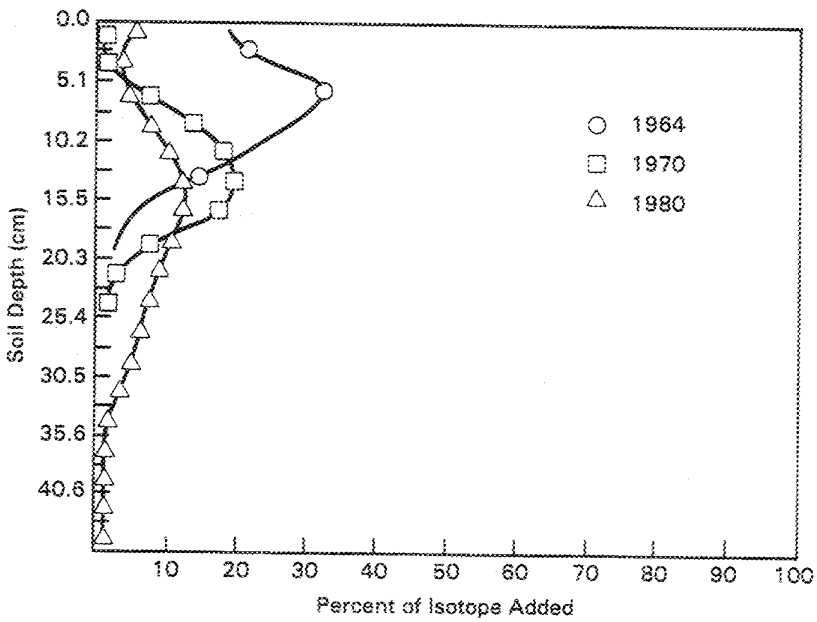


FIGURE 6.24. Changes in the Distribution of ^{90}Sr in an Untilled Soil Profile, from 1964 to 1980 (data from Cline and Rickard 1972b, Cline and Cadwell 1984)

peak less pronounced. After 26 years, ^{90}Sr previously moved downward by irrigation water appears to have been redistributing toward the upper one-third of the soil profile after irrigation ceased. How was the ^{90}Sr being dispersed?

Factors that might account for the redispersal observed in the years from 1970 to 1980 include 1) upward movement of soil solution during dry seasons by capillary actions, 2) freezing and thawing, 3) vertical mulching by soil-dwelling invertebrate animals, and 4) plant root uptake and translocation. Another factor to be considered is the possible change in chemical form of strontium due to micro-organism metabolic or geochemical processes. Such phenomena are known to occur for plutonium deposits after long residence time in soils, for example (see next section), but they are here ruled out for ^{90}Sr on the basis of laboratory experimentation (Cline 1981). Items 1) and 2) are difficult factors to quantify. More recently, models have been developed to deal with biotic transport, items 3) and 4) above, and these may be the most important factors to consider.

In analyses of various biotic transport factors (Kennedy et al. 1985), sufficient ecological data were available to develop a model. The computer code (BIOPORT) was developed to predict plant and macrofaunal translocations to the surface of shallowly buried radioactive wastes (Figure 6.25). The model is instructive because calculations clearly show that biotic processes are significant factors in distributing ^{90}Sr and ^{137}Cs to the surface. Previously, biotic transport by plants and burrowing small animals (rodents, ants, grasshoppers, etc.) was considered to be of negligible importance at shallow-land radioactive waste disposal sites.

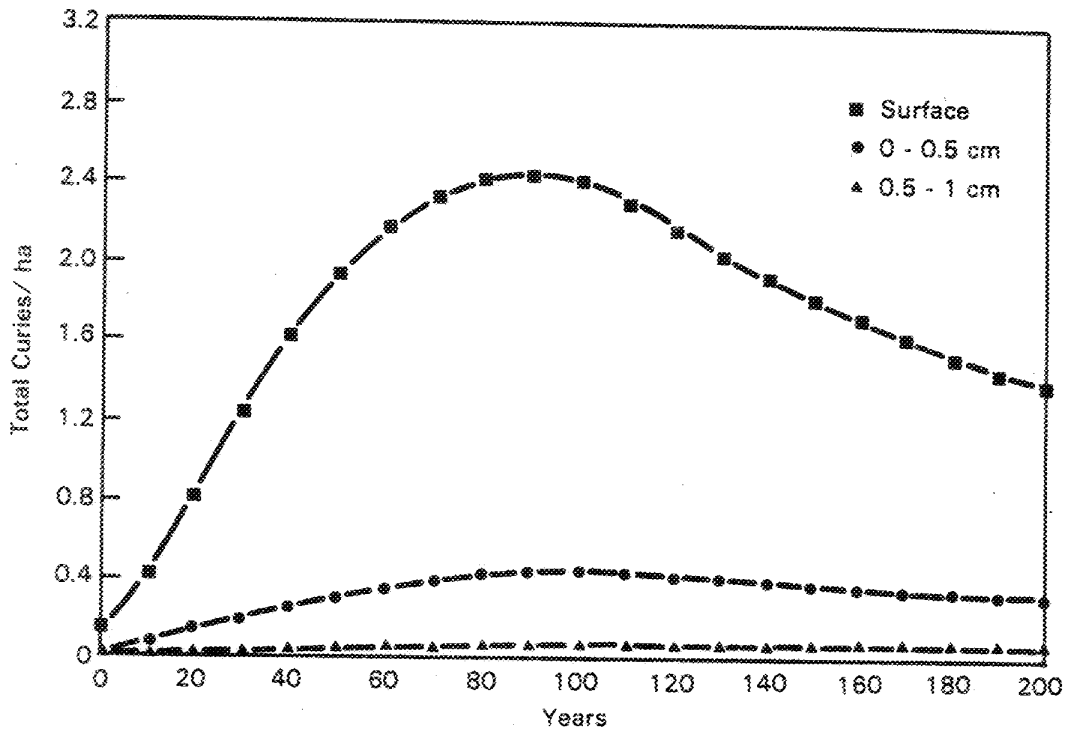


FIGURE 6.25. Estimated Total Curies per Hectare Present over 200 Years Resulting from Biotic Transport of Low-Level Radioactive Waste Buried 2 Meters Deep (from Kennedy et al. 1985)

The BIOPORT model simulates for each year 1) radioactive decay of the radionuclide inventory and release rates in each soil stratum, 2) the amount of soil brought to the surface from the soil strata by animal data, 3) the new concentrations of each radionuclide in each stratum based on data for soil/radionuclide movement, and 4) the new concentration of each radionuclide in each soil stratum, indicated by plant translocation data. The rise in the middle and upper graphs of Figure 6.25 represents the increase in availability of mixed radioactive wastes as their containers disintegrate. The decline after 100 years represents radioactive decay. What is important about the figure is that the wastes, originally buried at a 2-meter depth, are being redistributed to the surface as they are released. Twenty-three radionuclides

specified as low-level waste by the Nuclear Regulatory Commission are included in the model computations, but the most important dose contributor was ^{90}Sr because of its high biological availability. The next most important dose contributor was ^{137}Cs, accounting for about 5 percent of the dose contributions (Kennedy et al. 1985).

PLUTONIUM RESUSPENSION AND FOLIAR IMPINGEMENT

The biological importance of plutonium as an environmental contaminant centers on its long physical half-life (thousands of years) and long-term potential for human health. As to the latter concern, plutonium concentrations in surface soil and plants of the Hanford Site are negligible. The amounts in air are very small, e.g., 3-12 aCi/m^3 compared to DOE's environmental concentration guide (60,000 aCi/m^3), as are the concentrations measurable in vegetation, e.g., 0.2-1.0 fCi/g dry wt. (Price et al. 1985).

In the terrestrial environment, plutonium is impinged directly on surface soil and plant leaves in wet and/or dry depositions. It also enters the soil indirectly through decay of entire dead plants or senesced plant parts that provided the initial impingement surfaces. These are fundamental processes in ecosystem functioning for which it was hoped that radioactive tracers would provide quantitative information. This hope has been partially realized. A broad range of soil-plant concentration ratios, for example, has been reported for the transuranic elements (Adriano et al. 1980) as it has for other radioelements (Vaughan et al. 1981). Examination of the review by Adriano et al. is instructive. It shows that while the concentration ratios range over many orders of magnitude (10^{-2} to 10^{-7}), they also encompass and depend upon different source terms, soil types, plant species, plant

components, climatic conditions, extent of foliar contamination, and kinetic factors. Where experimental and environmental parameters remain unexplained, this extensive information is of little use in predicting long-term behavior of these elements, but significant progress has been made in delineating the various parameters (Hanson 1980).

Of the factors enumerated, perhaps the least quantitatively understood with relation to ecosystem function has been foliar uptake and translocation. Earlier investigations on world-wide fallout phenomenology showed its importance; they revealed that both fission and activation elements differ substantially, both in their uptake from foliar surfaces and in their mobility within plants (Aarkrog 1975, Athalye and Mistry 1972, Tukey et al. 1961). However, numerous confounding factors, particularly particle size distribution, made comparisons difficult for observations that were taken, as these were, at different times and places under varying weather conditions. Under conditions of better control, uptake and leaf translocation of primary plutonium particles (0.02 to 0.2 μm) from aerosols was measured using a wind tunnel exposure system (Cataldo et al. 1980). Plutonium was found to be translocated from the exposed leaves to seeds and to other plant parts. When the plutonium in seeds was determined relative to the plutonium on the exposed leaves, a translocation ratio of about 10^{-3} percent was found. When the data were compared to literature values for seed content of plutonium relative to soil, but transported via the roots, the values were found to equal or exceed estimated root transport, as shown in Figure 6.26. In these studies, the foliar absorption route represented an effective pathway for absorption of plutonium, and both chemical form and solubilization kinetics

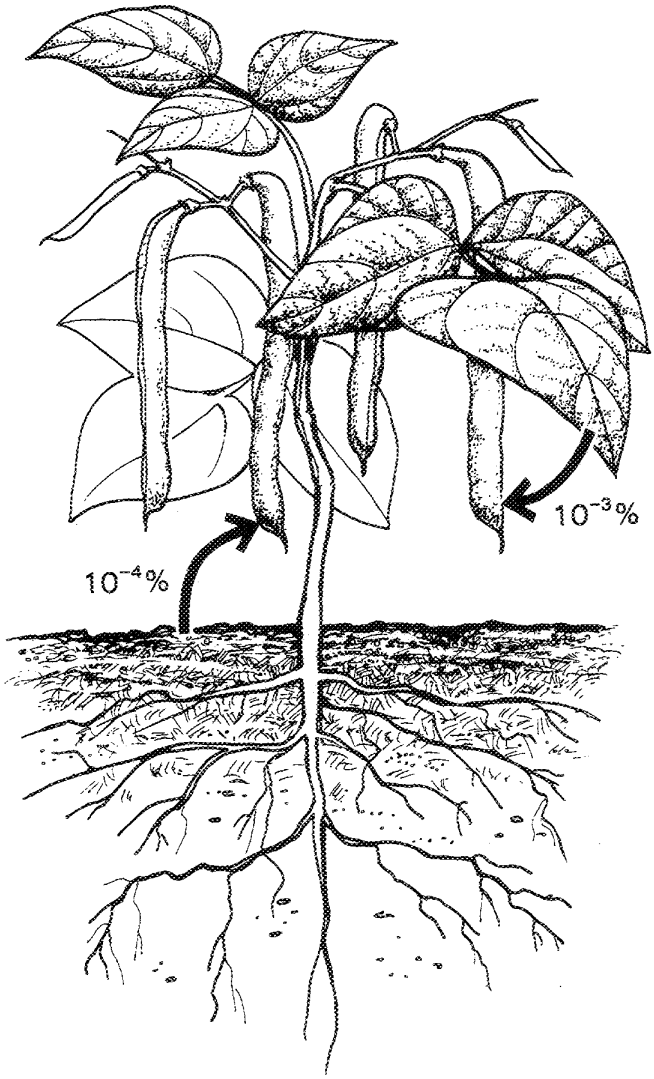


FIGURE 6.26. Plutonium Translocation Ratios to Bushbean Seeds from Foliar Deposits, Compared to Seed Translocation from Soil via Root Uptake (The foliar pathway can be the dominant factor in uptake of airborne trace elements.)

(humidity) affected the uptake (Cataldo et al. 1980). The significance of these findings lies in their implications with respect to resuspension of wind-driven soils.

The studies of Sehmel (1983) show that the plutonium activity in air and airborne particles at Hanford, e.g., as measured by Price et al. (1985), represents an old source subjected to wind resuspension. The source consists of accumulations from the early years of plutonium production at Hanford mixed with plutonium delivered as world-wide fallout. The plutonium isotopic ratios measured in Sehmel's study are indicative of releases from Hanford operations in early years, not the current operations of the Plutonium-Uranium Extraction (PUREX) facility.

If we assume that the soil inventory of plutonium has been in place for years and remains on the surface as wind-erodible particles, an appropriate uptake ratio from air to plant (annuals) may be inferred for the resuspension process. For the ALE Reserve, this ratio is 170, which probably represents the maximum air to plant uptake during the annual cycle of growth. The surface soil concentration ratio is much higher than would be expected from root uptake alone, e.g., 10^{-4} to 10^{-5} (Adriano et al. 1980), again pointing to the resuspension origin of plutonium. The findings are of wider significance. Earlier studies, for example, showed that 80 to 90 percent of ^{90}Sr and ^{137}Cs in crop plants were derived from foliar contamination, probably of wind resuspended origin, based on growing plants covered and uncovered in the field (Romney et al. 1973).

RESUSPENSION	RADIOACTIVITY CONCENTRATION	RATIO
a. Vegetation	0.6 fCi/g dry	---
b. Soil surface	1.6 fCi/g dry	a/b = 0.4
c. Air	3.5 aCi/m3	a/c = 170

(Price et al. 1985)

IODINE IN DESERT PLANTS AND SOIL

Iodine-129 is a long-lived radionuclide (1.6 x 107 years) produced in the nuclear fission process. Because of its low concentrations in the environment, low chemical toxicity and low-energy radiation emissions, it is not regarded as biologically hazardous (Soldat 1976). Iodine-129 occurs naturally, and is probably present in small amounts in all soil and terrestrial biota. In this respect, its introduction into the biosphere is not a new experience for biota. Only the magnitude has been altered by the release of artificially produced ^{129}I into the biosphere.

Most of the ^{129}I in soils and vegetation of the ALE Reserve has its origin in the fuel-reprocessing facilities located elsewhere on the Hanford Site. It was released to the air in controlled amounts, more or less continuously, during the operating years 1944 to 1972. In all, only about 0.46 curies were released (Anderson 1974).

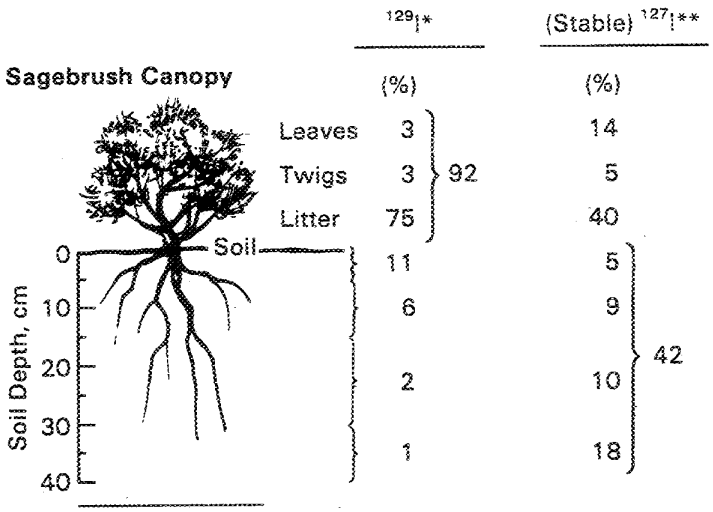
Two cheatgrass communities on the ALE Reserve were sampled for their concentrations of radioactive ^{129}I and stable ^{127}I. In addition, a sagebrush community was similarly sampled (Garland et al. 1983). The cheatgrass communities were located at elevations of 520 and 320 meters above mean sea level; the sagebrush community was located at an elevation of 240 meters. All locations were within a distance of 15 kilometers of the radiochemical processing facility.

Samples of plant parts and soil were chemically analyzed and measured for both ^{129}I and ^{127}I by mass spectroscopy (Brauer and Strebin 1979), and the resulting concentrations of iodine were converted to distribution percentages. Radioiodine concentrations were extremely low, not exceeding 40 fCi/g in sagebrush (which was located closest to the radiochemical

processing facility). The data show that ^{129}I concentrations were greatest in the litter and the upper 2.5 cm of soil (Figure 6.27). The greatest concentration of stable iodine was measured deep in the soil profile. The greatest concentration of stable iodine occurred at the highest elevation.

The present-day surface soils of the Hanford Site were strongly influenced by the land-shaping activity of the Spokane flood, which occurred about 16,000 years ago (U.S. Department of Interior 1976). The rooting substrate for plants at the low elevations of the ALE Reserve consists of fine-textured alluvial deposits layered over layers of gravels and cobbles. The rooting substrate at the high elevations is mostly fine-textured silt derived from loess and/or alluvial depositions layered over basalt. The differences in stable iodine as seen between the soil profiles at low and high elevations (Table 6.35) are undoubtedly due to differences inherent in the geological substrates and to geochemical equilibria controlling the availability of iodine to roots and other soil components (Garland et al. 1983). Airborne ^{129}I behaves differently in the plant-soil system than does the ^{127}I in the soil. Most of the ^{129}I found in the cheatgrass community has been delivered to sites as atmospheric deposition. The live and dead shoots of cheatgrass collect ^{129}I from the air. Although some externally impinged ^{129}I can probably enter the living leaves through stomatal apertures, most impingement is external.

The data clearly show a high affinity of airborne ^{129}I for plant foliage and litter (Figure 6.27). This affinity was most striking for sagebrush litter, compared to sagebrush leaves where the concentration was 24-fold



*Measured radioactivity ranged from 0.005 to 40 fCi/g

**Measured concentrations ranged from 0.4 to 3.0 pg/g
(Sagebrush data based on Gariand et. al., 1983)

FIGURE 6.27. Iodine Distributions for Sagebrush and Two Cheatgrass Communities

TABLE 6.35. Soil Profile Concentrations of (Stable)^{127}I Under Sagebrush and Cheatgrass Canopies at Three Elevations on the Hanford Site

Soil Profile Depth	Cheatgrass (520 m)	Cheatgrass (320 m)	Sagebrush (240 m)
(cm)	(ng/g)	(ng/g)	(ng/g)
0 - 2.5	600	520	150
10	720	410	310
25	---	---	340
35	---	---	580
60	2700	1300	---

(The data are for the same samples as are shown in Table 6.34)

higher in the litter. The chemical basis for this affinity of iodine for organic matrices is currently being investigated (also, see Wildung et al. 1974).

Foliar-impinged ^{129}I eventually reaches the ground as leaf-fall. It enters plant shoots via the soil → root → shoot uptake pathway. Stable iodine in cheatgrass shoots arises from both upper atmosphere and soil sources. With presently available observations, it is not possible to assign relative importance to these two pathways for stable iodine. Had the cheatgrass communities been actively recycling ^{127}I, one might expect that surface soil would be enriched in ^{127}I relative to deeper levels. This expectation does not appear to be the case.

CARBON-14 DENDROCHRONOLOGY IN SAGEBRUSH

Carbon-14 is a long-lived radionuclide (half-life 5,700 years). It occurs naturally, and it is also artificially produced at industrial facilities that process irradiated nuclear fuels, at operating nuclear reactors and during nuclear explosions. Carbon-14 is released into the air as carbon dioxide and it becomes available for incorporation into the cells of living plants during photosynthesis.

On the Hanford Site, ^{14}C has been released to the air through stacks at the REDOX and PUREX fuel-reprocessing facilities. In order to determine the ^{14}C concentrations in known-age wood of big sagebrush shrubs were collected at locations near and far from the chemical processing facilities on the Hanford Site. Concentrations of ^{14}C in wood were correlated with the pre- and post-operational years of the chemical processing plants and their shutdown in 1972.

One study location was on the Hanford Site, 0.5 kilometers east of the PUREX facility. Another was located offsite, 60 kilometers west, near the town of Moxee; and a third was located 26 kilometers southwest, near the town

of Benton City. At each study location, 10 sagebrush shrubs were cut off near the ground with a hand saw. A portion of the woody stem was saved for analysis and cut into a 2.5-centimeter cross section. The age of the stem was determined by counting the annual growth rings, and wood of certain age classes was carefully cut from the section with a knife. Ten grams of wood from each shrub were submitted for ^{14}C analysis.

The ^{14}C concentration in the wood from sagebrush shrubs growing close to the PUREX facility was enhanced during the years of facility operation. When the PUREX facility was closed in 1972, the ^{14}C concentrations in wood promptly declined to pre-PUREX levels. Sagebrush wood at the Benton City offsite location did not show increased ^{14}C concentrations during the years of PUREX operations (Table 6.36). The slightly enhanced values at the offsite locations since 1944 are probably due to ^{14}C-enriched carbon dioxide levels introduced on a global scale by nuclear weapons testing.

Carbon-14 was introduced into the air at the Hanford Site during operation of the PUREX chemical processing facilities. It occurs in the wood of big sagebrush, and probably other species of desert shrubs and trees on the Hanford Site as well. It can be returned to the air as CO_2 during plant respiration and also during microbial decomposition of dead plants. Plant-incorporated ^{14}C can also be released into the air during burning of sagebrush and other plants. The long half-life of ^{14}C indicates that artificially produced ^{14}C will participate in the carbon cycles of terrestrial and aquatic ecosystems for centuries.

TABLE 6.36. Average ^{14}C Concentrations (dpm/g Carbon) in Wood of Known Age from Big Sagebrush Shrubs at Three Locations in Southcentral Washington

Wood from Moxee	Wood from Benton City	Wood from the Hanford Site
Pre-1944	Pre-1944	Pre-1944
13.2	13.3	13.6
----	1945-1972	1945-1955
----	16.6	12.7
----	----	1956-1972
		67.2
1945-1978	1973-1978	1973-1979
17.8	18	17.2

Section IV. Summary

A portion of an extensive sagebrush-bunchgrass community on the Hanford Site in southcentral Washington was sampled to obtain estimates of annual shoot production. The chosen community is a remnant of a once-extensive vegetation type and it probably botanically resembles those communities that existed in the early 1800's, before the advent of livestock grazing and cultivated agriculture. Shoot production is low compared to other kinds of grass-dominated plant communities in other semi-arid regions of the western United States, indicating the harshness of the shrub-steppe environment particularly a long, hot, dry summer and occasional cold winters.

Livestock grazing that began in the mid-1800's was the first human-induced perturbation with region-wide impacts. Excessive grazing encouraged cheatgrass invasions. Three consecutive years of experimental cattle grazing beginning in a relatively undisturbed sagebrush-bunchgrass community did not impair the capacity of the community to sustain herbaceous shoot production, but trampling opened the community to invasion by cheatgrass and other alien annuals and impaired seed production of perennial grasses.

Plowing the sagebrush-bunchgrass community to raise dryland wheat in the 1870's created a second human-induced disturbance of regional magnitude. Thousands of hectares of sagebrush and native grasses were destroyed by plowing, and many of these fields are still farmed today. Because productive wheatland is seldom allowed to remain idle long enough to study the secondary plant succession process, there are few data on the natural rate of re-invasion by the native species, especially when good stands of native species are nearby and provide seed sources. On the ALE Reserve, abandoned dryland wheatfields

are now 40 years old, and they are still dominated by cheatgrass. Those communities produce three to four times more shoot biomass than the sagebrush-bunchgrass communities. Shoot production in cheatgrass communities varies greatly from year to year. Nevertheless, the data tend to support the hypothesis that cheatgrass communities are among the most efficient rangeland communities in the semi-arid and arid regions of the western United States, at least in terms of shoot biomass produced per centimeter of precipitation.

Wildfires are naturally occurring events in sagebrush-bunchgrass communities. Sagebrush is very sensitive to summer burning, but the herbaceous plants are resistant. Cheatgrass communities usually recover quickly after summer burning.

Greasewood differs from all other shrubs on the Hanford Site by accumulating sodium in its leaves. Over long periods of time, leaf fall and decay contributes additional nitrogen and sodium to the soil beneath greasewood canopies. In experimental studies, cheatgrass yields were increased when grown in the greasewood-influenced soil. Clearly, the beneficial effects of increased soil nitrogen offset the deleterious effects of soil sodium. Greasewood also promptly recovers from summer burning, so that the shrubs can maintain their position on the land for centuries. This stability provides an unusual opportunity to assess the role of long-lived shrubs in altering soil chemistry within their canopy spread.

Nitrogen and phosphorus are scarce resources in soils of arid and semi-arid lands; and when soil water is adequate for growth, the availability of those elements constrains shoot production. Because cheatgrass communities are more productive than sagebrush-bunchgrass communities, they also accumulate more N and P. It is especially important for cheatgrass communities to recycle

N and P from the dead roots shoots to the soil in a timely fashion in order to sustain production. Decomposition studies have shown that about 35 percent of the annual shoot production disappears in the first year; hence, a 3-year interval for mineral return could be inferred (see Chapter 4). Nevertheless, one of the most poorly known aspects of community production is mineral cycling.

In wet years, soil water below 4 decimeters is not fully exploited by cheatgrass (Cline et al. 1977). Only in dry years, when soil water has failed to penetrate below the 5-decimeter profile, is shoot production limited primarily by the scarcity of water, rather than by temperature or nitrogen.

Interrelationships among the factors controlling vegetational productivity were examined by Uresk et al. (1979). Biomass production, N content, soil water content, and soil temperature values collected on the same plot over 5 years were analyzed. From the initiation of growth to peak production of cheatgrass in the interval from April to May, soil temperature and N content showed a strong relationship to biomass production (Figure 6.28). For example, 44 percent of the variation in daily growth was accounted for by soil temperature during this interval; and, when N as well as soil temperature was taken into account, 77 percent of the variation was accounted for. A stepwise multiple regression model was used to analyze the multiple factor interactions. Only during the accelerated growth interval, from April to May, did soil water show a significant relationship with growth rates, and this was observed for a profile depth of 9 decimeters. In the period of senescence, soil water was no longer correlated, and soil temperature became the dominant factor.

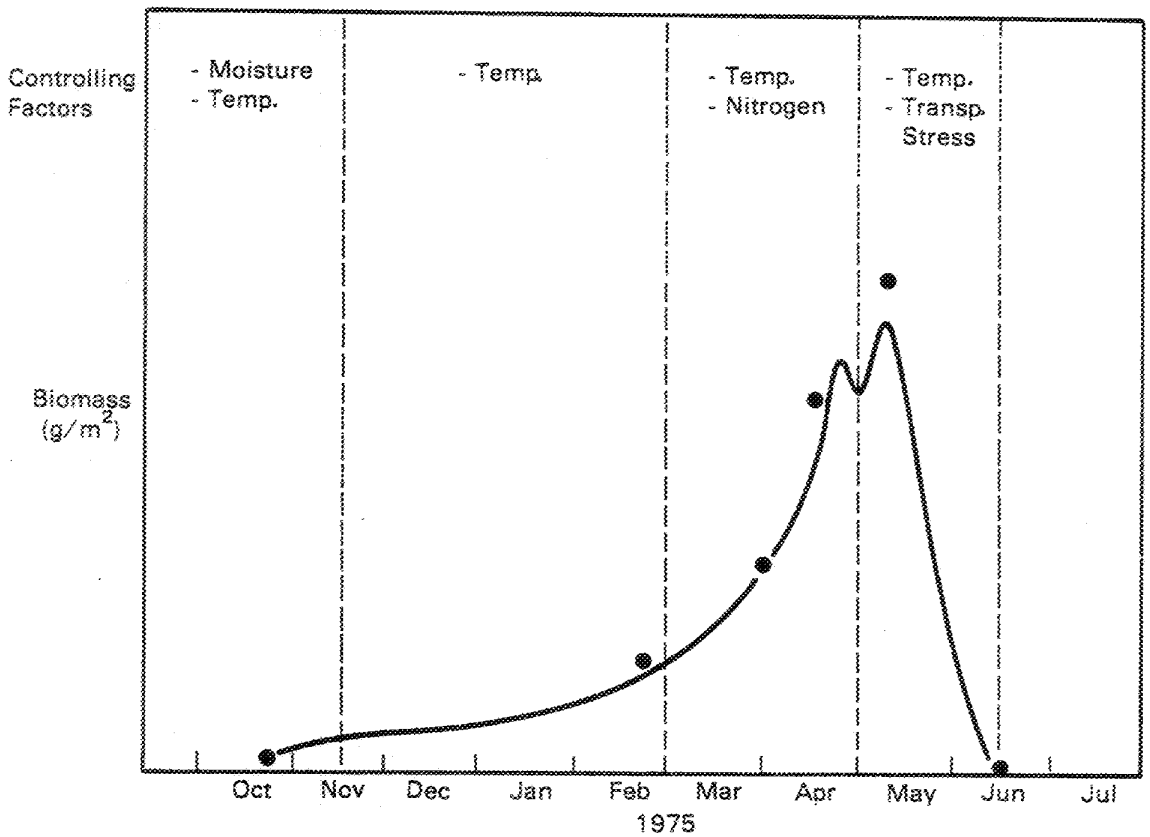


FIGURE 6.28. Factors Most Influential in Estimating the Growth of Cheatgrass at Different Points in the Seasonal Cycle [Factors are shown in relation to actual biomass data (.) and modeled data (-); dominant factors are based on a stepwise multiple regression model.]

There are many gaps in the available data sets needed for a more complete understanding of the functional aspects of sagebrush-bunchgrass and cheatgrass plant communities on a landscape scale. In general, the belowground dynamics of organic matter production and mineral nutrient behavior are poorly known, as are the rates of decomposition of dead plants and the rates of releases of nutrient mineral elements to the soil from dead plants and litter. Almost all the information obtained to date has been on plant communities rooted in non-stony soils located on gentle slopes. Nevertheless, much of the

shrub-steppe region consists of steep slopes and stony soils with different kinds of plant communities composition than those treated in this chapter.

A small-scale field experiment has been described in which the plant rooting substrate is controlled and the plants' microclimate is manipulated by growing plants on paired north-and south-slope exposures. In this way the effect of the rooting media is separate from the effects on plant growth induced by microclimate. The great effect of microclimate on the growth of cheatgrass was demonstrated under conditions of realistic sun, wind and temperate regimens associated with complex topography.

Radionuclides as tracers have been useful in several ways: 1) to measure the upward movement of ^{90}Sr to surface soil by root uptake processes, 2) to determine the dominance of foliar impingement and retention of airborne radioactive iodine from chronic low-level industrial releases, 3) to document the capture of $^{14}CO_2$ by radiocarbon analysis of known age sagebrush wood, and 4) to determine the magnitude of the wind resuspension pathway of $^{239-240}Pu$ contamination of foliar surfaces.

Future research needs to be directed towards understanding the role of landscapes (watersheds) in regulating surface and groundwater flows. Also in need of additional study are the roles of plants and plant communities in the evapotranspiration process, in soil erosion, and in the process of repairing damaged plant communities following different kinds of perturbations and stresses imposed on plant communities by various industrial and agricultural operations acting in concert.

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CHAPTER 8. THEORETICAL PERSPECTIVE ON ECOSYSTEM DISTURBANCE AND RECOVERY

P. A. Beedlow, P. Van Voris and L. E. Rogers

CHAPTER 7. TERRESTRIAL ANIMAL HABITATS AND POPULATION RESPONSES

L. E. Rogers, R. E. Fitzner, L. L. Cadwell and B. E. Vaughan

CHAPTER 7. TERRESTRIAL ANIMAL HABITATS AND POPULATION RESPONSES

L. E. Rogers, R. E. Fitzner, L. L. Cadwell and B. E. Vaughan

This chapter is about the animals that inhabit the shrub-steppe and how they cope with the harsh climate (cold winters and hot, dry summers), frequent wildfires, relatively low amounts of vegetative cover, and a pervasive, intruding, alien plant, cheatgrass. A final topic addresses the role of animals in environmental surveillance and as vectors of contaminant transport.

The problems of existence in the shrub-steppe are clearly exhibited by the relative sparseness of animal life. For example, the nesting passerine birds and microtine rodents, which are usually found in wide variety elsewhere, are represented in the shrub-steppe by only a few species. More importantly, while there is a wide range in body size for shrub-steppe animals, the balance between large animal and small animal biomass is tilted markedly towards the small ones such as rodents, and insects. In fact, insects and related arthropods are the dominant consumers of primary production. As shown in Figure 7.1, insect consumers from a shortgrass prairie site comprised over 80% of the first-level consumer component. This finding was also confirmed in studies on the ALE Reserve (L. E. Rogers, unpublished).

The abundance of larger animals in the shrub-steppe is largely controlled by the nature of their habitat, and habitat can be markedly altered by human intrusion. During 40 years of operation at one of the nation's major nuclear energy facilities, the impact of human intrusion has been minimal, so that the Hanford Site offers an attractive refuge for larger animal life. However,

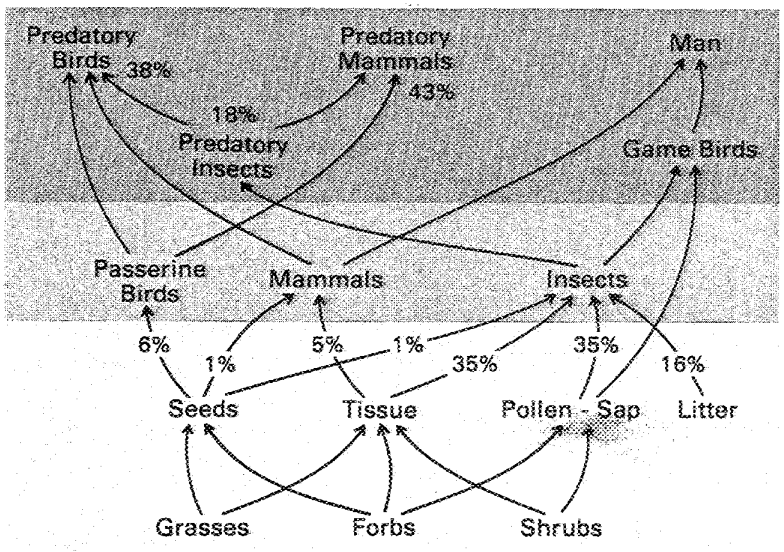

FIGURE 7.1. Consumption by Consumers from a Shortgrass Prairie Site (Data taken from Scott et al. 1979, Table 5.2.)

wildlife management options must sometimes be considered because of the large site; also, unexpected responses have sometimes occurred where habit modification or predator suppression has been instituted. For proposed controls to be effective, accurate information is needed on the habitat, the populations, and the ecosystem relationships of the animals.

Section I. Mammals and Reptiles

Mammals inhabiting the Hanford Site range in size from very large to very small (Figure 7.2). The large mammals are represented by deer and elk. They have considerable ability to move, and they usually travel over large areas in search of food and concealment cover. The mid-sized mammals are coyotes, bobcats and badgers, rabbits and hares. These mammals are also mobile, but their ranges, with the exception of bobcats and coyotes, are generally much smaller than those of deer and elk. Small mammals--mice, shrews, voles and ground squirrels--have limited home ranges, but their populations are usually large in contrast to the larger mammals. Mammals found on the Hanford Site are listed below along with their habitats.

Mammals Known to Inhabit the Hanford Site and Their General Habitat Preferences

Mammals That Use Several Terrestrial Habitats

Elk	*Cervus elaphus*
Mule deer	*Odocoileus hemionus*
Coyote	*Canis latrans*
Badger	*Taxidea taxus*
Deer mouse	*Peromyscus maniculatus*
Cottontail	*Sylvilagus nuttalli*

Mammals That Use Aquatic and Streamside Habitats

Raccoon	*Procyon lotor*
Muskrat	*Ondatra zibethica*
Porcupine	*Erethizon dorsatum*
Montane meadow mouse	*Microtus montanus*
Vagrant shrew	*Sorex vagrans*
Beaver	*Castor canadensis*
House mouse	*Mus musculus*
Weasel	*Mustela frenata*

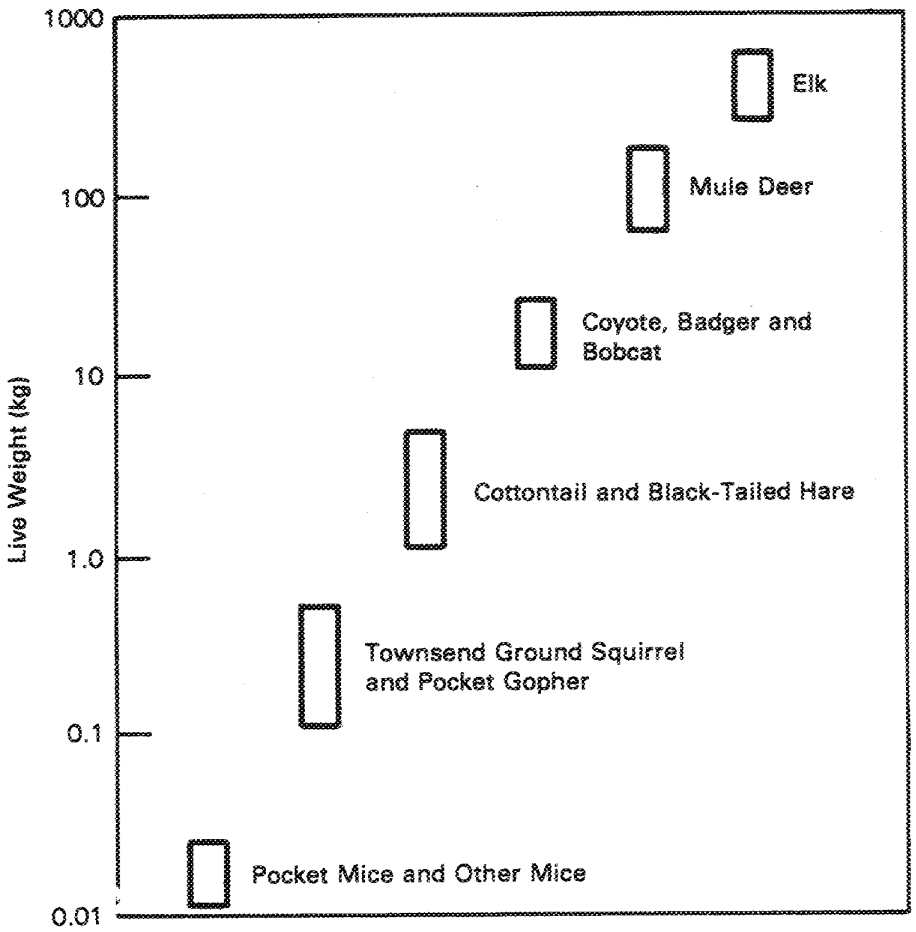

FIGURE 7.2. Weights of Mature Terrestrial Mammals on the Hanford Site

Mammals That Use Shrub-Steppe (Dryland) Habitats

Merriam's shrew	*Sorex merriami*
Bushy-tailed woodrat	*Neotoma cinerea*
Grasshopper mouse	*Onychomys leucogaster*
Harvest mouse	*Reithrodontomys megalotis*
Sagebrush vole	*Lagurus curtatus*
Great basin pocket mouse	*Perognathus parvus*
Black-tailed jackrabbit	*Lepus californicus*
White-tailed jackrabbit	*Lepus townsendi*
Pocket gopher	*Thomomys talpoides*
Least chipmunk	*Eutamias minimus*
Yellow-bellied marmot	*Marmota flaviventris*
Townsend ground squirrel	*Spermophilus townsendi*

Mammals That Can Fly

Little brown bat	*Myotis lucifugus*
Yuma myotis	*Myotis yumanensis*
California myotis	*Myotis californicus*
Silver-haired bat	*Lasionycteris noctivagans*
Western pipistrel	*Pipistrellus hesperus*
Big brown bat	*Eptesicus fuscus*
Hoary bat	*Lasiurus cinereus*
Pallid bat	*Antrozous pallidus*

Small mammals have been favorite subjects for studies of population responses to human-induced changes in plant communities. In recent years, research attention has also been directed to acute and chronic releases of biologically hazardous chemicals from industrial facilities and their potential for accumulation by animals through food webs. Wild mammals, either as biotic vectors of chemical contaminants or as indicators of a quality environment, are subjects of increased attention.

Lizards and snakes of several species occur throughout the shrub-steppe region. Ho ever, only a few species inhabit the Hanford Site and little is known about their population behavior. Snakes are important as foods for nesting hawks, in this way they contribute to the maintenance of a breeding population of high-tropic-level birds.

LARGE MAMMALS: HABITATS AND POPULATIONS OF DEER AND ELK ON THE HANFORD SITE

Mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) are year-round residents of the Hanford Site, (Hedlund 1975, McCorquodale 1985a). The absence of a resident human population and presence of a conservative land use as practiced on the Hanford Site by the U.S. Department of Energy for 40 years are important factors in keeping the landscape acceptable as habitat suitable for breeding populations of elk and deer (Rickard et al. 1982). Mule deer can be encountered almost anywhere on the Hanford Site; however, populations are centered mostly along the shorelines of the Columbia River and in the Rattlesnake Hills (ALE Reserve). Elk confine themselves to the ALE Reserve (McCorquodale 1985a).

Before 1943, during years prior to Federal acquisition of the land and the relocation of the resident human population, there were probably very few resident mule deer on the Hanford Site. The population was suppressed to a low level by farmers because of potential damage by foraging deer to young orchard trees and field crops. Also, concealment cover on the Hanford Site was sparse, making mule deer especially vulnerable to shooting. Mule deer populations increased with the relocation of the resident human population and the cessation of livestock grazing. By the mid-1950's, mule deer were present in substantial numbers.

In 1959, a study was initiated to capture and tag mule deer fawns as a way to obtain information on their dispersal movements (Hedlund 1975). Fawn tagging continued each year until 1979. These studies showed that female deer swam from the mainland to Columbia River islands to give birth to their fawns, that some of the tagged deer eventually moved offsite and were killed

by hunters, and that most of the kills were made in Franklin County immediately across the Columbia River from the Hanford Site. In all, 346 fawns were captured and tagged. Of these, 23 were eventually killed by people (17 shot, 6 killed in collision with automobiles) and 2 drowned in offsite irrigation canals. Two other deer died from unknown causes. Coyotes were a major source of fawn mortality (Steigers and Flinders 1980).

Movement patterns of 37 radio-collared mule deer were studied in the years from 1980 to 1982 (Eberhardt et al. 1984). This study showed that the Columbia River was not a permanent barrier to deer movements. Eight of the 37 tagged deer crossed the river at least once, and one deer crossed the river at least eight times in a 19-month period. The average home range was 39.3 square kilometers.

One of the puzzling aspects of the mule deer population on the Hanford Site is its ability remain relatively stable in the absence of any human-induced population control (i.e., hunting). This suggests that coyote predation and migration may be sufficiently balanced with fawn production to sustain a steady-state population. Nevertheless, this hypothesis remains untested because there has been no systematic census of the mule deer population that included determinations of sex ratios, age composition or general health.

The diets of mule deer have not been studied in detail. However, some information on plant species composition has been obtained from microscopic analysis of fecal pellets (Uresk and Uresk 1980).

The presence of elk in the semi-arid steppe region of Washington during the 1800's was never established. Elk first appeared on the Hanford Site in 1972 (Rickard et al. 1977), most likely as stray animals from existing herds in the Cascade Mountains 100 miles to the north and west of the Hanford Site.

In a 3-year period, the population increased from 26 to 72. The home ranges of elk are closely matched by the existing boundaries of the ALE Reserve (McCorquodale 1985a). The ALE population is free from predator mortality, and calf survival is very high.

The self-establishment of a breeding elk population on the ALE Reserve provides an unusual opportunity to study elk behavior in a hot, dry, treeless region that provides a minimal amount of vegetative concealment or thermal cover. The absence of resident elk in the shrub-steppe region of eastern Washington in the 1800's led to a general concensus that the environment was too severe for elk; excessive summer heat, lack of thermal cover and a forage base of low nutritional quality were suggested as plausible explanations for the historic absence of these animals. The research findings to date indicate that the elk on the ALE Reserve have larger home ranges in comparison to animals inhabiting forested mountain regions that are generally regarded as "characteristic" elk habitat (McCorquodale 1985a). One of the practical observations concerning the ALE Reserve elk is that they reside there year-round and successfully reproduce on rangeland vegetation that is suitable for cattle grazing for only a few weeks in the spring (as noted in Chapter 6). Also, elk do not tend to concentrate their activities around the spring streams and trample the vegetation in the manner of cattle. Elk use most of the available area, even though much of the land is remote from watering places.

The absence of livestock grazing on the Hanford Site since 1968--and in some parts since 1943--has probably benefited both mule deer and elk populations by providing more forage per unit area than would be available if the forage base were shared with livestock.

Wildfire presents some threat to deer and elk. In 1984, the largest fire in the 40-year history of the Hanford Site burned 80 percent of the ALE Reserve and a large section of the adjacent Hanford Site. There were no observed mortalities to elk, but at least a few mule deer were killed by the fire as it swept across the entire expanse of Rattlesnake Hills. The recovery of herbaceous plants following the fire was similar to that described in Chapter 6. Elk foraged in the burned areas during the winter and spring after the fire but seemed to spend more time in the unburned sectors.

Bitterbrush (Purshia tridentata) is regarded as an important mule deer forage plant, and it is most abundant on the sandy soils at the low elevations on the Hanford Site (Rickard and Rogers 1983). However, bitterbrush is vulnerable to wildfire, and is slow to recolonize areas that are burned. Therefore its role as a forage plant can be greatly diminished for many years following a wildfire unless some artificial restoration is practiced.

The Hanford Site serves as a refuge for small, mostly isolated populations of elk and mule deer. The regional landscape is generally dominated by intensive agriculture and urbanization, into which intrusions by deer and elk are not welcome. In 40 years of operation on the Hanford Site, however, there has been no need to practice population controls to reduce the number of intrusions by mule deer into adjacent farms lands. Knowledge of the various factors contributing to the relative stability of the population would be of use to managers of national parks, wildlife refuges, military installations, and other lands that normally support mule deer populations, where a potential exists for population eruptions and subsequent expenditures for damages claimed by adjacent land owners.

In contrast to mule deer, the elk population is increasing, largely due to the lack of predation. Coyotes can prey on deer fawns but appear unable to take elk calves. Information is being gathered concerning the rate of increase, sex ratios, diets and behavioral characteristics of individual animals. If some form of artificial population control is needed in future years, an assessment of the appropriate size of the herd must be made to match the available forage resource with the optimal herd size.

MID-SIZED MAMMALS

Coyotes, Bobcats and Badgers

The bobcat (*Lynx rufus*), badger (*Taxidea taxus*), and coyote (*Canis latrans*) are the largest wild predators on the Hanford Site. These animals range across the entire Site, but there is essentially no information concerning their population densities.

Bobcats are present on the Hanford Site in low but unquantified numbers. It is thought that most of animals are located in the varied topography of the ALE Reserve but they have not been studied. Some related research has been documented at the Idaho National Engineering Laboratory in southeastern Idaho (Knick and Ball 1983).

Badger populations on the Hanford Site have not been studied. Badgers prey mostly on small mammals, which they capture by digging into burrows. The badger's diet, like the coyote's, undergoes seasonal changes. Messic and Hornocker (1981) reported that badgers in the shrub-steppe of southwestern Idaho fed mostly on Townsend ground squirrels. When ground squirrels entered summer dormancy and became unavailable, the intake of other prey species

increased. Other badger foods noted in that study were deer mice, black-tailed hares, Nuttall's cottontails, kangaroo rats, montane meadow voles, snakes and insects.

Only two coyote-related studies have been conducted. Stoel (1976) examined coyote feces as an indication of diet, and Springer (1982) studied coyote movements through the use of radiotelemetry. Stoel found that the proportions of food items identified in the feces collected in the lowland areas of the Hanford Site (at and below 170 meters elevation) were different from those of the higher elevations. In the lowland collections, the principal foods were Great Basin pocket mice, black-tailed hares and Nuttall's cottontails. Other food items, listed in decreasing abundance, were pocket gophers, grasshoppers, orchard fruit, deer mice, darkling beetles, birds, Townsend ground squirrels, reptiles, voles, and livestock. At the higher elevations, the coyote's diet was dominated by sagebrush voles and montane voles. Other foods, in decreasing order of abundance, were pocket gophers, Great Basin pocket mice, birds, rabbits, and Townsend ground squirrels. Minor contribution to diets were provided by bushy-tailed woodrats (Neotoma cinerea), grasshoppers, darkling beetles, orchard fruit, grass and deer. Coyotes clearly are opportunistic feeders and can take advantage of a great variety of foods that become seasonally or opportunistically available.

McCracken and Hansen (1983) studied diets of coyotes at the Idaho National Engineering Laboratory, and found a predominance of leporids. Nuttall's cottontails and blacktailed hares comprised, respectively, 56 and 23 percent of the coyote diet. Pocket mice contributed less than one percent. Differences

in coyote diets between Idaho and the Hanford Site appear to be a reflection of different food bases. At Hanford, unlike Idaho, small rodents are important coyote food.

Coyotes on the Hanford Site forage large areas, e.g., 89 square kilometers, but they also spend relatively large amounts of time in "core" areas of about 6 square kilometers (Springer 1982). One interesting observation was that coyotes learned to catch fish (Cyprinus carpio) that had become stranded in small pools of water following a sudden draw-down of river flow (Springer 1980).

There is much scientific and practical interest in understanding the relationships of coyote populations, their exploitation by people, and their responses to a changing food base. For example, the coyote population in Curlew Valley (on the Utah-Idaho border) is under extreme duress from sports hunters, fur trappers and professional predator trappers. Even in years of low black-tailed-hare densities, coyote diet in the Curlew Valley was 60-70 percent hares (Hoffman 1979). At the Idaho National Engineering Laboratory where there is little coyote exploitation, coyotes kill very few hares during years of low hare density (Stoddart 1983).

Coyotes have been persistently killed by ranchers, farmers, and hunters since the shrub-steppe region was first settled more than 100 years ago. However, they are opportunists, which helps explain how they have been able to maintain populations in a rapidly changing environment. They are also wary, quick to avoid poisons and traps. On occasion they can be destructive to domestic livestock, especially young sheep.

There is virtually no information concerning the behavioral characteristics, population dynamics, or age structure of "unexploited" coyote populations in the shrub-steppe region. This is unfortunate because exploitation is known

to influence population parameters for many wild mammal species. The ALE Reserve offers a rare opportunity to study the dynamics of a relatively unexploited coyote population inhabiting a large land area neither grazed by domestic livestock nor containing a resident human population. To be sure, trapping and hunting normally occur on the lands bordering the ALE Reserve, and some of the coyotes that are born on the Reserve are killed when they make forays onto adjacent private lands. It seems likely that coyotes born on the adjacent lands also migrate onto the ALE Reserve. However, the magnitudes of these movements are unknown.

Black-tailed Hares and Cottontails

Nuttall's cottontails (*Sylvilagus nuttalli*) and black-tailed hares (*Lepus californicus*) are the most common leporids in the entire shrub-steppe region. The cottontail population is scattered throughout the Hanford Site, but black-tailed hares are absent (or nearly so) from the slopes of Rattlesnake Hills at elevations greater than 400 meters above mean sea level. The absence of hares from the slopes of the Rattlesnake Hills is puzzling. It seems unlikely that the slightly cooler, moister microclimate associated with increasing elevation could entirely account for their absence. High and low elevations support different kinds of plant communities. Bluebunch wheatgrass is the dominant grass on the slopes of the Rattlesnake Hills while cheatgrass and Sandberg's bluegrass are the dominant grasses on the plain, but the significance of these vegetal and topographic changes to hare behavior, population distribution and densities is unknown.

The population distribution of black-tailed hares on the mostly level topography of the Idaho National Engineering Laboratory appears to be related

to the amount of grass cover. In a study by Johnson and Anderson (1983), the greatest numbers of hares were associated with the greatest amount of grass cover. French et al. (1976) reported that hares were most numerous in dense stands of desert shrubs.

Black-tailed hares have no capacity for digging into the ground or retreating into burrows to escape inclement weather. However, hares do seek shade beneath sagebrush shrubs. Haug (1969) believes that the shrubs protect hares from direct exposure to summer sunlight and also from predators.

A study of the diets of black-tailed hares on the Hanford Site indicated that they do not eat cheatgrass (Uresk 1978). Forbs were the preferred forage plants, with smaller amounts of grasses and shrubs. At the Idaho National Engineering laboratory, black-tailed hares ate a wide variety of plants especially perennial grasses of the genera Agropyron, Sitanion, Oryzopsis, Poa and Elymus (Johnson and Andersen 1983). Cheatgrass was sparsely represented, as were shrubs.

One of the main differences between the hare populations on the Hanford Site and those of southeastern Idaho is the absence of massive population eruptions on the Hanford Site. The reasons for this surprising lack have not been elucidated; such an investigation might provide some valuable insights into population control mechanisms for hares and related animals.

SMALL MAMMALS: POPULATION RESPONSES TO DISTURBANCE

It is reasonable to expect that small-mammal populations in a particular community will change as the plant species composition and vegetative structure of the community change in response to burning, plowing or livestock grazing. To be able to assess population responses to these kinds of habitat changes,

it is necessary to know the species composition and the seasonal fluctuations of small mammal populations before perturbations are imposed. Small mammals have been studied using a variety of techniques, but snap-trapping and live-trapping has been employed in most studies in the shrub-steppe region.

Relative Abundance in Undisturbed Sagebrush-Bunchgrass Communities

In a study of small mammal populations in a large, homogeneous sagebrush-bunchgrass community on the ALE Reserve, a permanent grid of 144 live traps was established inside a 9-hectare study plot. The traps were spaced 15 meters apart, creating a trap zone of 3.2 hectares. The traps were open for 3 days each month. Three species of small mammals were trapped frequently enough to provide an indication of their abundance and seasonal periodicity (Table 7.1). These were the Townsend ground squirrel (*Spermophilus townsendii*), deer mouse (*Peromyscus maniculatus*) and grasshopper mouse (*Onychomys leucogaster*). The sagebrush vole (*Lagurus curtatus*) was only trapped during one trapping session. The northern pocket gopher, *Thomomys talpoides*, occurred within the trap grids, but gophers were not captured in live traps.

The trap data show that pocket mice were above ground from March through September. They remained below ground during the winter months. Ground squirrels were most active from March through May. They retired below ground during the hottest months, July and August, and also during the coldest months, December and January. Deer mice and grasshopper mice were active above ground at all months of the year, but their numbers were much lower than those of pocket mice or ground squirrels.

TABLE 7.1. Total Numbers of Individual Small Mammals Captured in an Undisturbed Sagebrush-Bunchgrass Community Between January and November 1972

Month	Pocket Mouse	Ground Squirrel	Deer Mouse	Grasshopper Mouse	Sagebrush Vole
Jan	0 (0)	(0) 5	1 (100)	0 (29)	0 (0)
Mar	33 (590)	12 (2000)	11 (190)	3 (71)	3 (87)
Apr	48 (790)	38 (3300)	7 (130)	1 (24)	0 (0)
May	41 (700)	20 (2600)	2 (43)	0 (0)	0 (0)
July	35 (540)	0 (0)	0 (0)	0 (0)	0 (0)
Sept	30 (440)	0 (0)	0 (0)	0 (0)	0 (0)
Nov	2 (35)	0 (0)	0 (0)	2 (44)	0 (0)
Peak Capture	48 (790)	38 (3300)	11 (190)	3 (71)	3 (87)

( ) = biomass

In terms of biomass, ground squirrels were the most abundant small mammal, followed by pocket mice and deer mice (Table 7.1). The above-ground activity of ground squirrels was confined to the period of most active plant growth, March, April and May. Ground squirrels are diurnal feeders, and they eat new plant growth, especially Sandberg's bluegrass (Johnson 1975, Rogers and Gano 1980). Pocket mice are also important contributors to biomass. They are active throughout the hot, dry summer, but the activity is nocturnal, allowing pocket mice to avoid the heat of day. Pocket mice rely primarily upon seeds as sources of chemical energy and water (Schreiber 1973). The deer mouse is active above ground year-round. Its diet is varied and includes insects as well as plant materials (Johnson 1975, Kritzman 1974). Other small rodents play lesser roles. The grasshopper mouse is also active above ground in all seasons, but it is never very abundant. It feeds on insects and also has the ability to kill and eat other mice. The only microtine rodent in the community

is the sagebrush vole. However, other grass-dominated (steppe) communities in North America support microtines of the genus Microtus which are often the most abundant small mammals (French et al. 1976).

The small-mammal component of the sagebrush-bunchgrass community is represented by an herbivore (ground squirrel), a granivore (pocket mouse), an insectivore (grasshopper mouse), and an omnivore (deer mouse). Of these, the granivore population is by far the most numerous. In this respect, the sagebrush-bunchgrass community more resembles the creosote bush community of the southwestern desert than it does the meadow-steppe (grasslands) east of the Rocky Mountains.

Comparative Data for Cattle-Grazed Plots

One of the most widespread disturbances to sagebrush-bunchgrass communities is cattle grazing (Rickard 1985a). Nevertheless, the long-term effects of cattle grazing on small mammal populations are not very well known. Cattle grazing reduces the amount of standing dead grass and removes at least some of the current year's shoot production that otherwise would be available as forage for wild herbivores (Chapter 6). Grazing also interferes with seed production of palatable grasses and forbs, and it reduces the amount of seed available as food for granivores.

To determine its impact on small mammal populations, experimental cattle grazing was administered to a 9-hectare portion of a previously undisturbed sagebrush-bunchgrass community for 3 consecutive years (Rickard 1985a). Small mammals were trapped on the grazed and ungrazed portions of the community, and the arrangement and numbers of live traps were identical in each area. The trap catches indicated that pocket mouse and deer mouse populations declined

between 1971 and 1973 in both the grazed and ungrazed portions of the study community, while the ground squirrels tended to increase (Table 7.2). These data indicate that 3 years of cattle grazing did not substantially change the population.

In the years before the introduction of domestic livestock to the shrub-steppe region, i.e., mid-1800's, the most important vertebrate herbivores were probably small mammals. Large ungulates were either absent or poorly represented (McCorquodale 1985b). In this respect, the shrub-steppe is different from the meadow-steppe region along the eastern edge of the Rocky Mountains, where plant communities developed under heavy grazing imposed by large ungulates; i.e., bison. The plants and small mammals associated with

TABLE 7.2. Pocket Mice, Deer Mice and Ground Squirrels Captured on Grazed and Ungrazed Study Plots During a 3-Year Study[a]

Species	1971	1972	1973
		Ungrazed	
Pocket mouse	271	189	129
Deer mouse	48	21	20
Ground squirrel	39	70	51
		Grazed	
Pocket mouse	236	143	110
Deer mouse	58	27	18
Ground squirrel	11	47	66

(a) Recaptures are not included for the third year. Following the fire, the trapping schedule was continued (Hedlund and Rickard 1981).

the shrub-steppe region had not experienced grazing by large herbivores (cattle). If there had ever been any impact from cattle grazing in that region, it occurred in the years before enough was known about small mammals to even pose the question.

Response to Summer Wildfire

Wildfire is a recurring event in shrub-steppe plant communities (Daubenmire 1968). Sagebrush-bunchgrass communities are especially vulnerable to wildfire in mid-summer when plants are dried, daytime temperatures are hot, and lightning storms occur with little accompanying rainfall. Summer wildfire kills sagebrush plants, but it destroys only the above-ground parts of herbaceous plants. Most herbaceous plants that survive summer burning send out new growth with the onset of autumn rains. Herbaceous shoot production is largely restored in the first season after burning.

A live-trap study of small mammals had been conducted for three consecutive years in a sagebrush-bunchgrass community on the ALE Reserve. The community was burned in late summer of 1973, the pocket mice emerging from their burrows after the fire were trapped until the onset of winter. In the spring, pocket mice were trapped in about the same numbers as during the previous spring. The trap catch declined with the onset of summer as it had during the years prior to burning. In September, larger numbers of juveniles were trapped than in the previous years (Figure 7.3). The young of the year were breeding, and the influx of juveniles added to the summer trap catch. This surge in population should not be attributed to burning. Increased precipitation in the 1973-1974 growing season contributed to increased shoot yields, and this was the likely impetus for the increased catches of pocket mice (Hedlund and

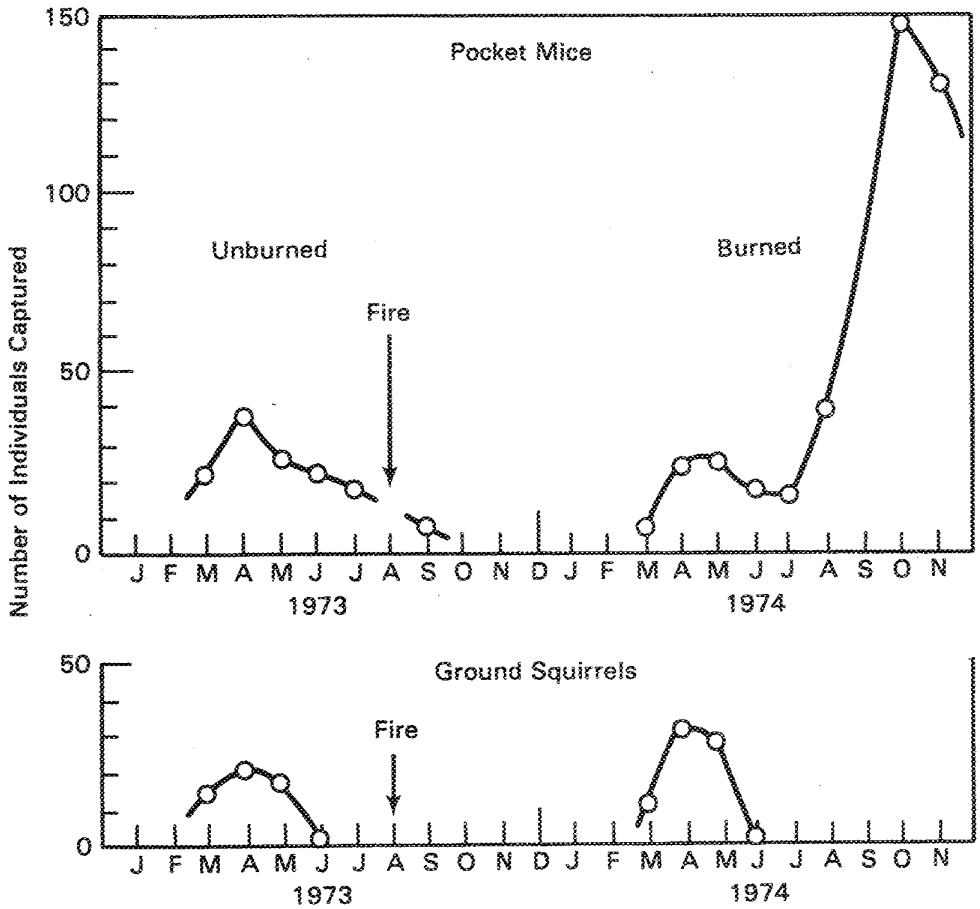

FIGURE 7.3. Total Numbers of Small Mammals Trapped in Burned and Unburned Sagebrush-Bunchgrass Communities on the ALE Reserve in the First Year Following Summer Wildfire

Rickard 1981). Fire *per se* was probably not responsible for the population surge; a surge was also observed in the adjacent, unburned portion of the community. Similar population surges were reported for other years by O'Farrell (1975). The factors responsible for population surges in desert rodent populations are not fully understood (Brown 1973).

The ground squirrel population, like the pocket mouse population, responded to the weather-induced increase in shoot production during the year following summer burning (Table 7.2). The deer mice and sagebrush voles were not trapped

in sufficient numbers to make reliable inferences about their response to summer burning. However, individually tagged deer mice remained on the study plot in the months after burning, and the trap catches showed no apparent increase or decrease that could be attributed to burning.

At the time of the wildfire, ground squirrels were in hibernation. When they emerged from their burrows in late winter (February-March), the new shoot growth of herbaceous plants--especially Sandberg's bluegrass--was available for eating as it had been in the years before burning. Pocket mice were mostly in hibernation or remained in their burrows during summer daytime hours, so they were well protected from burning mortality. In the following spring, they emerged from their winter hibernation and probably found seeds that did not burn, still on the ground and available. New seed became available throughout the spring as the surviving plants flowered and set seeds. Consequently, the ground squirrel and pocket mouse populations were not significantly affected by the summer wildfire.

Response in Cheatgrass Successional Community

Long-time-abandoned agricultural fields are scarce in southeastern Washington because even the nonirrigated land is productive for wheat farming. In the few cases where wheat fields have been abandoned, they have been quickly vegetated by a dense stand of alien annuals, especially cheatgrass and tumble mustard. On the ALE Reserve, such alien annuals have maintained vegetative dominance for decades, providing a different habitat for small mammals than do the sagebrush-bunchgrass communities. Small-mammal populations were studied in two 30-year-old cheatgrass communities and two adjacent sagebrush-bunchgrass communities. A grid system of 100 live traps spaced at 10-meter intervals

was used for 3 consecutive days, four times during the year (March, June, August and November) (Table 7.3). More animals were caught in the sagebrush-bunchgrass community than in the cheatgrass community, 283 as compared to 89. However, the taxonomic composition of the catch was the same in both communities except for the capture of a single house mouse (Mus musculus) in the cheatgrass community. Ground squirrels were not captured in either community and probably did not occur there. The presence of digs suggested that pocket gophers were present, but they were not trappable. In the sagebrush-bunchgrass community, 82 percent of the trapped animals were pocket mice; this compares with 75 percent in the cheatgrass community. Deer mice made up 10 percent of the catch in the sagebrush-bunchgrass community and only 2 percent in the cheatgrass community. In contrast, harvest mice contributed 5 percent of the total catch in the sagebrush-bunchgrass community, compared to 15 percent in the cheatgrass community. These proportions suggest that harvest mouse populations may be favored over deer mouse populations.

TABLE 7.3. Small Mammals Captured in Cheatgrass Communities and Adjacent Sagebrush-Bunchgrass Communities on the ALE Reserve, November 1978 to August 1980 (8000 trap nights per community)

Plant	Pocket Mouse	Deer Mouse	Harvest Mouse[a]	House Mouse	Montane Vole	Merriam's Shrew	Community Total
Cheatgrass	67(75)[b]	2(2)	12(15)	1	1	3	88
Sagebrush-Bunchgrass	231(82)	29(10)	15(5)	0	3	2	283

(a) Introduced Eurasian species.
(b) () = % of total.

As noted in Chapter 6, the cheatgrass community has fewer plant taxa than the sagebrush-bunchgrass community. Vegetational structure of the two communities also differs. Cheatgrass communities have a large number of plant stems per unit area. The stems are spaced so that there is little room for the movement by small mammals without touching stems. In contrast, the plants of the sagebrush-bunchgrass community are widely spaced (number of plants per unit area is low) with much open ground between plants. It would seem to be much easier for small mammals to move through a sagebrush-bunchgrass community than through a cheatgrass community. According to data presented in Chapter 6, cheatgrass communities are also much more productive in terms of shoot biomass and seed production.

The cheatgrass community appears to provide a habitat that is suitable for most if not all of the native species of small mammals that live in sagebrush-bunchgrass communities. However, their populations appear to be suppressed in cheatgrass communities. Pocket mice eat cheatgrass seed (Schreiber 1973). With the great abundance of seeds that can be produced in cheatgrass communities, especially those communities that are not grazed by livestock, there should be greater numbers of pocket mice in the cheatgrass communities if food supply is the limiting factor. However, the smaller trap catches in the cheatgrass community indicate that factors other than seed abundance (food) are involved. Perhaps the quality of forage is too low to sustain "normal" pocket mouse reproduction. Or pocket mice may be more vulnerable to predation while living in cheatgrass communities. Or, perhaps, "trappability" in cheatgrass communities, is simply much less efficient than in sagebrush-bunchgrass communities and the low trap catch is an artifact of the method. These kinds of questions must be addressed in order to obtain a

better understanding of the responses of small mammals to various human-induced perturbations. Such perturbations have altered plant communities over vast areas of the shrub-steppe region during the past 100 years and are continuing at the present time.

Relationships to the Larger Shrub-Steppe Region

The pocket mouse is by far the most abundant small mammal on the Hanford Site, and it occurs throughout the altitudinal gradient (O'Farrell 1975).

As shown in Table 7.4, it has dominated the trap catches in low altitude bitterbrush-sagebrush/cheatgrass, sagebrush-bunchgrass, and cheatgrass communities (Gano and Rickard 1982, Rogers and Hedlund 1980, Hedlund et al. 1975, O'Farrell et al. 1975).

In contrast, Table 7.5 shows trap catches of small mammals at the Idaho National Engineering Laboratory (INEL) to be dominated by deer mice. Although the plant communities at these sites are similar in floristic composition and vegetational structure, the fact that pocket mouse populations flourish on the Hanford Site suggests that an advantage is offered by its more moderate winter climate and lower altitude.

The hypothesis that cold winter temperature is the controlling factor for pocket mouse dominance is supported by the studies of O'Farrell (1975). With increasing elevation, pocket mouse catches declined and deer mice dominated the trap catches (Figure 7.4).

O'Farrell et al. (1975) thoroughly described the dynamics of a pocket mouse population on the ALE Reserve. Population was estimated from trap capture data by the Jolly-Seber stochastic model; for pocket mice on a 2.7-hectare grid it was 320 animals (1.8 kg/ha). Figure 7.5 displays data

TABLE 7.4. Percent Composition of Trap Catches of Small Mammals at Five Low-Altitude Locations on the Hanford Site

Species	Bitterbrush-Cheatgrass	Cheatgrass	Sagebrush-Cheatgrass	Sagebrush-Cheatgrass	Cheatgrass
Pocket mouse	84	84	83	91	89
Deer mouse	12	11	7	8	10
Grasshopper mouse	2	4	0	<1	<1
Harvest mouse	1	<1	0	<1	0

TABLE 7.5. Percent Composition of Trap Catches of Small Mammals in Different Plant Communities at the Idaho National Engineering Laboratory (Groves and Keller 1983)

	Plant Community		
Species	Sagebrush-Bunchgrass	Crested Wheatgrass	Russian Thistle
Deer Mouse	51	45	87
Ground Squirrel	17	6	<1
Chipmunk	12	0	0
Kangaroo Rat	10	10	23
Pocket Mouse	6	6	0
Montane Vole	3	31	0
Harvest Mouse	<1	<1	0
Grasshopper Mouse	<1	<1	0
Sagebrush Vole	<1	0	0

for total trap catches from this study. Over the 5-year study period, the estimated population ranged between 206 and 437. This represents a relatively small population fluctuation as compared to other kinds of small-mammal populations (Keller and Krebs 1970).

Subadults first appeared in the trap catches in June, and they usually dominated catches throughout the summer. Many of the adults retired below ground early in the summer, leaving the juveniles to forage without competition. In September, only 13 percent of the trapped animals were adults.

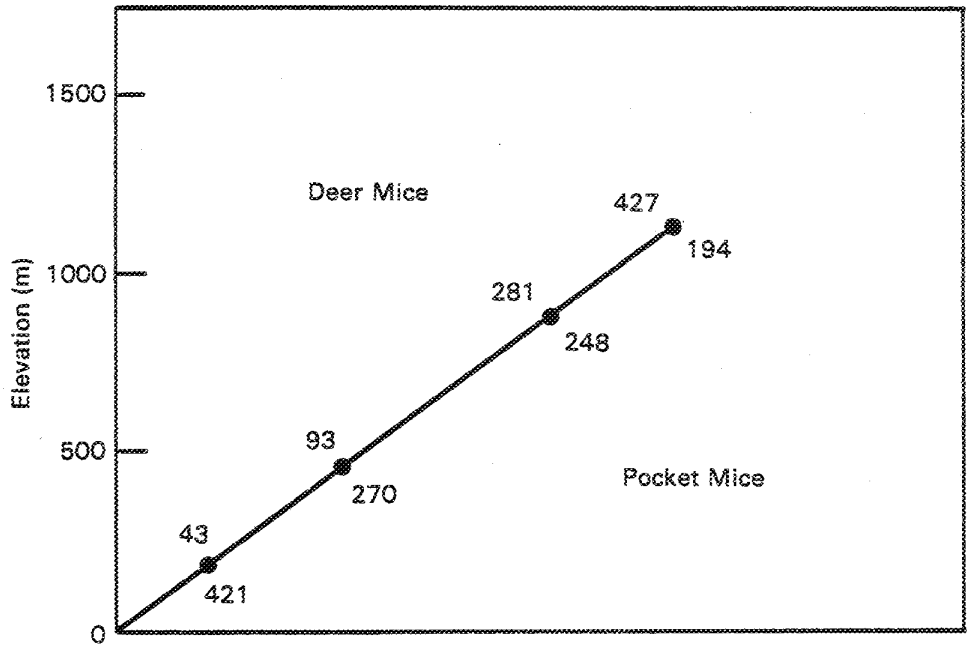

FIGURE 7.4. Trap Catches of Pocket Mice and Deer Mice with Increasing Elevation in the Rattlesnake Hills, Hanford Site (O'Farrell 1975)

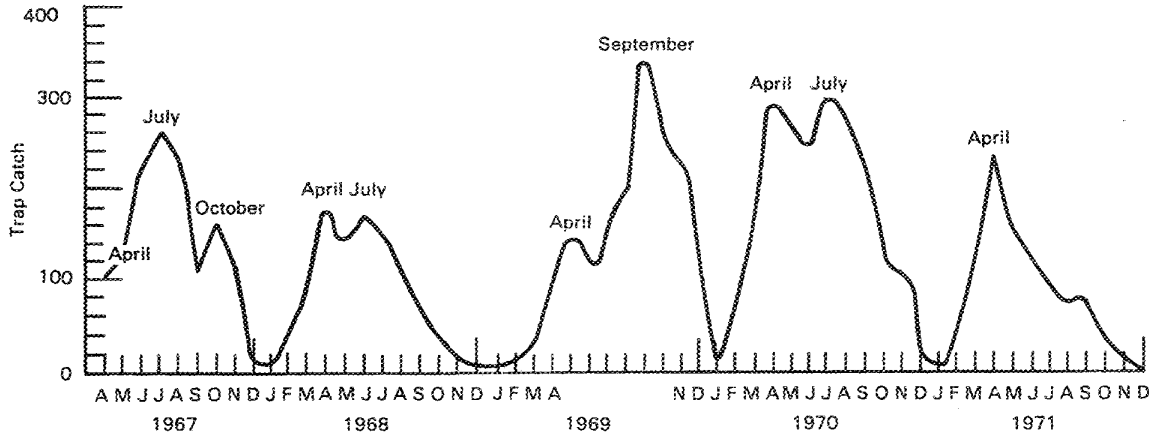

FIGURE 7.5. Monthly Trap Catches of Pocket Mice in the Same Study Plot in the Years 1967-71, Showing Months of Peak Trap Catches (Data from O'Farrell et al. 1975)

Male pocket mice characteristically emerged from winter torpor earlier in the year than females, but the behavioral significance of this is unknown.

The home ranges of males were larger than those of females, 1560-4000 square meters for males and 508-2301 square meters for females.

The study suggested that pocket mice have evolved strategies for survival that include temporal and spatial isolation of sexes and also of juveniles. This may reduce the frequencies of social contacts between individuals and help to reduce intraspecies conflict in the overall population structure (O'Farrell et al. 1975). Pocket mice are relatively long-lived compared to other small mammals, and their longevity may also contribute to population stability. According to O'Farrell et al., one of the least known aspects of the life history of pocket mice is the amount of time they spend below ground. Presumably, they are then in a state of torpor, their metabolic rate is diminished, and their energy is conserved.

The inadvertent introduction of alien winter annuals to the ALE Reserve a century ago may have had an effect on local populations of pocket mice, especially in those habitats that support cheatgrass as the dominant understory species to sagebrush. In the undisturbed sagebrush-bunchgrass community, as noted in Chapter 6, seeds are ripened over a relatively long period of time, i.e., April through November. In cheatgrass communities, however, ripe seeds are produced in a surge, in late May or early June. The effect of this sudden and abundant seed ripening upon pocket mice populations has not been systematically investigated. However, opportunity for such studies occurs where native plant communities and cheatgrass communities exist in close proximity to each other, with similar soils and microclimates.

Conclusions

Small mammals in the shrub-steppe region of eastern Washington seldom reach population densities that are injurious to vegetation and therefore deprive domestic livestock of forage. However, ground squirrels living near irrigated alfalfa fields can damage the crop, and population control is sometimes practiced. While pocket mice eat some wheat grains from dryland wheat fields, their overall economic damage to crops cannot be significant because of their low population densities. The conversion of native shrub-steppe vegetation to agricultural fields has been damaging to the overall population of ground squirrels, pocket mice, sagebrush voles and grasshopper mice. Deer mice and pocket gophers are probably more adaptable to agricultural land uses than the other small mammals.

The introduction of alien annual plants has changed the quality and quantity of plant foods available to small mammals. Cheatgrass communities apparently do not support as many small mammals as do the native sagebrush-bunchgrass communities, even though seed supplies are greater in the cheatgrass community.

Cattle and sheep grazing has probably not been an important force in changing the species composition of small mammals in sagebrush-bunchgrass communities. However, it may have had some impact on overall population densities.

Wildfires are natural events in sagebrush-bunchgrass communities, and it is reasonable to expect that small mammals have evolved behavioral adaptations that enhance their ability to survive the periodic burning of these communities. Indeed, small mammals, especially pocket mice and ground squirrels, are well adapted to survive the burning of plant communities,

although there may be some persistent impacts on deer mouse and grasshopper mouse populations in terms of food and concealment cover following the destruction of sagebrush shrubs. By retreating to their burrows, the mice and squirrels avoid immediate mortality. Following a summer burn, ground squirrels and pocket mice have a distinct advantage by entering winter torpor. Their food requirements are thus greatly reduced during a time of year when other small mammals, i.e., deer mice and grasshopper mice, require the usual food intake to maintain normal metabolic functions. The long time alloted to winter torpor allows the vegetation to undergo autummn-winter plant growth that is availiable as forage when the animals emerge in the spring.

SNAKES AND LIZARDS ON THE HANFORD SITE

As compared to the southern deserts, there are relatively few species of lizards and snakes in the shrub-steppe region, although snakes are important as prey for nesting raptors, especially Swainson's hawks. The snakes and lizard species inhabiting the Hanford Site are listed below.

Snakes and Lizards of Shrub-Steppe Habitats

Yellow-bellied racer	*Coluber constrictor*
Gopher snake	*Pituophis catenifer*
Western rattlesnake	*Crotalus viridis*
Desert night snake	*Hypsiglena torquata*
Striped whipsnake	*Masticophis taeniatus*
Side-blotched lizard	*Uta stansburiana*
Sagebrush lizard	*Scleoporus graciosus*
Short-horned lizard	*Phrynosoma douglasii*

Snakes of Riverine Habitats

Garter snake *Thamnophis sirtalis*

Snakes and lizards are active in the spring and summer months, but they retreat to dens in autumn and winter. Yellow-bellied racers, rattlesnakes and gopher snakes probably rely on pocket mice as a primary source of prey, but their food habits have not been confirmed through observations.

Garter snakes are confined to shorelines of the Columbia River. The yellow-bellied racer, western rattlesnake and gopher snake have been observed at locations scattered throughout the Hanford Site. The desert night snake and the striped whipsnake are rarely observed, and little is known about their distribution. The side-blotched lizard is the most abundant lizard on the Hanford Site. Its population is confined to the lower altitudes (Rickard 1968). The short-horned lizard ranges throughout the elevational gradient, but the sagebrush lizard appears to be limited to stabilized sand dunes at low elevations.

The cold winters of the shrub-steppe apparently are a major constraint to its occupancy by many species of terrestrial North American reptiles. By comparison, the winter climate at INEL is more extreme than that of the Hanford Site; the INEL area supports small populations of both the leopard lizard (*Crotophytus wizlesinii*) and the western skink (*Eumeces skiltonianus*), lizards that do not occur on the Hanford Site. However, there are apparently no side-blotched lizards or yellow-bellied racers on the Idaho site (Sehman and Linder 1978) as there are on the Hanford Site.

Section II. Birds

Birds are probably the most visible and readily recognized wild animals in the shrub-steppe region. The diversity of terrain (sand dunes, rock outcrops and cliffs, lakes and rivers) provides a great variety of bird habitats.

People generally show more interest in birds than in other wild animals. Many of the shrub-steppe species can be readily seen almost anywhere, e.g., meadowlarks and horned larks. Others, such as the mourning dove, chukar, and ducks and geese, are important as game animals. Some birds serve as indicators of environmental change. For example, an increase in starlings reflects the presence of human-manipulated habitats, and a decrease in sage sparrows reflects the loss or alteration of sagebrush-dominated habitats.

Birds are highly mobile, but their movements are restricted during the nesting season. Territory selection and defense, nest building, egg-laying, incubation and feeding the young occupies the full-time attention of parent birds for several weeks. After the young are fledged, the fledglings and parent birds disperse, often in loosely organized flocks. Some birds migrate to southern latitudes in late summer and autumn and return to nest the following spring.

This section summarizes the status of research findings for various bird populations on the Hanford Site and the various kinds of environmental stresses that have influenced the populations over the past 40 years.

PASSERINE BIRDS IN A SAGEBRUSH-BUNCHGRASS COMMUNITY

Passerine birds are probably the most conspicuous animals inhabiting sagebrush-bunchgrass communities, even though their contribution to total biomass is relatively small. Because they are most active during daylight hours, population censuses can be made by visual sightings under most field conditions. Over the years shrub-steppe and steppe birds have attracted a great deal of research attention (Rotenberry and Wiens 1978; Wiens 1974; Best 1972; Reynolds 1978, 1981; Olson 1974; McGee 1976; Castrale 1981).

It has been recognized for many years that only a few species of passerine birds successfully nest in sagebrush-bunchgrass communities. On the ALE Reserve, only the western meadowlark (*Sturnella neglecta*), horned lark (*Eremophila alpestris*) and sage sparrow (*Amphispiza belli*) nested in a sagebrush-bunchgrass community (Rotenberry 1978). Meadowlarks and horned larks construct their nests on the ground, but sage sparrows usually nest in the branches of sagebrush shrubs.

Human-induced changes in sagebrush-bunchgrass communities have centered around either the removal of sagebrush to enhance growth of the understory grasses most palatable to livestock, or the destruction of all the native plants by plowing and replacement with crop plants. Sagebrush destruction can be accomplished by mechanical means, herbicides, or burning. Removal of sagebrush, while preserving the native grasses, results in the displacement of those birds that prefer to place their nests inside shrubs, i.e., sage sparrows and Brewer's sparrows (Best 1972). However, the ground-nesting birds continue to nest in the absence of sagebrush. Following the destruction of sagebrush by a summer wildfire on the ALE Reserve, the numbers of sage sparrows declined in the following seasons but they were not completely eliminated (Figure 7.6). At

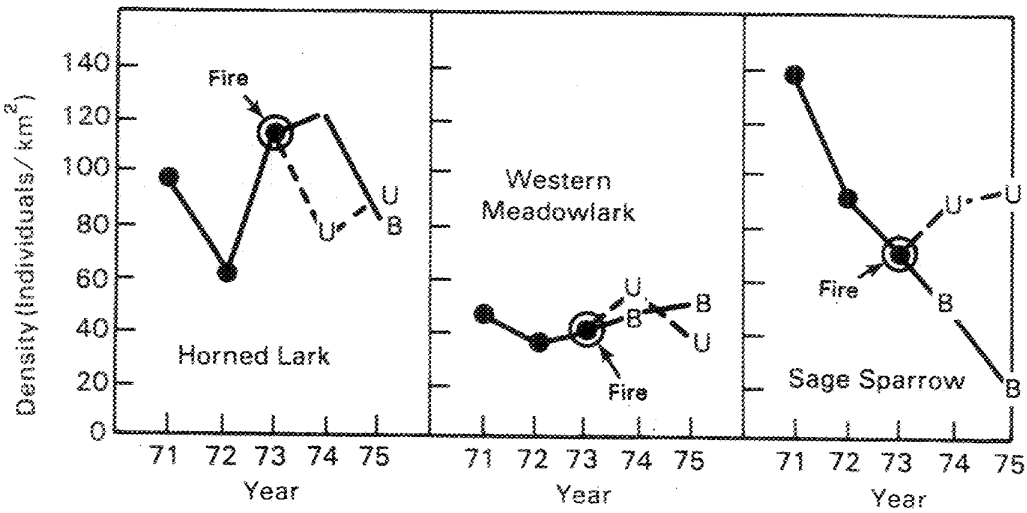

FIGURE 7.6. The Response of Meadowlarks, Horned Larks, and Sage Sparrows Found in Burned and Unburned Areas of a Sagebrush-Bunchgrass Community Following a Summer Wildfire (Rotenberry and Wiens 1978)

the same time, no apparent decrease or increase occurred in the numbers of horned larks or meadowlarks as a result of burning. Cheatgrass communities have a different floristic composition, physiognomy, phenology and productivity than do the sagebrush-bunchgrass communities (See Chapter 6). It seems logical that there would also be differences in nesting bird populations. On the ALE Reserve, only the ground-nesting birds (meadowlark, horned lark and savannah sparrow) nested in the cheatgrass communities (Table 7.6). These same species also nested in nearby sagebrush-bunchgrass communities, but Brewer's sparrows, vesper sparrows and sage sparrows also nested in these communities. Clearly, the sagebrush-bunchgrass community provided nesting habitat for more birds than did the cheatgrass community.

TABLE 7.6. Average Number of Passerine Birds Counted Along 500-Meter-Long Line Transects (2 each) in Cheatgrass and Sagebrush-Bunchgrass Communities on the ALE Reserve in the Spring of 1979 and 1980

Species	Cheatgrass Community	Sagebrush-Bunchgrass Community
Horned lark	16	12
Meadow lark	6	13
Vesper sparrow	0	88
Brewer's sparrow	0	3
Savannah sparrow	1	3
Sage sparrow	0	2
Total	23	41

Sagebrush shrubs maintain their leaves year-round, and the dead shoots of grasses also remain standing, thereby creating relatively little change in visual appearance from the beginning to end of the spring nesting season. This same feature also prevails in cheatgrass communities, suggesting that concealment cover for nest placement changes relatively little from year to year in these kinds of communities unless the plants are disrupted by fire, grazing, or plowing.

Cattle grazing can change the general appearance of sagebrush-bunchgrass and cheatgrass communities by reducing the amount of standing dead grass. Such a decrease may influence nesting birds, especially if grazing is practiced over a long period of time. During a 5-year study of meadowlarks, horned larks, and other nesting birds in a meadow-steppe community in Colorado, heavy summer grazing by cattle appeared to increase the nesting density of horned larks and to lower the nesting density of meadowlarks (Table 7.7).

TABLE 7.7. Five-Year Averages of Breeding Pairs of Horned Larks and Meadowlarks on 8.1-ha Study Plots in a Colorado Shortgrass Prairie Under Heavy and Light Cattle Grazing (Ryder 1980)

	Heavy Grazing		Light Grazing	
	Summer	Winter	Summer	Winter
Horned Lark	5.0	2.7	2.8	2.7
Meadowlark	0.1	1.1	1.2	1.5

Horned larks and meadowlarks are considered to be ecological generalists. At Hanford, they nest in both cheatgrass and sagebrush-bunchgrass communities. The sage sparrow is a specialist. It is closely associated with the presence of mature sagebrush shrubs. Clearly, a regional decline in abundance of sagebrush shrubs through wildifes and/or rangeland manipulation will diminish the total nesting population of sage sparrows. It seems likely that breeding populations of sage sparrows will, in future years, become more and more relegated to isolated sagebrush patches located on steep slopes or on stony soils that support too little fuel to carry a wildfire and where herbaceous plants are too sparse to economically justify the removal of sagebrush by chemical herbicide spraying. Nevertheless, even the most degraded rangeland condition of the sagebrush-bunchgrass community, i.e., a cheatgrass community, still supports nesting populations of horned larks and meadowlarks.

Horned larks and meadowlarks are among the most abundant of the nesting birds in shrub-steppe and meadow-steppe regions of the western United States. These ground-nesting birds are also resistant to changes in plant community structure induced by livestock grazing and by periodic wildfires. They are the first birds to establish nests in cheatgrass communities after cultivated fields have been abandoned. In contrast, sage sparrows are strongly dependent

upon the shrub component of sagebrush-bunchgrass plant communites, and are vulnerable to change, natural or human-induced, that destroys sagebrush.

It seems unlikely that passerine birds play any significant role in ecological succession processes or mineral cycling behavior in sagebrush-bunchgrass communities. They do serve as prey for predatory birds, but even this role is subordinate to that of the small mammals and snakes. Passerine birds do provide opportunities for basic research designed to determine the various environmental factors involved in habitat selection through various kinds of experimental manipulations of habitats.

LONG-BILLED CURLEW

The long-billed curlew (*Numenius americanus*) once occurred in large numbers in the semi-arid, meadow-steppe and shrub-steppe regions of the western United States and adjacent Canada. By the year 1900, breeding populations had markedly declined as a result of excessive killing by market hunting and by agricultural practices that converted thousands of square kilometers of native rangeland vegetation to cultivated crops (Allen 1980).

Pampush (1980) has estimated that 50 percent of the nesting long-billed curlews west of the Rocky Mountains are in the shrub-steppe region of Washington, Oregon and adjacent Idaho. Probably the single most important breeding area for curlews in this large region is located in southwestern Idaho (Jenni et al. 1981).

A study of the ecological behavior of the long-billed curlew on the Hanford Site was conducted by Allen (1980). The land, west of the Columbia River, supported approximately 100 curlews. Of this number, 60 were breeding birds. Curlews invariably nested on level or nearly level ground with sparse,

short grasses 1-2 decimeters tall (Figure 7.7). All curlew nest sites were dominated by cheatgrass, but two variations were noted. Type I vegetation consisted mostly of cheatgrass mixed with the short native bunchgrass, Sandberg's bluegrass. Type II vegetation consisted almost entirely of cheatgrass, essentially without Sandberg's bluegrass. A statistical description of the two kinds of vegetation is shown below.

	Type I % Cover	Type II % Cover
New-growth cheatgrass	6.7 ± 2.2	13.6 ± 1.6
Dead cheatgrass	65.4 ± 10.9	92.2 ± 2.8
New-growth Sandberg's bluegrass	16.6 ± 4.2	none
Old-growth Sandberg's bluegrass	4.6 ± 2.0	none

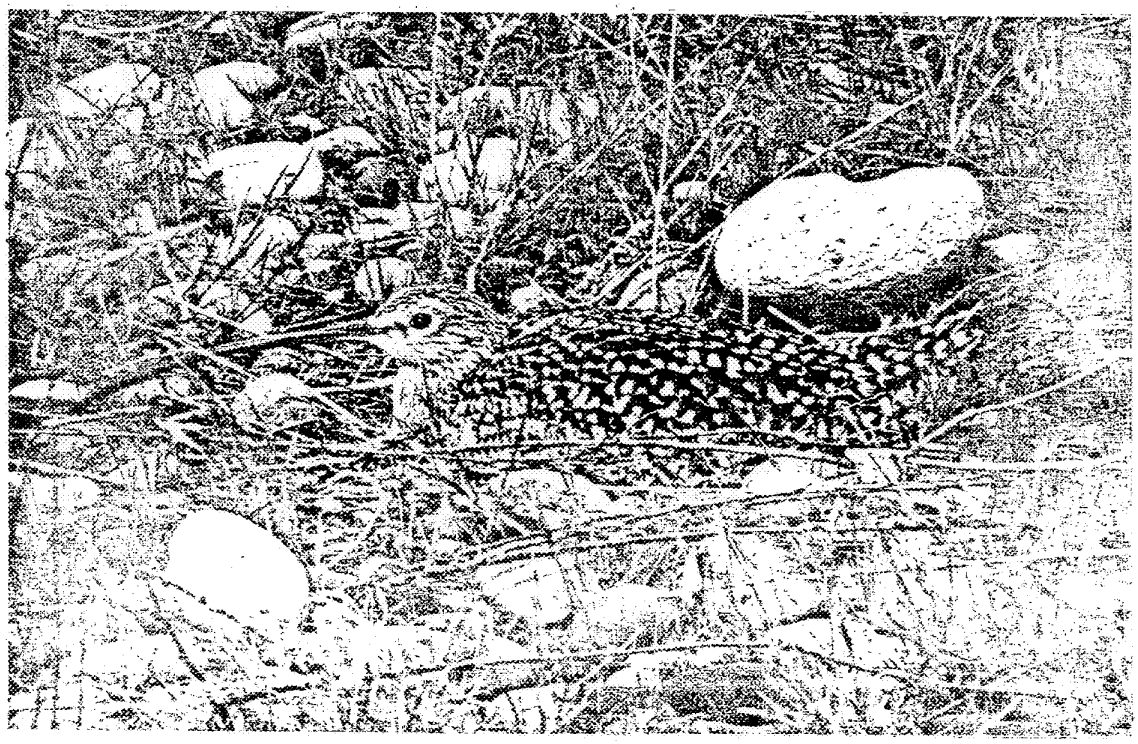

FIGURE 7.7. Long-Billed Curlew Nesting

Of 21 nesting areas, 71 percent were situated in Type I vegetation and 29 percent were in Type II vegetation. Some Type II locations with very dense stands of cheatgrass were not selected as nesting sites. Vegetation with a preponderance of relatively tall plants (0.3-0.5 meters), e.g., tumble mustard or bluebunch wheatgrass, were not selected as nesting areas. It is likely that curlews select communities of short-statured plants because these do not interfere with line-of-sight vision while the birds are on the ground.

Nesting curlews appeared to eat insects, but no dietary analyses were conducted. Allen found that curlew nests were vulnerable to vertebrate predators, particularly coyotes (Allen 1980).

The influence of summer wildfire on nesting curlews has not been investigated. However, it seems unlikely that wildfire would cause damage. Breeding, incubation and fledging of young would be accomplished before the usual onset of the fire season. Wildfire could create favorable nesting areas for curlews in the first year following a summer wildfire because cheatgrass communities would be sparser than usual. Burning destroys accumulations of standing dead stems, and it requires several growing seasons to accumulate maximum stand densities.

The nesting habitat of the long-billed curlew throughout the shrub-steppe region continues to be encroached upon by intensive agriculture and urban land uses that are not compatible with the wide open space and sparse vegetation requirements of nesting curlews. For example, thousands of hectares of shrub-steppe land in the most arid parts of the Columbia Basin region of eastern Washington have been converted to irrigated agriculture since 1952, and the irrigated area is still expanding. There is some evidence that cattle grazing in shrub-steppe communities may be favorable to nesting

curlews by helping to keep vegetation short and sparse (Jenni et al. 1981). Nevertheless, curlews have nested on the Hanford Site on lands that have been without livestock grazing for 40 years.

The Hanford Site can be expected to serve as a nesting habitat for long-billed curlews into the foreseeable future. The use of the land as a buffer zone around a few widely separated industrial buildings has been of benefit to the curlew population of eastern Washington for 40 years. It also contributes to the maintenance of a breeding population in the extreme western portion of the shrub-steppe region and helps to maintain genetic diversity in the overall population. It seems unlikely at this time that irrigated agriculture will be practiced on the Hanford Site, which should remain favorable to nesting curlews.

RAPTORS IN SHRUB-STEPPE AND MEADOW-STEPPE REGIONS

Buteonid Hawks, Prairie Falcon and Golden Eagle

The Hanford Site consists of 1400 square kilometers of mostly undeveloped land that still supports large, contiguous tracts of shrub-steppe plant communities. With the exception of a vigorous invasion by cheatgrass, especially at the lower elevations, those communities are visually and structurally much like they were in the 1850's. Historically, the land has supported very few trees. Native cottonwood trees (*Populus sp*) and tree-willows (*Salix amygdaloides*) are sparsely distributed along the banks of the Columbia River and at the few spring-streams (i.e., Rattlesnake and Snively Springs). Cliff locations suitable for nesting ledges are also scarce. However, Gable

Mountain, Gable Butte, Rattlesnake Hills and the riverine bluffs along the eastern shoreline of the Columbia River do provide a few ledges that are suitable for raptor nest sites.

Irrigated agriculture introduced in the late 1800's and early 1900's was followed by the planting of wind breaks in the villages of White Bluffs and Hanford. Following this abandonment, some of the planted trees have survived for over 40 years without benefit of irrigation water. These trees now provide nest sites for buteonid hawks (Olendorff 1973b, Fitzner 1980a). It is likely that these trees did not support many hawks' nests in the years prior to 1943, when hawks were commonly killed to protect flocks of domestic fowl or for sport. The most common tree-nesting buteos on the Hanford Site are the Swainson's hawk (Buteo swainsoni) and the red-tailed hawk (Buteo jamaicensis). From 1975 through 1978, nests of Swainson's and red-tailed hawks were present in nearly equal abundance, as indicated by a 4-year nest census summarized in Table 7.8 (Fitzner 1980b).

TABLE 7.8. Nests of Swainson's and Red-Tailed Hawks Located on the Hanford Site, 1975-1978

Species	1975	1976	1977	1978	Average	Number of Nests per km^2
Swainson's hawk	16	14	9	17	14.0	.0100
Red-tailed hawk	8	15	22	20	16.2	.0102
TOTAL	24	29	31	37	30.2	.0202

The Swainson's hawk tends to choose trees as its nesting sites, but the red-tailed hawk nests on power line towers, and on cliffs, as well as in trees. As shown in Table 7.9, over 50 percent of the red-tailed hawk nests have been found on power line towers.

TABLE 7.9. Nesting Sites of Swainson's and Red-Tailed Hawks on the Hanford Site

Species	Nesting Sites (%)		
	Tree	Cliff	Artificial
Swainson's Hawk	100	0	0
Red-Tailed Hawk	13	35	53

Under certain conditions, hawk nest placement on power line towers can cause power outages and sometimes results in electrocution of the birds. However, electrocution of hawks and power outages can be avoided by making structural modifications to the existing power line structures (Benson 1980).

Diets of nesting buteos in southeastern Washington consist of various reptile, mammal, and bird species (Fitzner et al. 1981). Most prey items are species that are allied to shrub-steppe plant communities rather than to agricultural land (Table 7.10). Snakes, especially the yellow-bellied racer and gopher snake, are well represented in the hawk diet. The ground squirrel, pocket gopher, cottontail, and black-tailed hare are the most important mammalian prey. The meadowlark is the most important bird in buteo diets. On the Hanford Site, snakes provide a large proportion of Swainson's hawk diets, but they are only a small part of the diet in Colorado (Olendorff 1973a) and in Idaho (Craig 1979).

The Swainson's hawk spends only the nesting season on the Hanford Site. Adults arrive in April. Nesting takes place in May, and the young birds and parents migrate south with the onset of autumn (Fitzner 1980b). It is believed that Hanford Site birds migrate as far South as Argentina; however, radio-telemetry studies of movements of nesting birds show relatively limited foraging

TABLE 7.10. Vertebrate Remains (individual animals) Identified in Regurgitated Pellets of Buteonoid Hawks in Southeastern Washington (Cadwell and Fitzner 1984)

Reptiles	Red-Tailed Hawk	Ferruginous Hawk	Swainson's Hawk
Yellow-bellied racer	67	22	120
Gopher snake	43	17	21
Prairie rattlesnake	3	0	0
Garter snake	1	0	0
Striped whipsnake	0	0	2
Small Mammals			
Ground squirrel	53	16	18
Pocket gopher	0	40	16
Pocket mouse	9	5	14
Montane vole	4	0	109
Sagebrush vole	17	0	0
Harvest mouse	1	0	0
Deer mouse	1	0	2
Kangaroo rat	0	1	8
House mouse	1	0	0
Hares & Rabbits			
Nuttall's cottontail	27	8	9
Black-tailed hare	17	5	19
Birds			
Meadowlark	5	22	21
Chukar	5	0	0
Black-billed magpie	5	1	10
California quail	3	0	0
Ring-necked pheasant	3	1	5
Mourning dove	2	0	0
Common flicker	2	0	0
Long-eared owl	1	0	0
Vesper sparrow	1	0	0
Long-billed curlew	0	1	0
Horned lark	0	1	0
Burrowing owl	0	1	0
Sage sparrow	0	0	2
Gray partridge	0	0	2
Starling	0	0	3
Mallard	0	0	1
Ring-billed gull	0	0	1

ranges. Fitzner found that ranges for females averaged 3.4 square kilometers (range 2.6 - 4.8, n=4), while males ranged over an average of 9.1 square kilometers (range 3.1 - 20.3, n=4).

Tree planting on the Hanford Site has allowed nesting buteos, especially Swainson's hawks, to exploit the prey populations of the surrounding shrub-steppe plant communities much more effectively than was possible before trees were artificially planted. There are probably more Swainson's hawks nesting on the Hanford Site today than there were in the 1850's, suggesting that nesting pairs of Swainson's hawks might be purposefully manipulated by selective placement of nest trees.

The Birds of Prey Study Area (BPSA) is a 1211-square-kilometer area of mostly undeveloped but grazed shrub-steppe land located in southwestern Idaho. The BPSA was established to provide a sanctuary for nesting raptors and also to obtain factual information on their ecological behavior. The many miles of basalt cliffs along the deep and precipitous-walled Snake River Canyon provides numerous nesting ledges, and vast acreages of shrub-steppe plant communities support small mammals and birds that provide a renewable food base for raptors. On the BPSA, the prairie falcon (Falco mexicanus) provided 55 percent of the nesting population (Table 7.11). The red-tailed hawk and the ferruginous hawk comprised 16 and 5 percent of the nesting population, respectively. The Swainson's hawk population was represented by a single nest. Clearly the ecological feature of the BPSA that contributes most to its high density of nesting birds of prey is the large number of nesting ledges for prairie falcons, provided by steep basalt cliffs and an abundance of Townsend ground squirrels.

TABLE 7.11. Active Nests of Hawks and Eagles on the Birds of Prey Study Area in Southern Idaho, 1975-1978 (USDI/BLM 1979)

Species	Years 1975	1976	1977	1978	Average	Percent	Number of Nests/km^2
Prairie falcon	186	207	209	183	196	55.3	0.162
Red-Tailed hawk	50	57	62	59	57	16.1	0.047
Kestrel	24	25	44	44	34	9.6	0.028
Golden eagle	32	34	33	32	33	9.3	0.027
Northern harrier	8	21	23	23	19	5.4	0.016
Ferruginous hawk	8	14	19	18	15	4.2	0.012
Swainson's hawk	0	1	1	1	1	1	Trace

The Pawnee National Grassland tract encompasses 1073 square kilometers of mostly undeveloped but grazed land in the semi-arid, meadow-steppe (short-grass prairie) of northeastern Colorado. Unlike the BPSA, the Pawnee site is devoid of cliffs. This lack of cliffs accounts for the absence of nesting prairie falcons at that site. Nevertheless, praire falcons do nest on cliffs in other places in northeastern Colorado adjacent to the Pawnee Site (Olendorff 1973a). Olendorff's study found the Swainson's hawk as the dominant buteo at Pawnee, where it accounted for 74 percent of the hawk and eagle nests (Table 7.12). The nesting density of Swainson's hawks at Pawnee greatly exceeded that of the BPSA, but there were twice as many nesting ferruginous hawks at the BPSA.

TABLE 7.12. Active Hawk and Eagle Nests on the Pawnee National Grassland, 1971-1972 (Olendorff 1973a)

Species	1971	1972	Average	Percent	Number of Nests/km^2
Swainson's hawk	24	35	29.5	73.7	0.0275
Ferruginous hawk	10	6	8.0	20.0	0.0075
Golden eagle	2	3	2.5	6.3	0.0023
TOTAL	36	44	40.0	100.0	0.0373

The total absence of nesting red-tailed hawks at Pawnee corresponds to the virtual absence of nesting Swainson's hawks at the BPSA and the near absence of nesting ferruginous hawks on the Hanford Site.

The Idaho National Engineering Laboratory (INEL) occupies 2315 square kilometers of land on the upper Snake River plain in southeastern Idaho. The vegetation is very similar to that of the Hanford Site, but the number of nesting buteonid hawks at the INEL is not as large. In 1976, only 8 active nests were counted (Table 7.13), whereas 30 were counted on the Hanford Site.

Few buteos nest on the Hanford Site. Prairie falcons nest on steep, basalt cliffs overlooking the Columbia River, but no more than three active nests have been observed in any one year. The absence of nesting golden eagles on the Hanford Site is something of an enigma. Eagles do nest in trees, and suitable nest trees seem to be available on the Hanford Site. However, the ferruginous hawk may be absent because of a lack of suitable nest sites. It nests in juniper trees (*Juniperus occidentalis*) in nearby Franklin County (Fitzner et al. 1977), but juniper trees are absent from the Hanford Site.

More needs to be learned about the way that hawks, eagles and falcons select their nesting sites and their foraging ranges if population management of raptors is to be successful in the shrub-steppe region of the western

TABLE 7.13. Active Hawk Nests on the Idaho National Engineering Laboratory, 1974-1976 (Craig 1979)

Species	Years		
	1974	1975	1976
Swainson's hawk	5	2	5
Red-Tailed hawk	no data	no data	1
Ferruginous hawk	no data	1	2

United States. Large land areas such as the Hanford Site, which still supports shrub-steppe plant communities with their characteristic components of small mammals and snakes, provide habitat suitable for nesting and raising of young. However, once parent birds and their young leave the Site, they travel to other places, some as far as South America. Raptorial birds are such highly mobile animals that even such very large land areas provide only a small part of their habitat requirements.

Northern Harrier Nesting

The northern harrier (*Circus cyaneus*) is a medium-sized hawk with a wide geographic range in North America and Eurasia. It is noted for its low-flying foraging tactics and its remarkable flying stamina (Thompson-Hanson 1984). It differs from most other North American hawks because it nests on the ground, usually in dense cattail and reed communities associated with wetlands or pond margins.

The construction of artifical ponds on the Hanford Site has provided new nesting sites for harriers (Rickard et al. 1982). Harriers have nested on the Hanford Site at Gable Mountain Pond and at ponds on the Wahluke Slope (Thompson-Hanson 1984). These ponds have permitted harriers to occupy parts of the Site that were not available to them prior to 1943. More harriers have nested on the Wahluke slope than at Gable Mountain Pond, but the percentage of successful nests has been greater at Gable Mountain Pond (Table 7.14).

Nesting harriers on the Hanford Site appear to have extremely large foraging ranges compared to harriers at other places in the United States (Table 7.15). In a study by Thompson-Hanson (1984), the foraging ranges of harriers on the Hanford Site were determined by monitoring their movements

TABLE 7.14. Active Nests of the Northern Harrier at Two Artificial Ponds on the Hanford Site

Year	Gable Mountain Pond	Wahluke Slope Pond
1981	4 (75)	7 (29)
1982	6 (50)	9 (44)
Average	5 (62)	8 (36)

() = percentage of nests with successful hatches.

TABLE 7.15. Foraging Ranges of Northern Harriers, Calculated by Various Methods

Location	Foraging Area, km^2	Source of Data	Method Used
Minnesota	2.6	Breckenridge (1935)	Visual
Wisconsin	8.8	Hammerstrom and Wilde (1973)	Ground telemetry
E. Washington	9.4	Rees (1976)	Visual
Idaho	19.9	USDI 1981	Ground telemetry
Southcentral Washington	(72 - 336)	Thompson-Hanson (1984)	Aerial telemetry

with radio transmitters and keeping pace with flying birds by means of a fixed wing aircraft. It is believed that the large foraging ranges are real and that the smaller ranges obtained by ground-based monitoring are probably artifacts of the method rather than representative of harriers' true range sizes. Reliable estimates of foraging ranges are required if bioenergetic budgets of nesting populations in different environments are to be obtained for comparison.

It appears that the foraging ranges of northern harriers nesting on the Hanford Site are many times greater than those of Swainson's hawks. The harrier is much better adapted to survival on agriculturally modified lands than the Swainson's hawk, other buteonid hawks, and prairie falcons, in part because

of the habitat it selects for nest locations (semi-aquatic reeds and rushes) and because of its ability to exploit prey associated with agricultural crops as well as native shrub-steppe plant communities. In this way, harrier populations are maintained while populations of other raptors tend to decline.

Nesting Owls

Five species of owls regularly nest on the Hanford Site (Fitzner et al. 1981). These are the great-horned owl, (*Bubo virginianus*), long-eared owl (*Asio otus*), short-eared owl (*Asio flammeus*), barn owl (*Tyto alba*) and burrowing owl (*Athene cunicularia*). The burrowing owl is the most numerous and the short-eared owl the least numerous (Table 7.16).

The nesting sites of Hanford owl species vary considerably. Trees provide sites for great-horned owls and long-eared owls; abandoned buildings serve as nest structures for great horned owls and barn owls. The burrowing owls nest in holes dug into the ground by burrowing mammals and in other kinds of ground cavities. The short-eared owl nests on ground under dense vegetative cover.

TABLE 7.16. Active Owl Nests on the Hanford Site, 1976-1978 (Fitzner et al. 1981)

Species	1976	1977	1978	Average	Number of of Nests/km^2
Great Horned owl	5	5	5	5.0	.0036
Long-eared owl	3	8	8	6.3	.0045
Short-eared owl	2	1	2	1.7	.0012
Barn owl	2	2	2	2.0	.0015
Burrowing owl	26	20	25	23.7	.0170

The diets of the owl species vary in proportion to their size. Owls' prey is identified through regurgitated pellets. A sample is shown in Table 7.17. The great-horned owl is the largest of the Hanford Site owls,

TABLE 7.17. Vertebrate Animals Identified in the Regurgitated Pellets of Owls (Fitzner et al. 1981)

	Barn Owl (pellets)	Burrowing Owl[a] (pellets)	Great-horned Owl (pellets)	Long-eared Owl (pellets)
Small Mammals				
Pocket mouse	526	251	514	175
Deer mouse	78	68	36	51
Pocket gopher	53	0	5	4
Montane vole	0	17	7	4
Woodrat	0	3	0	2
Merriam shrew	1	0	1	0
Lagomorphs				
Black-tailed hare	--	10	2	0
Nuttalls' cottontail	--	12	2	9
Unknown(b)	22	6	0	0
Birds				
Rock dove	0	7	0	6
Mallard	0	5	0	0
American coot	0	5	0	0
California quail	0	4	0	0
Long-billed curlew	0	2	0	0
Starling	0	2	1	0
Black-billed magpie	0	2	0	0
Common flicker	0	1	0	0
Burrowing owl	0	1	0	0
Ring-billed gull	0	1	0	0
Eared grebe	0	1	0	0
Sage sparrow	0	0	3	0
Meadowlark	0	0	3	0
Chukar	0	0	1	0
Unknown	22	6	0	0
Reptiles				
Yellow-bellied racer	0	2	0	0
Gopher snake	0	1	0	0

(a) The burrowing owl also ate insects.
(b) Uncertain category.

and it kills relatively large-sized mammals and birds. The burrowing owl is a small bird; its diet consists largely of pocket mice supplemented by insects. While pocket mice are relatively unimportant items in the diets of hawks, they are important to owls. The nocturnal activities of pocket mice may make them especially vulnerable to the night-hunting owls.

There is no information concerning movements and foraging ranges of nesting owls, so comparisons with Swainson's hawks and northern harriers cannot be made at this time. However, owls on the Hanford Site have access to an abundant prey source (pocket mice) that is not as readily available to hawks. If food is indeed a limiting factor, there should be more owls than hawks on the Hanford Site. However, nest counts show that the large Swainson's and red-tailed hawks are more abundant than the larger owls, i.e., great-horned and long-eared owls. This apparent paradox suggests that factors other than food availability are operating to favor the population of hawks over owls.

The nest locations of the small hawks, i.e., kestrel (Falco sparverius), and burrowing owls are more difficult to locate than those of the larger hawks and owls. Therefore, nesting densities of these birds have not been so well documented.

If, indeed, there are more large owls on the Hanford Site today than there were in the years before settlement, the increase may have resulted from the proliferation of suitable nest sites--planted trees and more buildings. Growing numbers of large owls, in turn, may have reduced the populations of smaller owls (i.e, burrowing owls) through competition for an important food source (pocket mice)--and perhaps by intimidation and outright predation.

BIRD POPULATIONS ASSOCIATED WITH SURFACE WATERS

A distinction occurs, between semi-arid and arid ecosystems, in the amount and diversity of water systems. Three such systems are found on the Hanford Site: streams, a river (the Columbia River), and various artificial ponds. Eash system offers specific opportunities for bird study.

Streamside Thickets

The attractiveness of streamside thickets to nesting birds in vast expanses of otherwise treeless shrub-steppe surroundings has been known to western ornithologists since the late-1800's. On the ALE Reserve, spring streams and streamside thickets are restricted to two main locations, Rattlesnake Springs and Snively Springs, described in Chapter 5. Of the two areas, the streamside vegetation at Snively Springs has been less influenced by the past activities of people (Rickard and Cushing 1982). Spring stream vegetation in the Snively area consists of a narrow zone of broad-leaved deciduous trees and shrubs, mostly shrub-willows (*Salix spp*), and a few scattered cottonwood trees (*Populus sp*). The important shrubs are chokecherry (*Prunus sp*), blue elderberry (*Sambucus sp*), mock orange (*Philadelphis lewisii*), wild rose (*Rosa spp*), and service berry (*Amelanchier sp*). The trees and shrubs along the spring-stream are all natives. However, at its source, a few white poplar trees (*Populus alba*) and black locust trees (*Robinia pseudacacia*) were planted around farm buildings prior to government acquisition of the land. These trees are still living, but the buildings have been destroyed by wildfire. Surveys were made to determine the kinds and numbers of birds that regularly use the streamside thickets bordering Snively Spring (Rotenberry et al. 1979). A narrow dirt road paralleling the spring for a distance of about 1.5 kilometers was used

as the travel path for a walking census. For 2 consecutive years, 11 census trips were made during the spring and summer, 10 during the autumn and winter. The spring season census data infer that the birds seen were nesting there, although nests of some species were not actually seen (Table 7.18). The data

TABLE 7.18. Birds Observed in the Streamside Community at Snively Springs (from Rotenberry et al. 1979)

Bird Species	Number of Censuses With Sightings	Average Number of Birds Sighted
Summer Census (n=11) (nesting birds)		
Northern oriole	10	7.6
Starling(a)	5	5.6
Lazuli bunting	10	5.5
Black-billed magpie	10	5.2
Wilson's warbler	4	3.7
Brewer's blackbird	6	2.8
Eastern kingbird	5	1.9
California quail	6	1.8
Song sparrow	7	1.4
Yellow-breasted chat	6	1.1
Kestrel	2	1.0
Winter Census (n=10)		
Dark-eyed junco	9	26.5
Yellow-rumped warbler	2	4.7
American robin	6	2.6
Black-billed magpie	8	2.2
White-crowned sparrow	5	1.8
Ring-necked pheasant	5	1.7
Song sparrow	7	1.6
Ruby-crowned kinglet	6	1.2

(a) Alien species.

show that the northern oriole, starling, lazuli bunting and black-billed magpie were the most abundant nesting birds. The year-round resident birds were black-billed magpies, starlings, California quail and song sparrows. The most abundant winter birds were dark-eyed juncos, yellow-rumped warblers and American robins.

Although the streamside thicket occupies only a tiny fraction of the landscape of the ALE Reserve, it provides nesting sites for birds that otherwise would not be able to maintain breeding populations. Presumably the foods for the nesting birds and their nestlings are derived from food webs generated within the thickets, as well as from foraging forays into the adjacent sagebrush-bunchgrass community. A great deal of summer use of the thickets has been noted for mourning dove and chukar partridge, but these birds were probably attracted by the access to free water rather than by the thickets themselves as nesting habitat or foraging area.

Streamside thickets provide nesting habitat for passerine birds that cannot successfully nest in the surrounding sagebrush-bunchgrass communities. Furthermore, different species use the thickets in winter than in summer, indicating that the streamside communities play a year-round role in maintenance of bird populations.

Columbia River

One of the most conspicuous geographic features of the Hanford Site is the Columbia River, which flows for a distance of approximately 60 kilometers through the Site (Figure 7.8). In 1943, the year the Hanford Site was first established, the mainstream Columbia River had only two hydroelectric dams: Bonneville, west of the Hanford Site near Portland, Oregon; and Grand Coulee,

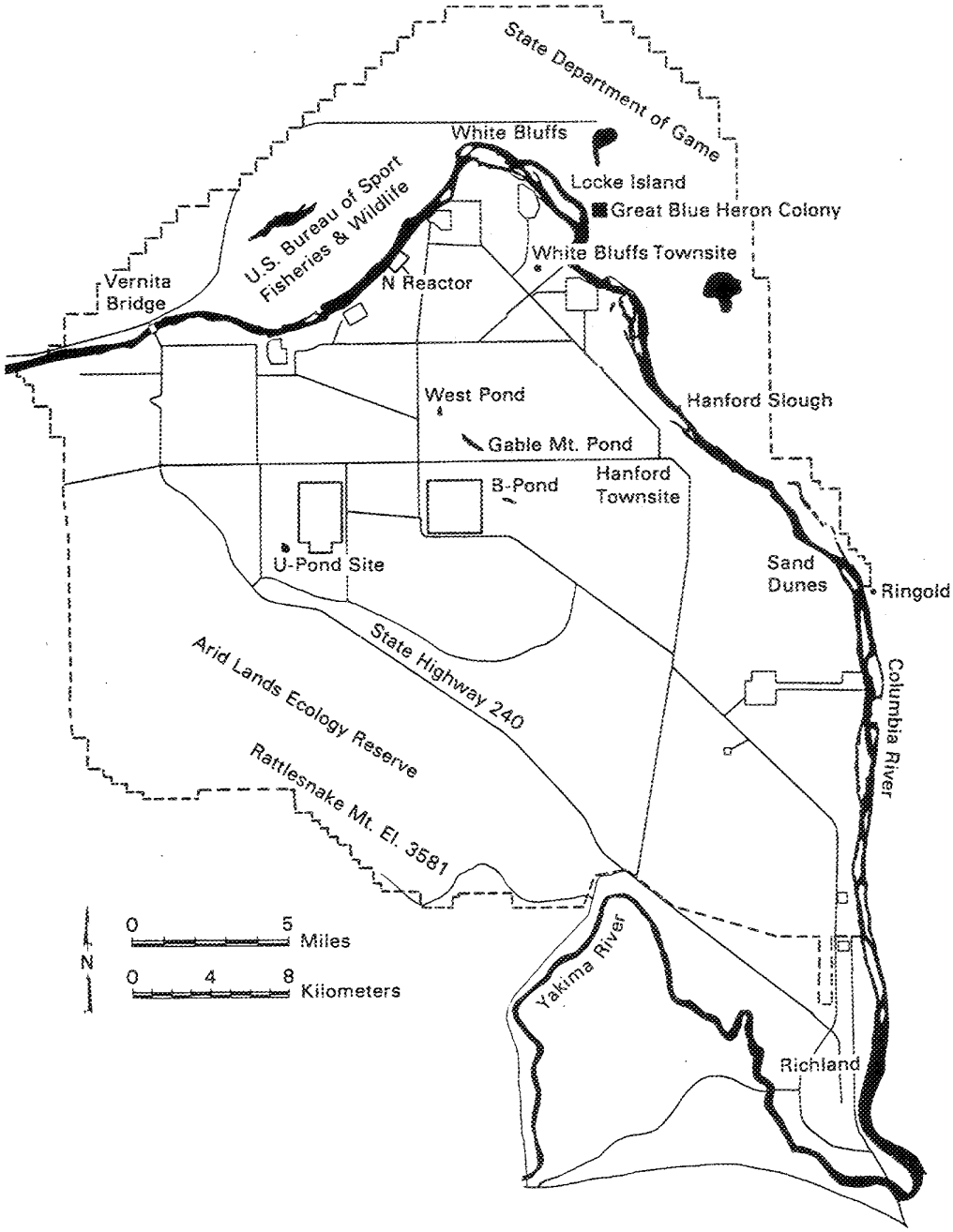

FIGURE 7.8. Map of the Hanford Reach of the Columbia River (includes the location of artificial ponds and river islands, heron colonies, and other locations mentioned in text)

located upstream in northeastern Washington. Since then, other dams have been built upstream and downstream from the Hanford Site. Today the Hanford reach is the only unimpounded section of the Columbia River in Washington upstream from Bonneville Dam (Rickard and Watson 1985).

Nine nuclear reactors were built on the banks of the Columbia River between the years 1943 and 1965. Eight of these were shut down by 1972; only one is operating today. In the early years of the Hanford Site, the river was closed to public boating. Boating has been accessible to the public since 1972, although shoreline traffic on the Hanford Site remains restricted.

Since 1943, the Hanford Reach has served as a major concentration area for Pacific Flyway migratory waterfowl in winter. In 1984, according to an unpublished census by R. E. Fitzner, 80,000 waterfowl were wintering along the Hanford Reach. Waterfowl hunting is permitted during the hunting season along a portion of the Reach, extending from the power line at the abandoned village of Hanford, downstream to the town of Richland (Figure 7.8). For the most part, waterfowl populations tend to be concentrated in the upstream segment that is closed for hunting. Waterfowl that rest on the river fly to nearby agricultural fields to forage. During these foraging visits, some are killed by sports hunters.

Surveys of Canada geese (Branta canadensis moffitti) that nest on 20 sparsely vegetated sand and cobble islands located in the Hanford Reach have been conducted yearly since 1953, (Hanson and Eberhardt 1971, Ball et al. 1981, Dewaard 1981, Fitzner and Rickard 1983). Although daily and seasonal water level flows in the Hanford Reach became more and more regulated over the years as additional hydroelectric dams were built, the river islands show relatively little morphological change. Nevertheless, there has been a tendency

for woody plants to become self-established along the shorelines of river islands, especially near Richland. Nest numbers reached their historical peak in 1958, when 306 nests were counted. Since this high point, the numbers of nests have ranged between a low of 110 in 1975 and a high of 240 in 1961. In 1957, 129 nests were counted on Locke Island alone. However, the presence of a few resident coyotes on Locke Island has effectively eliminated it as an effective goose-nesting habitat. Not more than eight nests have hatched successfully on Locke Island in any single year over the past decade. In most years no active nests have been established (Fitzner and Rickard 1983).

Although the Hanford Reach has been a faithful producer of Canada geese each year, for nearly 40 years it has produced only a few ducks. Apparently, the Reach is not a suitable nesting habitat for most species of ducks. A few mallard (Anas platyrhynchos) nests are discovered during the annual goose nest survey, but total mallard production is low.

Great blue herons (Ardea herodias) are year-round residents along the Hanford Reach. In the early days, only a few great blue herons nested there. In the 1980's two colonies had become established; one, with 62 active nests, is located near the abandoned townsite of White Bluffs, and the other, with 16 active nests, is located upstream from the abandoned townsite of Hanford (Figure 7.8). The increase in nesting herons, especially over the past decade, may be related to an increasing abundance of resident "trash fish" such as carp, which may be more amenable to heron capture than are juvenile, anadromous salmonids. The nesting herons on the Hanford Site are entirely dependent on the presence of trees planted in the years before 1943. Without these trees, there would likely be no heron colonies on the Hanford Site.

In the early years of the Hanford Site, the American Bald Eagle (Haliaeetus leucocephalus) was sparsely represented among the wintering birds along the Hanford Reach (Fitzner and Hanson 1979). However, in the past 10 years, the number of wintering bald eagles has greatly increased; 41 were counted in fall and winter 1984-85. The expanded eagle population is attributed partly to large increases in spawned-out salmon carcasses, especially during the past decade (Rickard and Watson 1985). The abundance of wintering ducks and geese and the presence of planted trees that serve as night-time roosts also contributes to the attractiveness of the Hanford Reach for wintering eagles (Fitzner and Hanson 1979).

Several islands in the lower section of the Hanford Reach serve as nesting sites for ring-billed gulls (Larus delawarensis), California gulls (L. californicus), and Forster terns (Sterna forsteri). The nesting colonies are large, 19,000 gulls (Conover et al. 1979) and several hundred terns have nested on the islands in recent years. These colonies are protected from human intrusion during the nesting season by the U.S. Bureau of Sports Fisheries and Wildlife, which manages the islands as bird refuges.

Although the daily and seasonal flow patterns of the Columbia River have been greatly changed by upstream dams, there is little information on the effects of these water fluctuations on birds that inhabit the Hanford Reach shoreline (Books 1984). The frequent wetting and rewetting of shorelines by the dam-regulated water flows have provided a food source for birds of the ground-feeding guild (Table 7.19). Receding water levels strand aquatic invertebrates and other bird foods on the shoreline, and these are eaten by red-winged blackbirds and others (Books 1984). Young geese hatched from nests in the Hanford Reach depend upon shoreline plants for forage in the weeks

TABLE 7.19. Statistical Analysis of Ground-feeding Birds in Relation to Fluctuating Water Levels Along the Hanford Reach of the Columbia River (data from Books 1984)

Type of Ground Feeding	Number of Observations	Observations During Receding Water Levels (%)	Chi-Square Values[a]
Rock Pickers	166	78	55.5[b]
Gravel Pickers	250	87	135.4[b]
Sand Pickers	110	89	67.2[b]
Mud (Silt Deposits)	878	59	29.2[b]
Grass Pickers	988	82	396.6[b]
Wading Bottom-Probers	35	27	8.3[c]

(a) Ho: P=| testing whether observations of ground-feeding occur randomly with respect to receding water-levels.
(b) Rejection at p.001, critical value = 10.8, df = 1.
(c) Rejection at p.01, critical value = 6.6, df = 1.

before they are old enough to fly (Eberhardt 1987). However, we do not yet know the influence of regulated daily fluctuations in water level on shoreline vegetation as a forage resource for young geese or its implications for future goose populations. The dam-regulated water level fluctuations do not directly affect most of the shoreline-nesting birds because these birds tend to nest above the influence of high-extremes. However, daily fluctuations in water level have changed the shoreline-vegetation by enhancing the growth of woody plants. While it is likely that this vegetative change will provide increased habitat for tree and thicket nesting birds in future years, it also could have a detrimental impact on nesting geese, gulls and terns because thickets provide cover for predators such as the coyote, raccoon and skunk.

At this time, the long-range implications of human-induced fluctuations in water level are not fully understood. The role of the Hanford Reach as an important nesting habitat for geese, gulls and terns will likely continue into the foreseeable future. However, most of the nesting islands could be inundated with water should a future hydro-electric dam be constructed across the Columbia River near Richland.

Artificial Ponds

When the Hanford Site was established in 1943, the only pond on the Site was located near Gable Mountain. Today this pond is called "West Pond" (Figure 7.8). It is a typical shallow-basin seep lake with white alkali deposits forming a distinctive border around its margins. The shoreline supports a zone of short-statured, salt-tolerant herbaceous plants, but no deciduous trees or shrubs. The source of pond water is a "window" in the groundwater (Meinhardt and Frostensen 1979). Over long periods of time, minerals dissolved in the groundwater have accumulated as water evaporated from the pond surface and became replenished from subterranean flows. Since the 1940's, the water levels of West Pond have varied with the changing elevations of groundwater resulting from water use at industrial facilities located on the Hanford Site (Meinhardt and Frostensen 1979, Cline et al. 1985).

Other shallow ponds have been formed on the Hanford Site as a result of energy-producing operations. Large quantities of water have been pumped from the Columbia River and used for cooling in the Site's industrial facilities. After use, the water is released to shallow basins in the land. Water entering

the ponds has much the same chemical composition as Columbia River water, except that very small quantities of radionuclides may be present from time to time.

The water input rate to the ponds closely matches the rate of percolation through the pond bottoms, and water levels tend to be stable. Some ponds have been in existence for more than 20 years (e.g., U-Pond, Gable Mountain Pond and B-Pond). Over this time span, zones of emergent plants have developed, especially cattails (Typha latifolia) and reeds (Scirpus spp). A few deciduous trees that are commonly associated with freshwater ponds and lakes elsewhere in the Columbia Basin, e.g., Russian olive (Eleagnus angustifolia) and peach leaf willow (Salix amygdaloides), have also become self-established along the pond margins (Rickard et al. 1981).

At all stages in their relatively short history, the artificial ponds have been attractive to water fowl, including dabbling ducks, diving ducks, American coots and Canada Geese (Fitzner and Rickard 1975). Waterfowl are generally most abundant during autumn and spring migration periods (Figure 7.9). Fitzner and Schreckhise (1979) found coots to be the most numerous of the waterfowl that actually nest on the pond and successfully produce young. Cattails and reeds provide nesting places for yellow-headed and red-winged blackbirds, marsh wrens, northern harriers and other birds. Birds associated with the artifical ponds on the Hanford Site are listed below.[a]

(a) Common names are listed in the AOU checklist 1983.

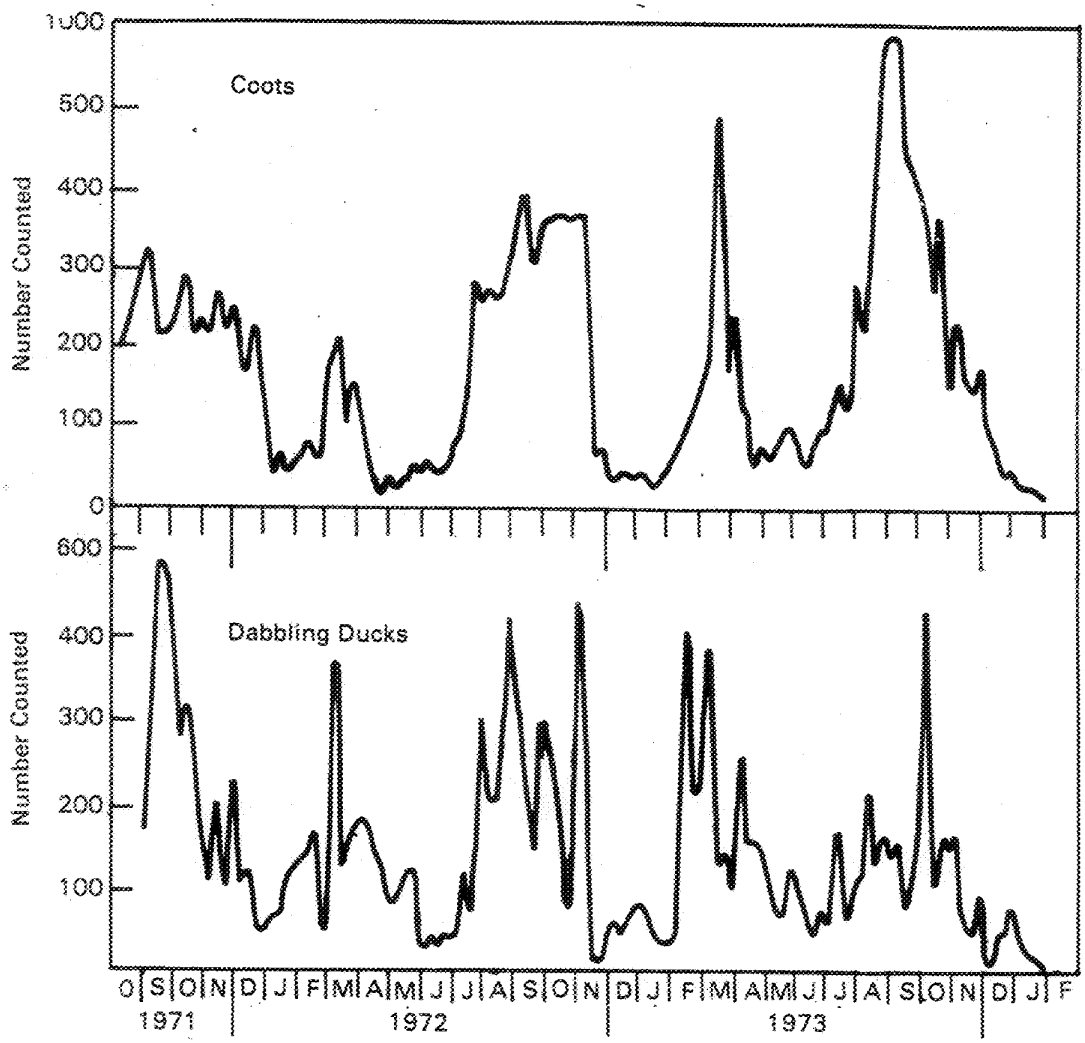

FIGURE 7.9. Waterfowl Abundance on Artificial Ponds (1971-1973)

Birds of Open Water

Horned grebe, eared grebe, western grebe, pied-billed grebe, whistling swan, Canada goose, mallard, gadwall, pintail, green-winged teal, blue-winged teal, cinnamon teal, American wigeon, northern shoveler, redhead, ring-necked duck, canvasback, greater scaup, lesser scaup, common goldeneye, Barrow's goldeneye, bufflehead, old squaw, ruddy duck, hooded merganser, ring-billed gull, California gull, Bonaparte's gull, American coot.

Wading Birds

American bittern, great blue heron, black crowned night heron, killdeer, common snipe, long-billed curlew, spotted sandpiper, greater yellowlegs, least sandpiper, dunlin, long-billed dowitcher, western sandpiper, sanderling, American avocet, Wilson's phalarope, red-necked phalarope, water pipit.

Birds of Reed Habitats

Sora, northern harrier, yellow-headed blackbird, red-winged blackbird, song sparrow, marsh wren.

One of the important environmental aspects of Gable Mountain Pond is its capacity to deliver radionuclides to summer-resident coots through food webs. Coots are quite mobile; they may fly to other ponds in the Columbia Basin, where they could be killed and eaten by humans. Radiocesium (^{137}Cs) is nearly absent from West Pond, which does not receive direct inputs of industrial coolant water, but it is present in the bottom sediments of Gable Mountain Pond (Meinhardt and Frostenson 1979). The ^{137}Cs is assimilated by the vegetation growing in Gable Mountain pond in quantities that vary according to where it is rooted, as follows:

Pond	Concentration (^{137}Cs pCi/g dry wt.) Sediment	Vegetation
West	1.5	1.5
Gable Mountain(a)	68	6.4
Gable Mountain	240	160

(a) Sampled near inlet stream.

In a special study, Cadwell et al. (1979) compared concentrations of radiocesium in tissues of coots collected from Gable Mountain Pond with those collected at the Columbia National Wildlife Refuge located in the Columbia

Basin Northeast of the Hanford Site and remote from Gable Mountain Pond. Radiocesium was present in enhanced concentrations in the tissues of coots collected at Gable Mountain Pond, as indicated below.

Pond	Tissue Concentration (^{137}Cs pCi/g dry wt.)		
	Bone	Liver	Muscle
Gable Mountain (n = 103)[a]	200 ± 30	440 ± 40	570 ± 40
Columbia Refuge (n = 13)	1.0 ± .30	.70 ± .20	.02 ± .05

(a) n = number of samples SE.

These data clearly show the capacity of coots to obtain body burdens of ^{137}Cs while in residence on Gable Mountain Pond. However, the amounts of ^{137}Cs delivered to people that might kill and eat the flesh of these birds as they leave the pond are not of sufficient magnitude to present a human health hazard according to conventional radiological dose modeling procedures (Cadwell et al. 1979).

The industrial ponds on the Hanford Site were never intended to become a permanent part of the landscape. At the time of this writing, U-Pond has been drained, the sediments are covered with earth, and drought-resistant grasses have been planted. Gable Mountain Pond is currently undergoing this same process. B-Pond is being expanded and modified to accomodate water flows that once were shunted to Gable Mountain Pond. Because of the potential for at least some biotic transport of radionuclides to offsite locations by waterfowl that have access to industrial ponds, methods are being considered to eliminate ponds entirely or to engineer them to be less attractive to waterfowl (Cadwell and Rickard 1979).

The U.S. Bureau of Reclamation's Columbia Basin water project has brought water to one-half million acres in the Columbia Basin for crop irrigation since 1952. Water is taken from the Columbia River at Grand Coulee Dam and delivered in a series of canals and connected reservoirs. When water first moved through the ground on delivery to these canals and reservoirs, a large number of seep lakes appeared on the landscape. Seep lakes first appeared on the land of the Hanford Site north and east of the Columbia River in the 1970's as the U.S. Bureau of Land Reclamation improved and extended a canal system to irrigate additional land north of the Hanford Site.

The early use of these new ponds and lakes by nesting waterfowl was reported by Johnsgard (1956). A concensus of wildlife managers today is that seep lakes originating from water diversions created for large scale irrigation purposes are beneficial to both breeding and migratory waterfowl populations of eastern Washington, and that these lakes now provide a wildlife resource of regional significance. Under a use permit from the U.S. Department of Energy Richland Operations Office, some of the seep lakes are managed as a waterfowl refuge by the U.S. Bureau of Sports Fisheries and Wildlife. Other ponds are managed by the Washington State Game Department as public hunting and fishing areas. Although these lakes provide valuable habitats for waterfowl and other birds, they also contribute to the diminishment of dryland habitat suitable for native shrub-steppe plants and animals.

UPLAND GAME BIRDS

During the 40 years of Hanford Site operation, no studies have been made of its populations of upland game birds. A few birds are killed each year to

provide tissues for radiochemical analyses for the Hanford Site environmental surveillance programs (Price et al. 1985).

Four of the species of upland game birds with self-sustaining populations on the Hanford Site are alien introductions, released into the general region for sports hunting purposes long before the Hanford Site was established (Rickard et al. 1982). These are the California quail (Lophortyx californicus), Chinese ring-necked pheasant (Phasianus colchicus), chukar partridge (Alectoris chukar), and gray partridge (Perdix perdix). The quail and ring-necked pheasant populations are mostly restricted to the vicinity of thickets along the Columbia River and the Snively Spring and Rattlesnake Spring areas on the ALE Reserve.

The chukar is probably the most abundant resident game bird, and its greatest populations are centered in the Rattlesnake Hills. The gray partridge population is probably smaller than the chukar population, but its greatest population densities are also located in and near the Rattlesnake Hills.

The native upland game birds are the mourning dove (Zenaida macroura), a migrant, and the sage grouse (Centrocercus urophasianus), a resident. The mourning dove nests on the ground and occasionally in the trees scattered throughout the Hanford Site. A few doves spend the entire winter in the Hanford Site.

The future of the sage grouse population on the Hanford Site is not favorable. The grouse population has not been hunted for 40 years, and the land has not been grazed by livestock; yet the population is very small, perhaps less than 20 birds, and it appears to be wholly confined to the ALE Reserve. In contrast, there are sizable sage grouse populations on the

Yakima Firing Center, a large military reservation located northwest of the Hanford Site. There the land is used for livestock grazing as well as military maneuvers including live artillery practice.

The Idaho National Engineering Laboratory supports a relatively large sage grouse population under a land use that is very similar to that of the Hanford Site (Connelly and Ball 1983), suggesting that a more suitable climate and/or vegetation exists at the INEL for sage grouse. Irrigated grass lawns (*Poa sp.*) and irrigated alfalfa (*Medicago sp.*) fields on and adjacent to INEL property are thought to provide a foraging habitat substitute for natural wet meadows that historically were of great importance to sage grouse. These kinds of artificial habitats are not available to the sage grouse living on the Hanford Site. It is possible that the few remaining grouse are restricted to the ALE Reserve in response to unfavorable land uses, especially dryland wheat, that adjoin the Reserve. However, the Reserve land apparently does not provide all the habitat requirements necessary to support a vigorous sage grouse population.

The sage grouse is clearly not as successful on the ALE Reserve as is the chukar partridge. The chukar does not require succulent plants as forage in summer, nor does it normally eat sagebrush leaves in winter as does the sage grouse. In this case, the native upland bird of the Hanford Site has been replaced by an alien game bird. At the same time, the sage grouse population at the INEL is vigorous and the chukar population is small, indicating that the Hanford Site is more favorable for chukars.

CARRION EATERS (MAGPIES, CROWS AND RAVENS)

Three carrion-eating birds, or corvids, are found on the Hanford Site. Probably the most visually distinctive bird in the entire shrub-steppe region is one of these, the long-tailed, black and white colored magpie (*Pica pica*). The magpie nests in deciduous trees and thickets scattered throughout the Hanford Site, but there have been no special surveys to determine the size of the nesting population. Magpies are often seen feeding on road-killed animals, sometimes accompanied by ravens (*Corax corax*) and coyotes.

The raven nests in trees, on powerline towers and on buildings on the Hanford Site. Like the magpie, there have been no surveys of nesting raven populations on the Hanford Site. The raven is a predator at goose nests located on islands in the Columbia River, where it damages goose eggs when parent geese are temporarily away from the nest.

There are very few crows (*Corvus brachyrhynchos*) on the Hanford Site. Crows are generally more abundant on the agricultural lands surrounding the Site, and they nest in ornamental trees in the city of Richland. While ravens seem to favor the open, shrub-steppe land of the Hanford Site, crows prefer cultivated lands and even more urban environments.

Corvids are widely distributed throughout the shrub-steppe region. They often forage upon the carcasses of vertebrate animals killed by accident, disease or predation. They also can destroy bird eggs and kill the young of other birds. They are regarded as pests by fur trappers and other humans. Corvids sometimes are killed when they trigger the meat-baited traps, but more often they simply set off the trap, which necessitates resetting. Corvids are often poisoned as nontarget organisms during vertebrate pest control programs. Field researchers are also often vexed by Corvids that remove or

mutilate aluminum foil tags used in marking plants or special locations in field studies. Even with their penchant to be nuisances, however, the Corvids appear to be "holding their own" in the shrub-steppe region.

Section III. Insects and Related Arthropods

Insects and related arthropods (mites, spiders, etc.) are ubiquitously distributed in the semi-arid, shrub-steppe regions of the world. Insects are most conspicuous when population eruptions result in damages to rangeland vegetation or crops. Consequently, most applied research has been directed toward understanding "pest" species, especially Orthoptera (Wakeland 1959, Smith 1954, Mulkhern et. al 1964, Rogers and Uresk 1974); Hymenoptera, mostly ants (Hewitt et. al 1974, Lavigne 1969); Coleoptera, beetles (Graber et al. 1931, Rickard 1970a and b, Ahearn 1971); and Lepidoptera (Wildermuth and Caffrey 1916, Walkden 1943, 1950).

The ecological role of insects in sagebrush-bunchgrass communities is that of consumers. Sometimes they become so abundant that they can completely defoliate sagebrush shrubs as does the sagebrush moth (Aroga websteri), or they compete with grazing livestock for shoots of grasses and forbs as does the migratory grasshopper (Melanoplus sanguinipes). Insects are important food sources for birds. Much of the food that horned larks, meadowlarks and sage sparrows feed their young is insects (Rotenberry 1978). Small birds of prey such as burrowing owls also rely heavily on insects as a food base (Fitzner et al. 1981).

In this section, we examine the seasonal abundance and taxonomic composition of some important insects and related arthropod groups inhabiting the Hanford Site and their population responses to wildfire, cattle grazing and to long-time-abandoned wheat fields that have been occupied by nearly pure stands of cheatgrass for 40 years.

BIOMASS IN A SAGEBRUSH-BUNCHGRASS COMMUNITY

The insects and related arthropod populations inhabiting a relatively undisturbed sagebrush-bunchgrass community on the ALE Reserve were investigated as a part of an ecological characterization study that included plants, small mammals and birds (described earlier in this book). The techniques used for collecting and analyzing samples are described by Rogers (1977) and Rogers and Woodley (1978). The general procedure was a circular-framed drop-trap (0.5 m^2), followed by Berlese funnel extraction of plant materials vacuumed from the ground surface.

Peak aboveground biomass in a 3-year study period, 1972-1974, occurred in June 1973 and averaged 400±152 mg/m^2 (Figure 7.10). However, values of

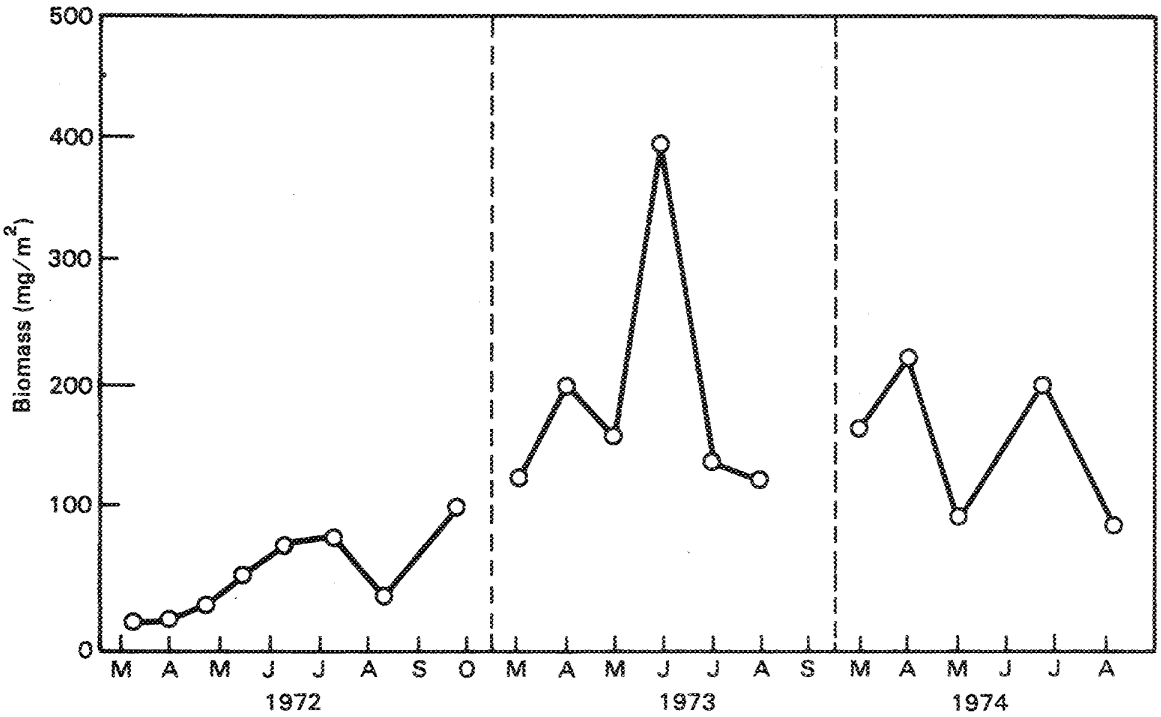

FIGURE 7.10. Biomass of Insects and Related Arthropods at Monthly Intervals in a Sagebrush-Bunchgrass Community, Spring and Summer 1972, 1973 and 1974

200 mg/m^2 were more representative. These values are similar to those reported for other semi-arid regions: 506 mg/m^2 for a shortgrass prairie community in Texas (Huddleston et al. 1972), about 270 mg/m^2 for a tallgrass community in Oklahoma; (Risser et al. 1981), and 200 mg/m^2 for a shortgrass community in Colorado (Kirchner 1977).

The beetles (Coleoptera), flies (Diptera), butterflies and moths (Lepidoptera), and grasshoppers (Orthoptera) accounted for over 70 percent of the total insect-arthropod biomass (Figure 7.11). The beetle biomass was contributed mostly by a single family, the Tenebrionidae (darkling beetles). One species, Philolithus densicollis, was particularly abundant.

Herbivores (tissue feeders, sap feeders, and pollen and nectar feeders) and omnivores accounted for most of the biomass (Figure 7.11). The herbivore, omnivore, and predator groups ranked first, second, and third, respectively, for each of the 3 study years. The rankings of the trophic groups did not differ significantly between years ($\alpha = 0.05$); indeed, a rank order analysis found them nearly identical (Dixon and Massey 1969). Kirchner (1977) reported similar findings for a shortgrass prairie community in Colorado.

Insects and related arthropods were not uniformly distributed in the sagebrush-bunchgrass community. The greatest numbers occurred within the bunchgrass clumps. Grass clumps occupied 15 percent of the ground but contributed 93 percent of the insect-arthropod biomass (Table 7.20). Sagebrush canopies occupied only 5 percent of the ground area, and these contributed only 3 percent of the biomass. However, individual shrubs support a greater biomass by virtue of their greater size. The "bare" areas that occur between

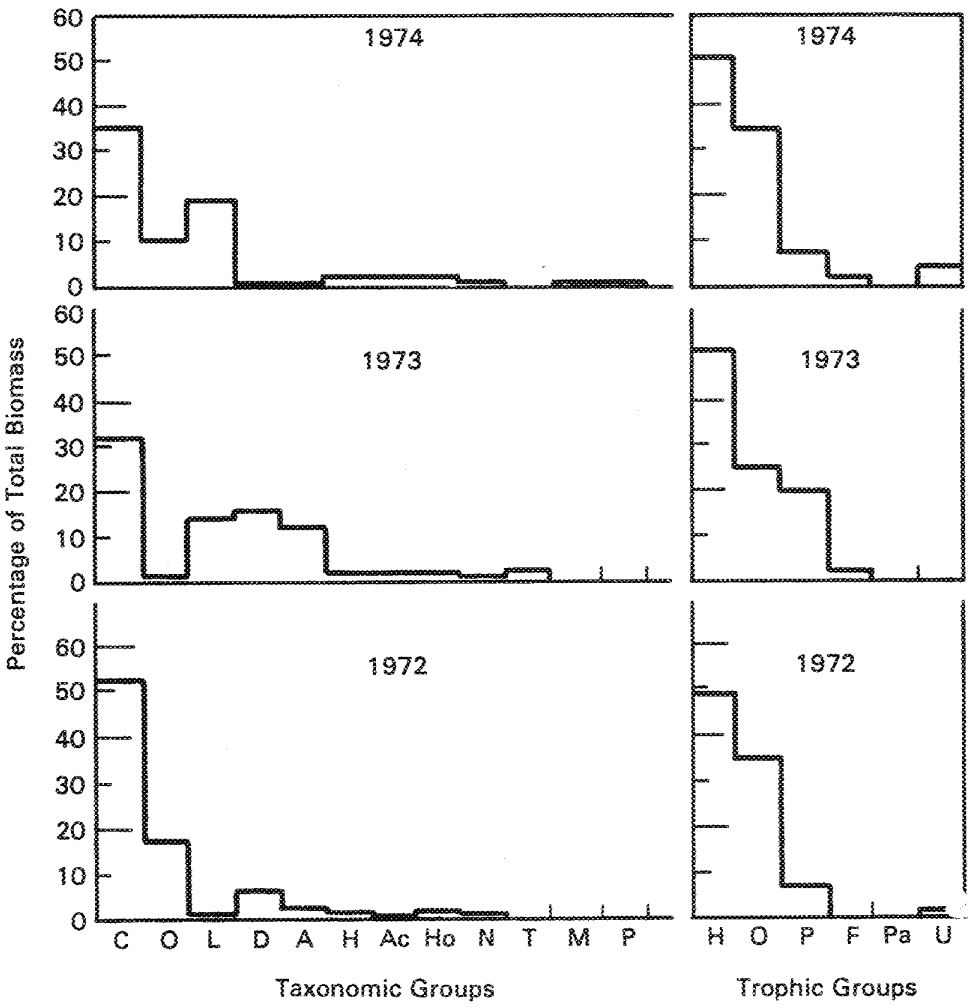

FIGURE 7.11. Percentage of Total Biomass Contributed by Various Taxonomic and Trophic Groups of Insects and Related Arthropods in a Relatively Undisturbed Sagebrush-Bunchgrass Community, 1972, 1973, and 1974

C =	Coleoptera	Ac =	Acarina
O =	Orthoptera	Ho =	Homoptera
L =	Lepidoptera	N =	Neuroptera
D =	Diptera	T =	Thysanura
α =	Areneida	M =	Mecoptera
H =	Hymenoptera	P =	Psocoptera

Trophic Groups: H = Herbivore O = Omnivore F = Fungivore
P = Predator U = Unknown

TABLE 7.20. Percentage of Insect and Related Arthropod Biomass in Relation to Microhabitats in the Sagebrush-Bunchgrass Community

Microhabitat	Total Area Occupied by Microhabitat (%)	Insect and Related Arthropod Biomass Contributed (%)
Bunchgrass Clumps	15	93
Sagebrush Shrubs	5	3
"Bare" Area(a)	80	3
Flying Insects(b)	100	1

(a) Areas between sagebrush and bunchgrass clumps.
(b) Insects that could not be associated with a particular microhabitat.

the bunchgrass clumps and sagebrush shrubs (80 percent of the ground area) also contributed 3 percent of the biomass. Flying insects accounted for only 1 percent of the total biomass.

The beetles were by far the major contributors to biomass in both grass clumps and in shrubs. The rankings of the various taxonomic groups associated with grass clumps and sagebrush shrubs did not differ significantly between years for either category ($\alpha = 0.05$, based on rank order analysis; Dixon and Massey 1969). The darkling beetles (*Oxygonodera hispidula*, *Coniontis setosa*, *Eleodes granulata* and other *Eleodes*) were especially abundant in the leaf litter associated with grass clumps and beneath sagebrush shrubs.

Of all the animals in the shrub-steppe, the insects and related arthropods are represented by the greatest number of species (several hundred currently documented). At times, they occur in overwhelming numbers and can consume large quantities of plant material, including leaves, stems, flowers and seeds.

Insect-arthropod populations are thought to have important roles in community dynamics. The breakdown of dead plant materials is accelerated by their foraging activities. This provides space for the establishment of new

plants and also accelerates the rate at which essential mineral nutrients are released to the soil for reuse by plants. The infiltration of rainfall and snowmelt into the soil profile is also improved and sustained by burrowing activities. This way insects and related arthropods help to regulate the rates of shoot and root production, decomposition of dead plants and the sustenance of soluble mineral nutrients within the root zone.

Most sagebrush-bunchgrass communities in Western North America have been modified to some degree by a variety of human activities practiced over the past 150 years. It therefore often remains unclear whether the wide variations observed in insect-arthropod populations are within the "normal" range of flux or whether the populations are responding to some externally imposed human-induced perturbation.

Relatively large segments of undisturbed plant communities such as those on the Arid Lands Ecology Reserve are useful places to study the dynamics of insect and related arthropod populations because they can provide insights as to population performances in the virtual absence of human-induced perturbations.

RESPONSE TO WILDFIRE

The purpose here is to describe, as completely as limited data permit, the influence of summer wildfire on the insect-arthropod populations inhabiting a relatively undisturbed (by human influences) sagebrush-bunchgrass community. In the first plant-growing season following a wildfire during the summer of 1973, density and biomass of insects and related arthropods associated with the bunchgrass clumps and sagebrush shrubs was greater on the unburned (control) area than it was on the burned area (Figure 7.12). Burning suppressed the

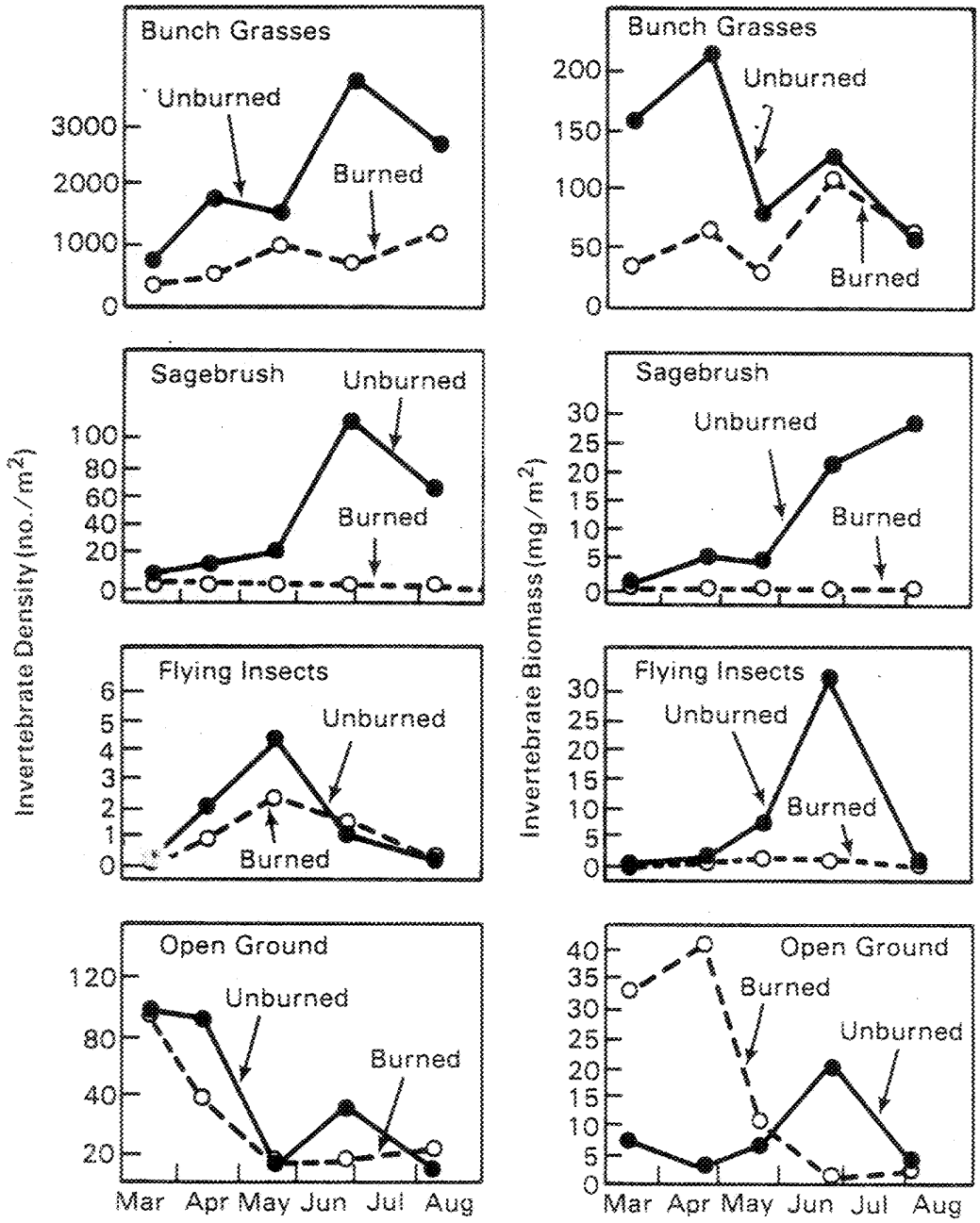

FIGURE 7.12. Density and Biomass of Insects and Related Arthropods in Bunchgrass Tussocks, Sagebrush Shrubs and Open Areas Between Grasses and Shrubs in Burned and Unburned Portions of a Sagebrush-Bunchgrass Community

populations that had been associated with grass clumps and shrubs. The biomass of flying insects on the unburned plot peaked in June, but there was no corresponding peak for the burned plot. Population densities in burned and unburned portions followed a similar trend, and peak density occurred in May. The insects and arthropods associated with the open ground peaked early in the spring and declined steadily with the onset of summer.

Other studies have produced varied results. Rice (1932) described a reduction (exclusive of ants) following a fire in an Illinois prairie. Bulan and Barrett (1971) reported a long-term reduction in arthropod density and biomass from a burned grassland in Ohio. A burned site in Kansas produced a significantly greater biomass of arthropods, but the collections were made by sweep nets, and did not include populations dwelling on the surface or in the litter (Nagel 1973).

Percentages of total biomass for the major taxonomic groups are summarized in Figure 7.13. A statistical comparison (using Spearman's rank order analysis) failed to detect statistically significant differences ($\alpha = 0.05$) between burned and unburned areas in the sagebrush-bunchgrass communities (Dixon and Massey 1969), suggesting that relationships between the taxonomic categories did not change after summer burning. The lack of a statistically significant change in taxonomic or trophic rankings of insects and related arthropods indicates that the population diversity was not altered by summer burning; only the magnitude was diminished as measured by biomass. Burning did not appreciably change the dominant taxonomic categories, but it did favor the Hymenopterans and depress the Lepidopterans. The Lepidopterans, mostly noctuid moths, were mostly associated with the bunchgrass clumps. Moths are relatively

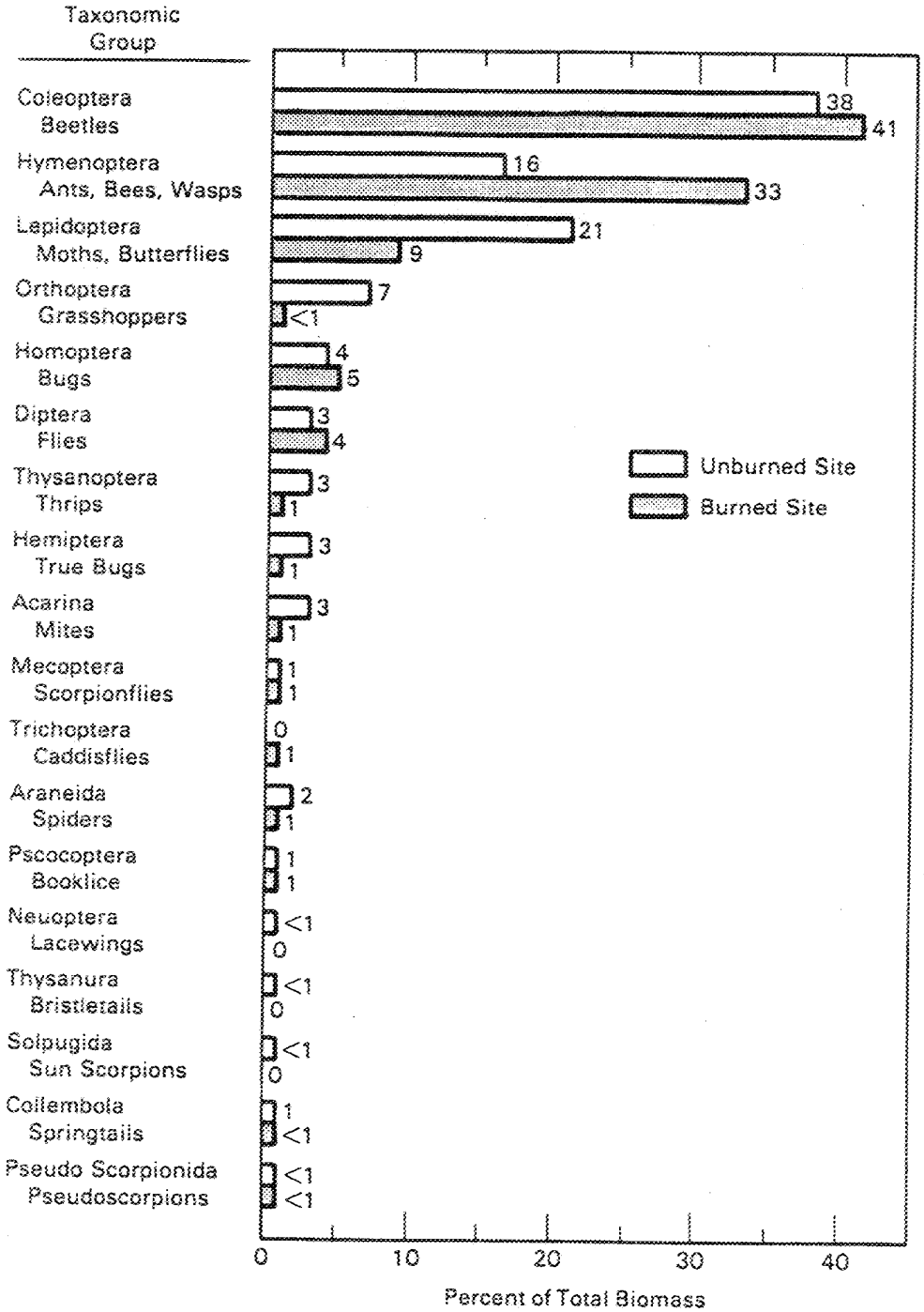

FIGURE 7.13. Contribution of Various Taxonomic Groups to the Percentage of Total Biomass of Insects and Related Arthropods in Burned and Unburned Portions of a Sagebrush-Bunchgrass Community During the First Growing Season Following a Summer Wildfire

large, so only a few of these included in a sample can appreciably influence the biomass. The observed increase in hymenopteran biomass was contributed by ants.

On the trophic level, the herbivores and omnivores dominated the total biomass (Figure 7.14). The herbivores, mostly tissue-feeding insects, contributed 60 and 50 percent for the burned and unburned areas, respectively. Herbivores also dominated the population density values, contributing 25 percent in the unburned portions of the plant community. There was, however, less of a distinction among the other trophic levels. Many of the predators and

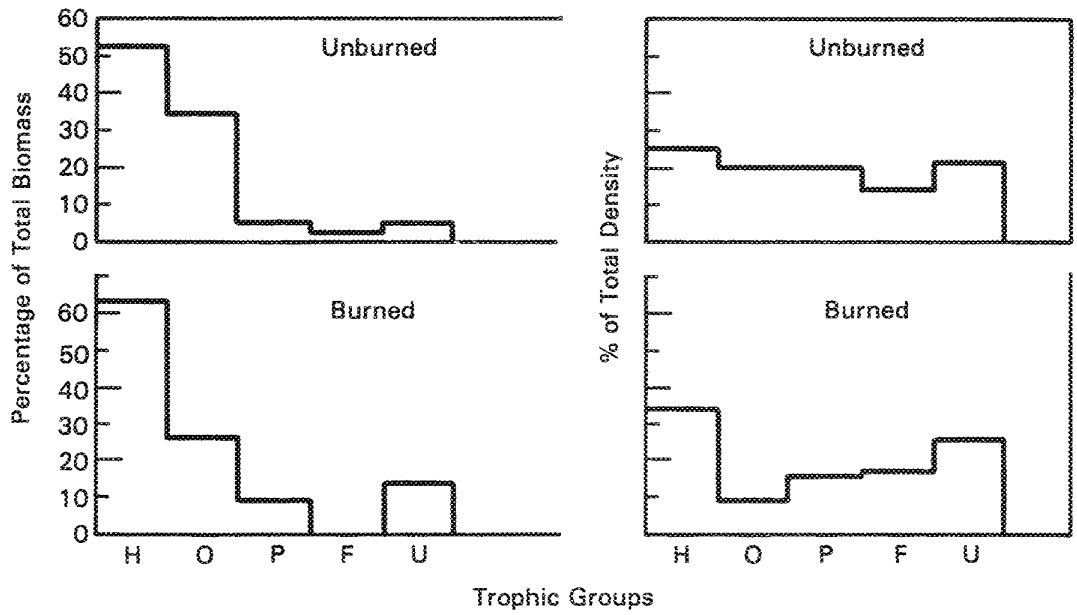

FIGURE 7.14. Contribution of Major Trophic Groups to the Percentage of Total Insect and Related Arthropod Biomass in Burned and Unburned Portions of a Sagebrush-Bunchgrass Community During the First Growing Season Following a Summer Wildfire

(H = Herbivore, O = Omnivore, P = Predator, F = Fungivore, U = Unknown)

fungivores were mites, so while their densities contributed 15 and 20 percent of total density, their contributions to total biomass were much smaller. The unknown category was primarily comprised of immature mites, and a trophic determination was not attempted for this group.

Fire has been used as a means of controlling insects pests since the early days of civilization (Komarek 1970). Nevertheless, the responses of insect populations have received only limited study (Bulan and Barrett 1971). While it seems clear that summer wildfire creates changes in the biomass of sagebrush-bunchgrass communities, the reasons for the observed suppression of insects and related arthropods cannot be fully explained. The heat generated during burns is mostly of light to moderate intensity and may especially damage the summer-dormant populations. The microclimate changes associated with the habitat after burning may be the most important factor regulating the population response. Burning alters the microclimate, and the burned zones are probably less favorable than the unburned zones. The rates at which the various insect populations are restored to burned portions of the community are therefore likely to be closely allied with rates of vegetation recovery and the amount of time required to restore microenvironments. If so, it may require many decades to restore sagebrush shrubs and their characteristic insect-arthropod populations.

RESPONSE TO CATTLE GRAZING

The influence of 3 consecutive years of moderately intensive spring grazing by steers upon the plants of a typical sagebrush-bunchgrass community

was discussed in Chapter 6. The purpose here is to compare insect and related arthropod populations in ungrazed (control) and grazed portions of the community.

Population densities of insects and related arthropods for the shrub, grass and open areas of the community were found to be similar for the grazed and ungrazed portions with the exception of bunchgrass clumps (Figure 7.15). During April and May 1974, population densities within bunchgrass clumps were much greater in the grazed area (Table 7.21). Densities of Acari (mites) were substantially greater during April and May, but not for the other months (more details on Acari densities in Table 7.22). Glycyrphagidae densities were relatively low in May. At the same time, members of the Caligonellidae were abundant. The Caligonellidae inhabit litter layers and may be either predaceous or phytophagous. There is little information in the published scientific literature concerning the behavior of glycerphagids in arid and semi-arid regions, but they are probably detritus feeders. Krantz (1971) noted that they often occur in grain warehouses and feed storage sheds on farms, where they feed on organic debris.

Both beetles and book lice (Psocoptera) were significantly (α = .05) more abundant within grass clumps that had been grazed by cattle. Anthicidae, Tenebrionidae, and a group of unidentified Coleoptera larvae accounted for most of the increase in beetle density. The anticids were all of the genus Notoxus and were mostly present as larvae. The feeding strategies of anthicid larvae are unknown. Oxygonodera hispidula was an abundant tenebrionid in the grass clumps. Adults feed mostly on cryptogams (Rogers et al. 1978).

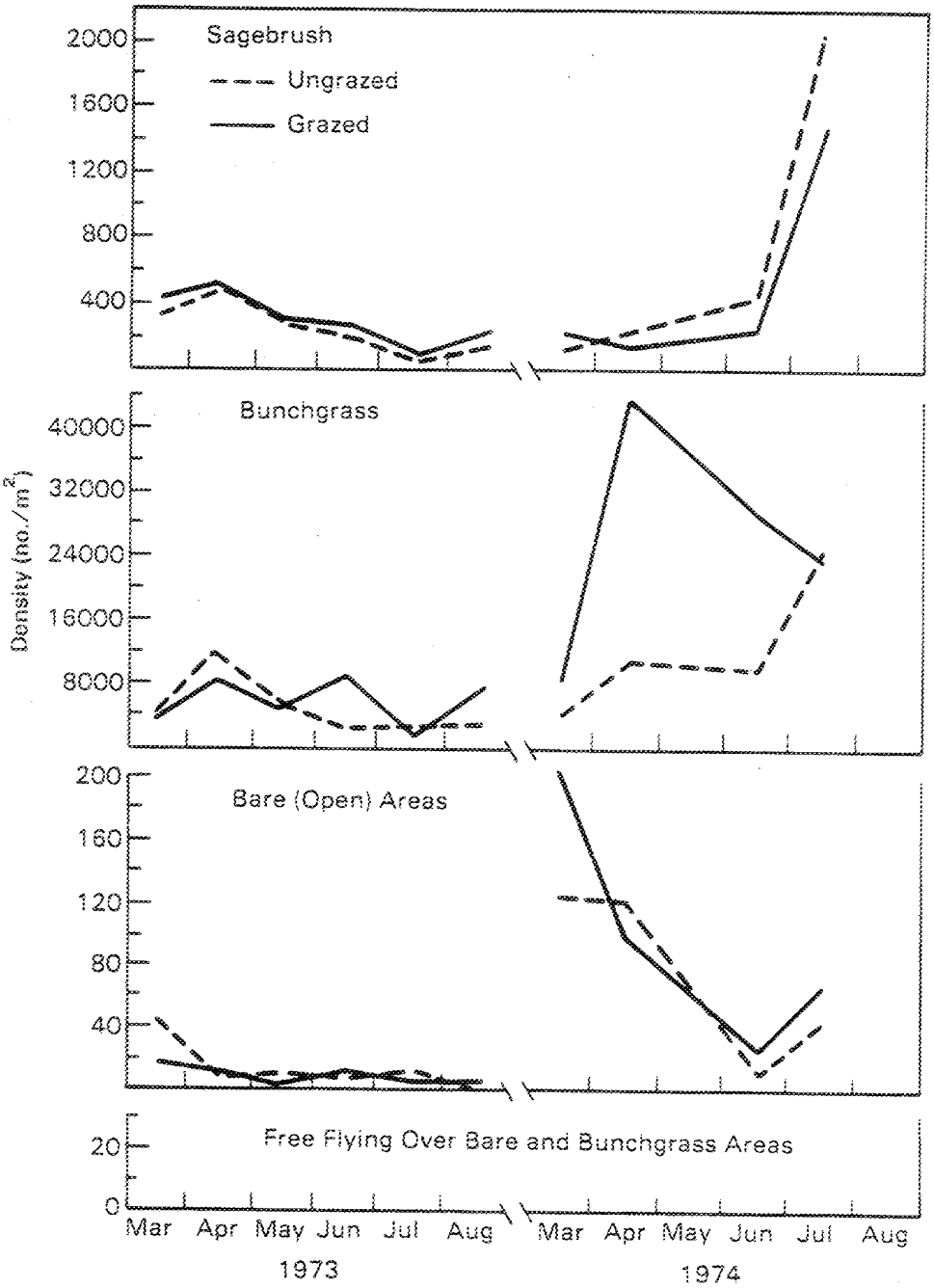

FIGURE 7.15. Densities of Insects and Related Arthropods for Sagebrush, Bunchgrass and Open Microhabitat in Grazed and Ungrazed Portions of a Sagebrush-Bunchgrass Community

TABLE 7.21. Insect and Related Arthropod Density by Major Taxonomic Groups for the Bunchgrass Clump Microhabitat in Grazed and Ungrazed Portions of a Sagebrush-Bunchgrass Community[a]

Taxonomic Group	April		May	
	Grazed[b]	Ungrazed[c]	Grazed[d]	Ungrazed[e]
Acari	4570 ± 1841	1389 ± 353	2638 ± 1364	1030 ± 205
Araneida	0	0	3 ± 2	5 ± 3
Coleoptera	10 ± 5	4 ± 3	95 ± 175	42 ± 14
Diptera	24 ± 18	26 ± 14	31 ± 13	10 ± 3
Hemiptera	10 ± 5	4 ± 3	18 ± 7	17 ± 2
Collembola	2 ± 2	61 ± 58	7 ± 55	79 ± 24
Homoptera	29 ± 16	46 ± 29	97 ± 38	173 ± 100
Hymenoptera	82 ± 43	232 ± 152	94 ± 96	32 ± 16
Lepidoptera	2 ± 2	4 ± 3	24 ± 10	22 ± 12
Psocoptera	2 ± 2	15 ± 15	138 ± 36[5]	30 ± 13
Thysanoptera	0	4 ± 4	12 ± 75	107 ± 35
Diplopoda	2 ± 2	0	0	0
Mecoptera	0	0	0	2 ± 2

(a) Values expressed in terms of no/m2 (x ± SE)
(b) n = 7 for all taxa
(c) n = 8 for all taxa
(d) Significantly different from ungrazed value (α = .10)
(e) Significantly different from ungrazed value (α = .05)

The Psocopterans in the samples were of the family Liposcelidae. Book lice are general feeders, consuming a variety of plant materials including fungi and detritus (Imms 1957).

Other investigators have reported a relationship between livestock grazing and increased abundance of insects. The increases appear to be most pronounced on pastures with a long history of grazing. Smith (1940) reported that insect abundance in a grazed pasture in Oklahoma was four times greater than in an ungrazed pasture. Hays (1927) and Crawford and Harwood (1964) found that

TABLE 7.22. Acari Density for the Bunchgrass Clump Microhabitat in Grazed and Ungrazed Portions of a Sagebrush-Bunchgrass Community[a]

Taxonomic Group / Taxa	April		May	
	Grazed[b]	Ungrazed	Grazed	Ungrazed
Astigmatidae				
Acaridae	0	0	306 ± 55	40 ± 37
Glycyrphagidae	4322 ± 1781	986 ± 428	3 ± 3	10 ± 10
Unknown	58 ± 34	13 ± 9	0	0
Cryptostigmata				
Camisiidae	0[b]	13 ± 4	39 ± 39	22 ± 7
Cosmochthoniidae	0	2 ± 2	10 ± 6	10 ± 5
Gymnodamaeidae	17 ± 7	61 ± 21	73 ± 32	72 ± 31
Haplochthoniidae	17 ± 17	4 ± 3	83 ± 73	37 ± 24
Oribatulidae	0	2 ± 2	46 ± 27	5 ± 2
Passalozetidae	2 ± 2	0	7 ± 7	37 ± 20
Mesostigmata				
Laelapidae	0	0	6 ± 6	2 ± 2
Parasitidae	0	15 ± 15	3 ± 3	15 ± 8
Zerconidae	22 ± 11	22 ± 17	0	2 ± 2
Unknown	0	2 ± 2	0	0
Prostigmata				
Anystidae	0	0	9 ± 6	5 ± 3
Bdellidae	3 ± 2[b]	35 ± 10	238 ± 84	421 ± 110
Caligonellidae	14 ± 8	11 ± 5	1706 ± 1205	114 ± 52
Cryptognathidae	0	0	1 ± 1	2 ± 2
Cunaxidae	12 ± 10	41 ± 17	4 ± 4	0
Erythraeidae	5 ± 5	0	6 ± 3	2 ± 2
Eupodidae	0	0	0	2 ± 2
Nanorchestidae	0	0	25 ± 10	2 ± 2
Penthaleidae	3 ± 3	9 ± 5	0	0
Raphignathidae	0	0	0	5 ± 5
Smaridiidae	0	0	0	2 ± 2
Tenuipalpidae	2 ± 2	0	0	0
Tetranychidae	19 ± 8	41 ± 9	7 ± 5	20 ± 14
Trombidiidae	0	4 ± 4	0	0
Unknown	0	0	1 ± 1	10 ± 7
Unknown Acari (Mostly immature)	75 ± 40	128 ± 70	62 ± 6+	195 ± 55
Total	4571 ± 1841	1389 ± 353	2635 ± 1364	1028 ± 205

(a) Density expressed as no/m^2 (x ± SE); n = 7 for April and N = 8 for May
(b) Significantly different from ungrazed value (α = .05)

insect populations were consistently higher on grazed pastures. Reed and Blocker (1972) noted a peak density of 1700 and 1346 insects per square meter for grazed and ungrazed pastures in a tallgrass prairie pasture. Peak abundances of 320 and 499 individuals per square meter for ungrazed and grazed pastures, respectively, were reported for a Texas pasture (Huddleston et al. 1972). On the basis of these data, it seems likely that cattle grazing favors the abundance of certain insects.

In fact, it appears that chronic cattle grazing has a greater impact on populations of insects and related arthropods than does occasional wildfire. The greatest impact of cattle grazing in the sagebrush-bunchgrass community is depletion in the amount of standing dead grass and leaf litter associated with grass clumps. Unlike wildfire, which increases in the summer when grasses are mature and dormant, cattle grazing occurs in the spring months when shoots are physiologically most active. Furthermore, wildfire is an erratic event, but cattle grazing is chronic--it usually occurs year after year. Wildfire is damaging to sagebrush shrubs; cattle grazing does little direct damage. Fire temporarily removes standing dead grass, but shoot production is not greatly impaired. In some ways it may be actually enhanced for a few growing seasons.

INSECTS AND RELATED ARTHROPODS IN A CHEATGRASS COMMUNITY

As was emphasized in Chapter 6, one of the most dramatic botanical changes that has taken place in the shrub-steppe region of southeastern Washington has been the massive invasion of cheatgrass following the introduction of domestic livestock grazing and plowing more than 100 years ago. Cheatgrass dominates abandoned agricultural fields (old-fields) for decades, and shoot

production consistently exceeds that of the native sagebrush-bunchgrass communities (Rickard et al. 1976). Seed production is also greater, as is the amount of dead shoot material (standing dead and litter). The purpose here is to compare taxonomic, trophic and seasonal variations of insect and related arthropod populations in a cheatgrass community with those of an adjacent sagebrush-bunchgrass community that supports very little cheatgrass.

Peak insect-arthropod biomass occurred in May in the old-field cheatgrass community and in June in the sagebrush-bunchgrass community, but the peak biomass was greater in the sagebrush-bunchgrass community (Figure 7.16).

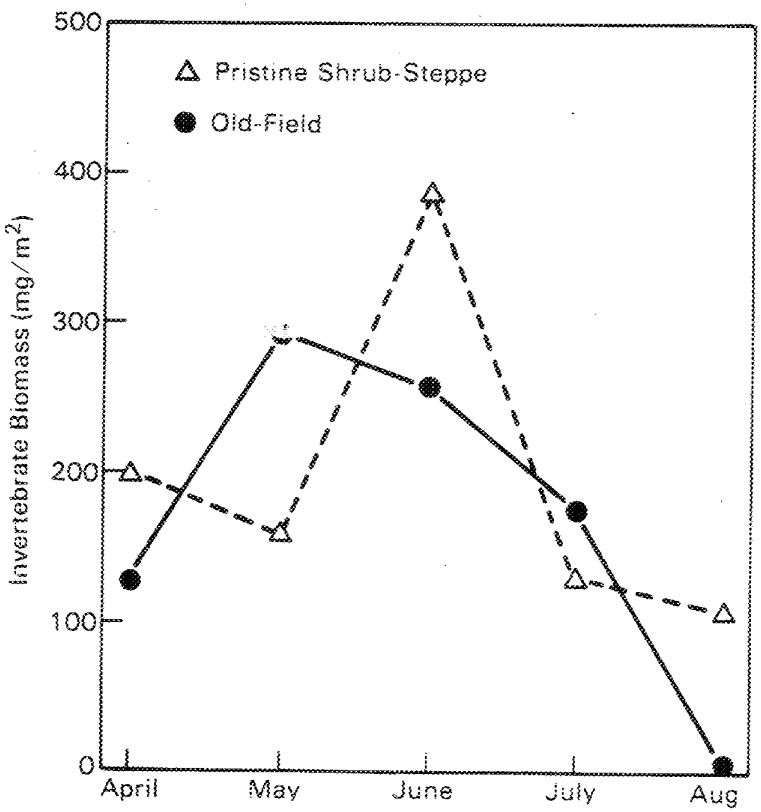

FIGURE 7.16. Insect and Related Arthropod Biomass Associated with Undisturbed Sagebrush-Bunchgrass and Cheatgrass Communities on the ALE Reserve

Biomass declined in both communities, as the plants matured and shoots dried from summer drought. Minimum values were recorded in August for the cheatgrass community; the decline in biomass in the sagebrush-bunchgrass community was not so precipitous. These patterns may indicate a response to the tendency of the sagebrush-bunchgrass community to remain green and succulent for a longer time than the cheatgrass community.

The most rapid increase in insect-arthropod biomass corresponded to the period of plant growth. As was noted in Chapter 6, shoot growth was accelerated in April and May in the cheatgrass community and in May and June for the large bunchgrasses in the sagebrush-bunchgrass community.

In the cheatgrass community, two taxonomic groups, beetles and grasshoppers, accounted for 71 percent of the total biomass (Figure 7.17). None of the other 10 taxonomic groups contributed greater than 7 percent of the total biomass. In the sagebrush-bunchgrass community, Coleoptera, Diptera, Lepidoptera, Hymenoptera (ants, bees and wasps), and Araneida (spiders) contributed 90 percent of the insect-arthropod biomass. The herbivores and omnivores dominated the biomass in both communities. A test rank order did not indicate significant differences among the various trophic groups in the two communities (Dixon and Massey 1969). However, predators comprised a much larger proportion of the population in the sagebrush-bunchgrass community (20 percent) than in the cheatgrass community (4 percent).

Cheatgrass communities appear to be less acceptable as habitat for some insect-arthropod taxa that inhabit native sagebrush-bunchgrass communities. If cheatgrass-dominated communities continue to occupy more and more of the rangeland area in the shrub-steppe region, the overall populations of insects and related arthropods may become less diverse. However, total biomass may

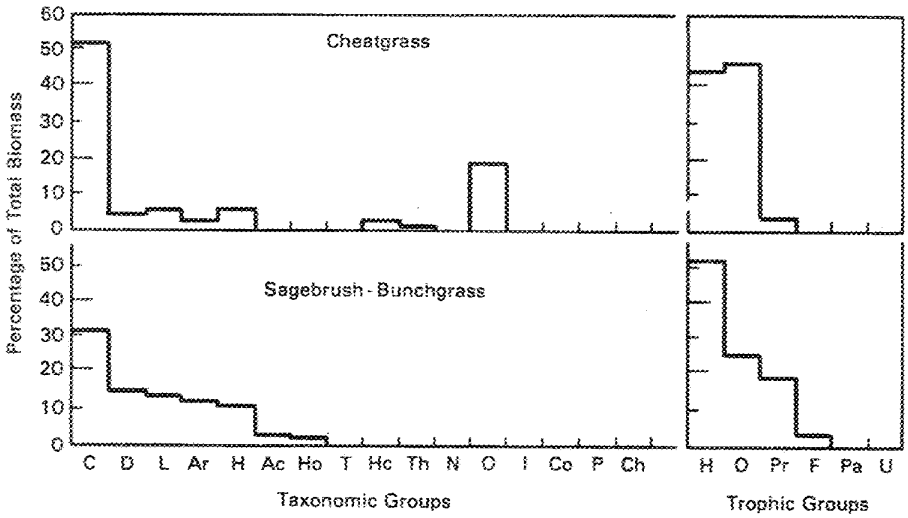

FIGURE 7.17. Percentage of Total Biomass of Insects and Related Arthropods Contributed by Taxonomic and Trophic Groups in Sagebrush-Bunchgrass and Cheatgrass Communities

C = Coleoptera	D = Diptera	L = Lepidoptera
Ar = Areneida	H = Hymenoptera	Ac = Acarina
Ho = Homoptera	T = Thysanura	He = Hemiptera
Th = Thysanoptera	N = Neuroptera	O = Orthoptera
I = Isoptera	Co = Collembola	P = Psocoptera
Ch = Chilopoda		

Trophic Groups: H = Herbivore, O = Omnivore, P = Predator, F = Fungivore, Pa = Parasite, U = Unknown

tend to increase in response to the greater shoot production provided by the cheatgrass communities. As an example, the grasshoppers Melanoplus sanguinipes can be very abundant in cheatgrass communities (Rogers and Uresk 1974).

BEETLES ON THE HANFORD SITE

Beetles are among the most conspicuous of the ground-dwelling insects in dryland plant communities on the Hanford site. According to Rickard (1970a and b) the larger beetles are represented by four genera, Eleodes, Philolithus, Stenomorpha (Tenebrionidae) and Calosoma (Carabidae).

Their abundance varies according to the season of the year and also from place to place. To determine the influence of elevation and its change in microclimate upon the distribution and relative abundance of beetles a pitfall trap survey was conducted at eight stations arranged along an altitudinal gradient ranging from 100 to 1100 meters (Rickard 1970b). In general, the catch of beetles was greatest at low altitudes and least at the highest altitudes (Figure 7.18). The data indicate that the cooler and moister microclimates associated with higher elevations are less favorable for beetles than are the warmer and drier microclimates at the lower altitudes. Trap catches of Elodes, Philolithus, and Calosoma generally were greater at the low altitudes; however, Stenomorpha did not occur in bitterbrush-sagebrush-cheatgrass stations at the lowest altitude. At the same time, Philolithus was barely represented at the highest altitude. Trapping at other locations on the Hanford Site has supported the validity of general observations that Philolithus populations are absent (or nearly so) at the higher elevations and that Stenomorpha is absent from the lowest elevations (Rickard 1970b and 1971, Rickard et al. 1974).

Eleodes species were trapped in greatest numbers in May, but the populations remained active from March through November (Figure 7.19). Calosoma catches were greatest in April, and they disappeared from the catch in July. Stenomorpha and Philolithus were trapped in September, October, and November. Beetles were not active in winter. Stenomorpha and Philolithus were very abundant at times, which seems to be characteristic of this group of tenebrionids. However, there had been no long-term studies of the year-to-year changes in abundance of beetles in the same location until a study was

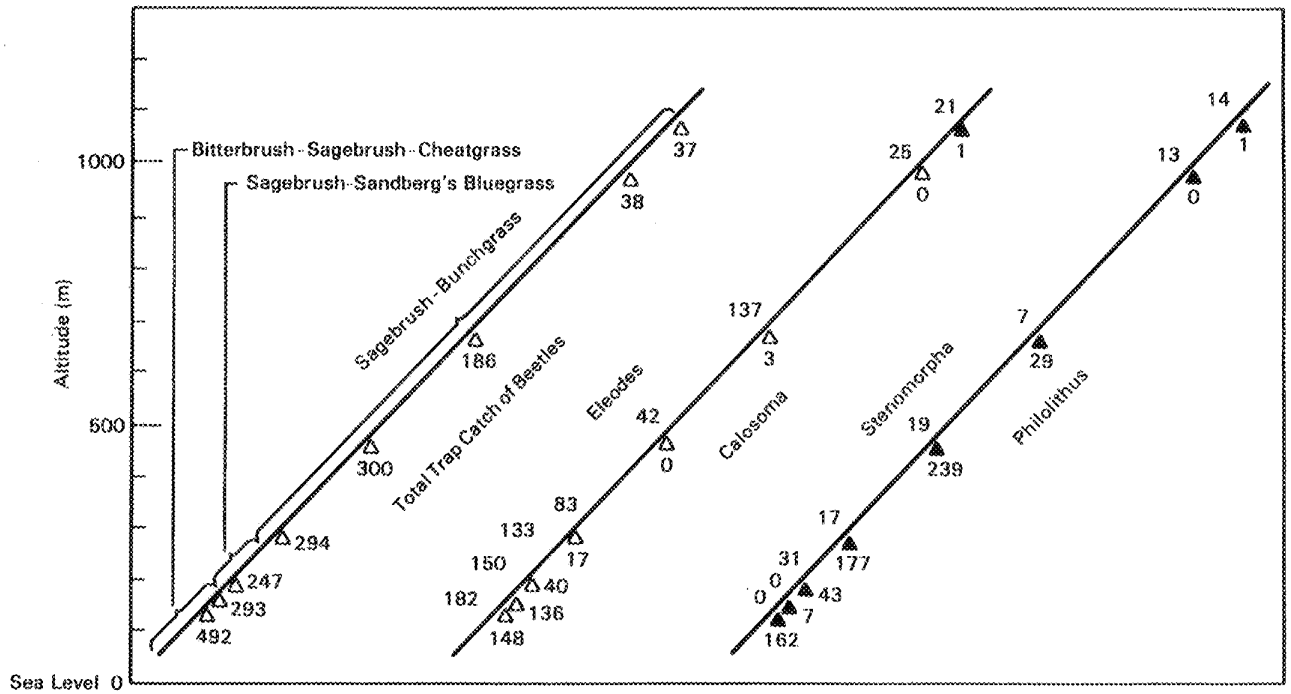

FIGURE 7.18. Trap Catches of Beetles at Eight Stations Along an Altitudinal Gradient Ranging from 100 to 1100 Meters

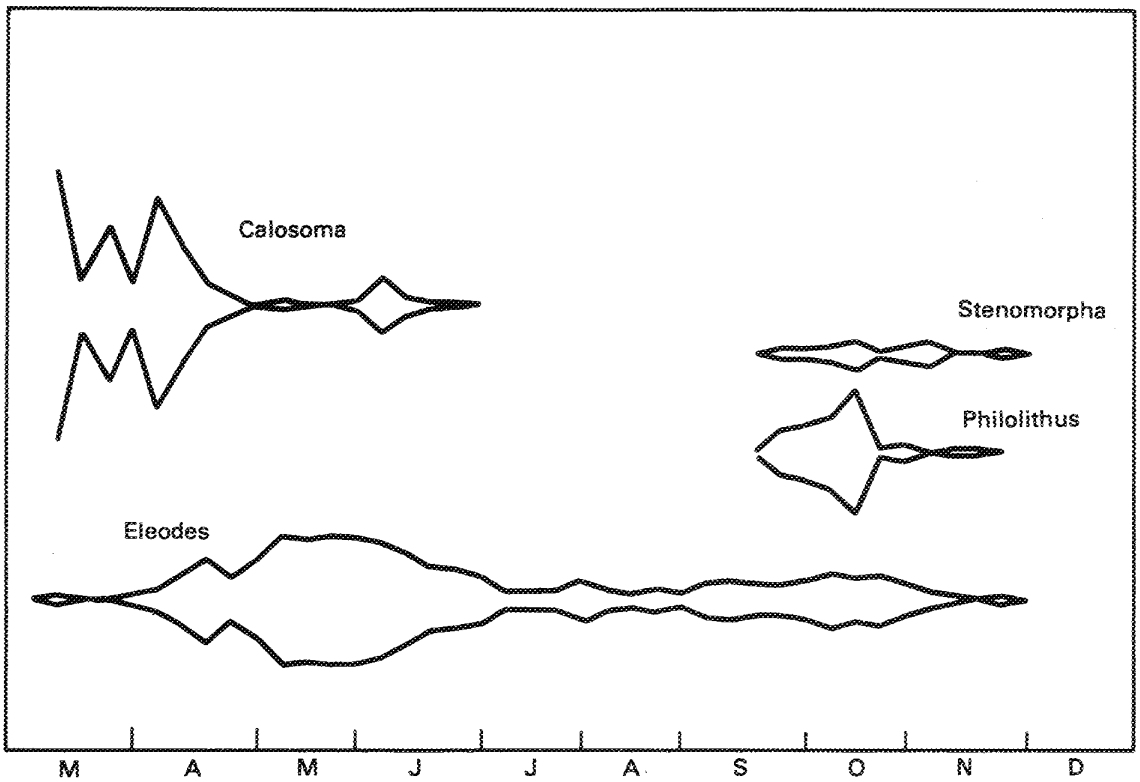

FIGURE 7.19. Seasonal Distributions of Ground-Dwelling Beetles (The areas of one polygone are indices of beetle abundance as judged from pitfall trap catches.)

initiated on the ALE Reserve in 1963 (Rickard and Haverfield 1965, Rogers and Rickard 1977). During 21 years of trapping, the peak trap catches have ranged between a low of 10 in 1984 to a high of 1235 in 1963 for Philolithus and between a low of 23 in 1982 and a high of 1223 in 1963 for Stenomorpha (Figure 7.20). At no time has the catch of either species been as great as it was in 1963. It is not unreasonable to expect that beetle populations will again attain a similar population peak. The plant community has not been grazed by livestock nor has it been burned by wildfire. The only human

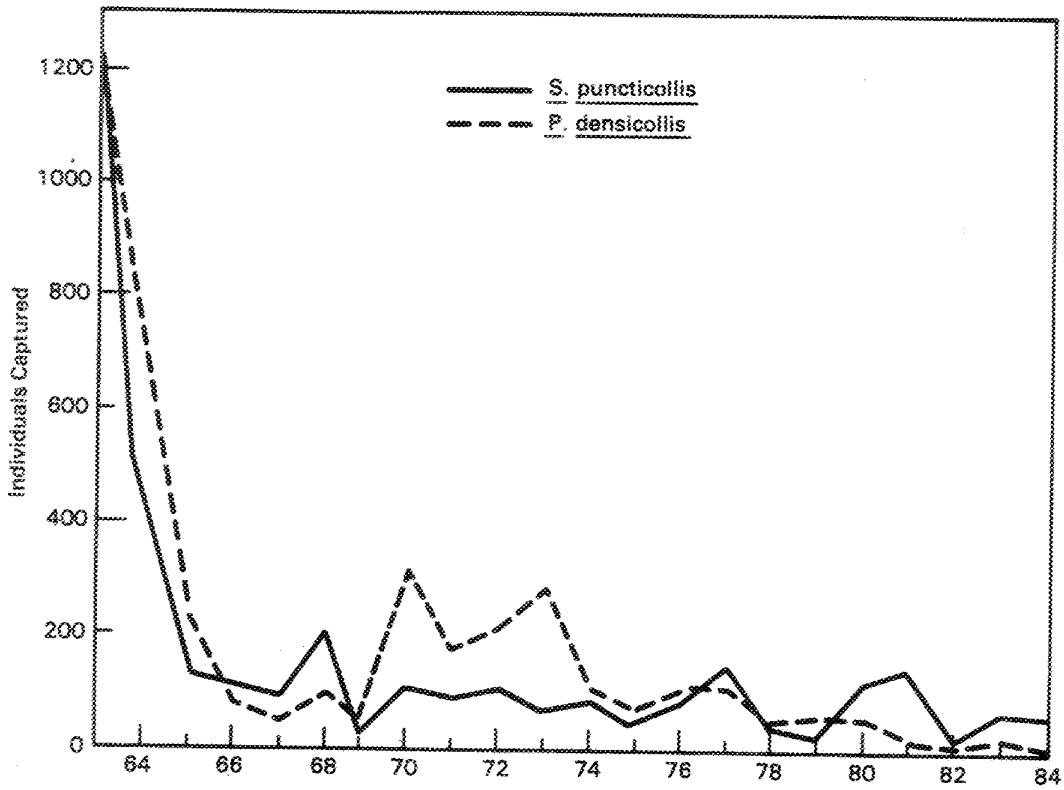

FIGURE 7.20. Total Numbers of Stenomorpha puncticollis and Philolithus densicollis Beetles Captured from 1963 Through 1984

intrusion is by investigators that briefly visit the community for trap-and-release beetle trapping. It appears that large variances in year-to-year populations are "normal" for these beetles.

The combinations of abiotic and biotic factors that are required to produce extreme beetle population peaks are mostly unknown. Hinds and Rickard (1973) conducted a multiple regression analysis for the first 9 years of data in this set. The general decline in the catch of Philolithus was primarily correlated with November minimum soil temperatures and October precipitation

2 years prior to the emergence of adults. A secondary correlation followed October minimum soil temperatures during the trapping period. Ninety percent of the variability was attributed to these three factors.

However, the same factors have not been reliable predictors of Philolithus populations in the years after 1973. Population eruptions of Philolithus have occurred from year to year at different places on the ALE Reserve. Apparently, variations in temperature and precipation are not highly corrleated with peak beetle populations especially since temperatures and precipitation are relatively uniform over broad zones on the ALE reserve (Rotenberry et al. 1976). Localized population eruptions are probably determined by more subtle factors. Diseases, parasites, predation, and competition are possible contributors to population suppression, but little is known about these factors in darkling beetle populations.

Life histories of Stenomorpha and Philolithus are characterized by a short-lived adult stage. Adults live for about 30 days (Brown 1973). They begin to emerge from the soil in September and remain active aboveground until the onset of freezing weather in November or December. The adults do not overwinter. The females of both species have long ovipositors, and females deposit their eggs a few millimeters below the soil surface. The eggs of Philolithus hatch in 14 days; the eggs of Stenomorpha require about 60 days. The behavior of the larvae is mostly unknown but they are probably detritivores, moving laterally and vertically on the soil profile and confining most foraging to the upper decimeter of soil. The adults forage upon a variety of plants, including mosses and lichens, but they are capable of laying eggs without benefit of feeding (Rogers et al. 1978).

Although Philolithus and Stenomorpha populations have been associated with sagebrush-bunchgrass communities for centuries, they have had access to pure cheatgrass communities on the Hanford Site for only about 40 years. According to Rickard et al. (1974), Philolithus and Stenomorpha both occur in cheatgrass communities. Adult beetles move relatively slowly and deliberately, so they can be counted inside frames surrounding square-meter plots. They were particularly abundant in a cheatgrass community in 1968 (Figure 7.21). At peak count, 11.2 beetles were present per square meter, 7.8 Stenomorpha and 3.4 Philolithus. Beetle biomass at peak counts was estimated at 2.4 g/m^2. This amounts to about 24 kg/ha. Of this amount, 20 kilograms was provided by Stenomorpha, attributable to its greater density and also to its greater size, 240 milligrams per individual as compared to 118 milligrams for Philolithus. The beetle biomass exceeded that of all vertebrate animals combined.

In the autumn of 1969 there were very few adult Philolithus in the cheatgrass community (Figure 7.21). The trap catch of Stenomorpha was also much less in 1969 than in 1968 but the decline was proportionally not as great for Stenomorpha as it was for Philolithus. Direct counts of beetles in 1968 showed Stenomorpha to be more abundant than Philolithus, but pitfall traps showed the opposite trend (Figure 7.21). This evidence suggests that pitfall trapping overestimates Philolithus populations in relation to Stenomorpha populations. Clearly, sampling methodology continues to plague efficient and meaningful studies of wild animal populations.

The tenebrionid beetles are important contributors to animal biomass in dryland plant communities throughout the Hanford Site. Populations vary greatly from year to year and from place to place. There are two general

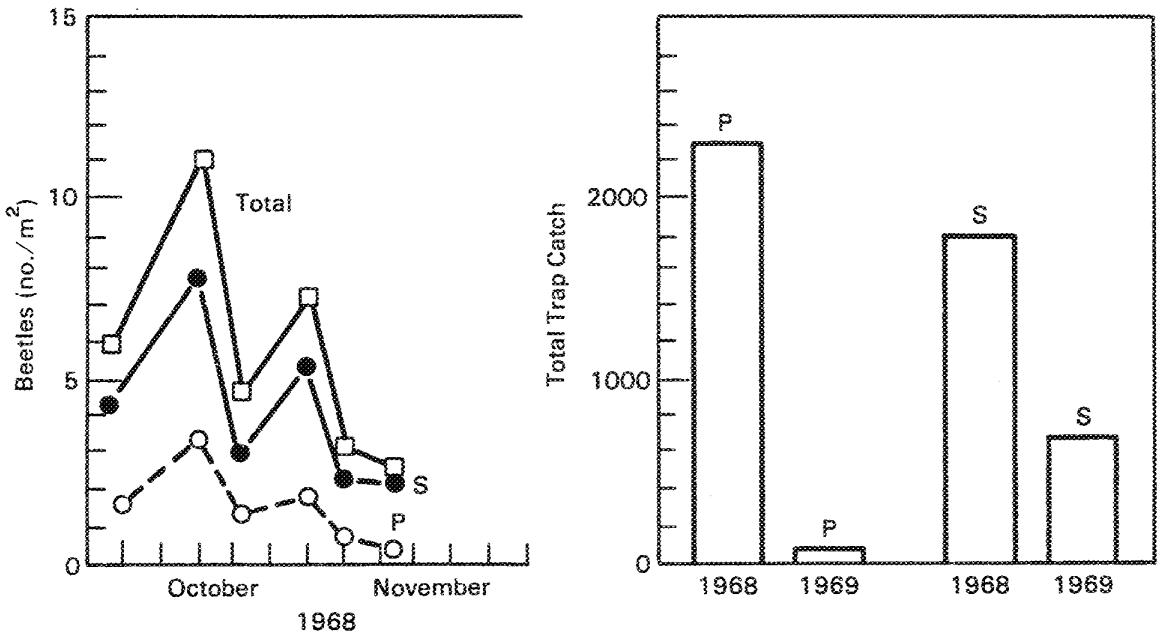

FIGURE 7.21. Trap Catches and Direct Counts of Philolithus (P), and Stenomorpha (S) in a Cheatgrass Community, 1968 and 1969

survival strategies. Eleodes species breed in spring and summer and are long-lived as adults. As adults, they also have malodorous "defensive" secretions that probably help to protect them from direct predation by mammals, birds and snakes. Adults of Philolithus and Stenomorpha are active for only a few weeks in the early autumn. They have no offensive odor. Of the two survival strategies, autumn breeding appears to be the most successful in terms of biomass production but not so effective at producing different species e.g., Eleodes. Autumn breeders place the eggs in the soil at the onset of autumn rains; soil moisture is present throughout the winter and early spring so that the early larvae stages are not subjected to extreme dessication. However, the larvae are subjected to the coldest temperatures of each year.

The ecological role of beetles in plant communities is manifested mostly by the larval populations. The larvae eat plant detritus and burrow through the soil profile, and these activities hasten the breakdown of dead plants and aid in moisture percolation.

GRASSHOPPERS (ACRIDIDAE) OF THE HANFORD SITE

Grasshoppers are among the most conspicuous of the large flying insects on the Hanford Site. They occur in all dryland plant communities. Like the beetles, grasshopper populations vary from place to place and also from year to year. On the Hanford Site, grasshoppers have been studied only to the extent that taxonomic collections have been made and the diets of a few species examined (Sheldon and Rogers 1978, Rogers and Uresk 1974). A list of the Acrididae inhabiting the ALE Reserve is shown below.

Ageneotettix deorum (Thomas)
Amphitornus coloradus (Thomas)
Arphia pseudonietana (Thomas)
Aulocara elliotti (Thomas)
Circotettix undulatus (Thomas)
Conozoa wallula (Scudder)
Cratypedes neglectus (Thomas)
Hesperotettis viridis (Thomas)
Melanoplus bivittatus (Say)
Melanoplus cinereus (Scudder)
Melanoplus packardii (Scudder)
Melanoplus sanguinipes (F.)
Melanoplus yarrowii (Thomas)
Oedaleonotus enigma (Scudder)
Parapomala pallida (Bruner)
Psoloessa delicatula (Rehn)
Trimerotropis bilobata (Rehn and Heban)
Trimerotropis caeruleipennis (Brunner)
Trimerotropis fontana (Thomas)
Trimerotropis gracilis (Walker)
Trimerotropis pallidipennis (Burmeister)
Trimerotropis sparsa (Thomas)
Xanthippus lateritius (Saussure)

On the Ale Reserve, adult grasshoppers appear in late May, and peak populations usually occur in July. Populations of Melanoplus sanguinipes have attained densities of $50/m^2$ in cheatgrass communities (Rogers and Uresk 1974). However, peak populations are usually less than $4/m^2$. The feeding habitats of most grasshoppers have not been investigated, but some species are known to be selective (Mulkern 1967, Banfill and Brusven 1973, Ueckert and Hansen 1971). Grasshoppers inhabiting a cheatgrass community on the ALE Reserve were found to eat proportionally large amounts of yellow salsify (Tragopogon dubius) and prickly lettuce (Lactuca scariola) that were not as abundant in the community as were mustards (Sisymbrium and Descurainea) and cheatgrass (Rogers and Uresk 1974). Salsify and prickly lettuce tend to remain greener longer into the summer than the other plants, which may account for their greater use by grasshoppers.

Only a few of the many grasshopper species of shrub-steppe regions ever become abundant enough to damage crops or rangeland vegetation; as a consequence, the life history details of many grasshopper species are not well known. Clearly, because of their potential abundance, grasshoppers play at least some role in the long-term functions of shrub-steppe communities. Of all the insects, grasshoppers are generally thought to be the most important from the standpoint of shoot consumption. They are eaten by many birds and mammals, and are particularly important in the spring-summer diet of chukar partridges.

Section IV. Animals as Indicators of Radionuclide and Chemical Contamination

One of the most difficult problems of modern industrial technology is the long-term assessment of potentially toxic materials released to the environment. While it is desirable to avoid such releases, it is not always technologically possible in practice to contain all the waste materials that are generated. However, environmental concentrations of radionuclides, which are typically present in surface environments at nuclear industrial sites, have had little effect on either ecosystem function or on specific wildlife forms (Whicker 1980). For example, the long-lived, low-energy ^{129}I isotope discussed in Chapter 6 was found to be enriched over background in the thyroid glands of mule-deer on the Site, but at levels far too low to expect any deleterious health effect (Rickard and Price 1984). Radiocesium and other nuclides have been found in owl pellets and in the fecal debris cast from nests of the great blue heron, but at concentrations of no known biological significance (Cadwell and Fitzner 1984, Rickard et al. 1974).

Interest currently centers on the utility of wildlife for specialized monitoring purposes (e.g., determining patterns of concentration and dispersal) and the modeling of biotic transport, as described in Chapter 2 (Kennedy et al. 1985). Earlier studies pointed to minor but unexpected radionuclide dispersal patterns by black-tailed hares and mule deer on the Hanford Site (O'Farrell and Gilbert 1975, Eberhardt et al. 1984). In recent years, some success has been had in quantifying the foraging ranges of animals in relation to contaminant distributions and source locations, and in then using this information as an efficient way to map the dissemination patterns of contaminants. Bees, ants and some birds appear promising for such purposes,

both because of their potential bioconcentration and biomagnification and because their foraging ranges are appropriate to the scale of typical contaminated areas.

INSECTS

For example, research indicated that the extensive distribution of honeybee colonies (*Apis millifera*) in parts of the Northwest could provide an in-place and accessible network from which contaminants could be monitored. The concept was tested in 1983 by determining concentrations of heavy metals in 100 bee colonies distributed over a 7500-square-kilometer area impacted by smelter operation (Bromenshenk et al. 1985). Isopleths of concentration over the area were established by kriging (Figure 7.22). The maps so produced

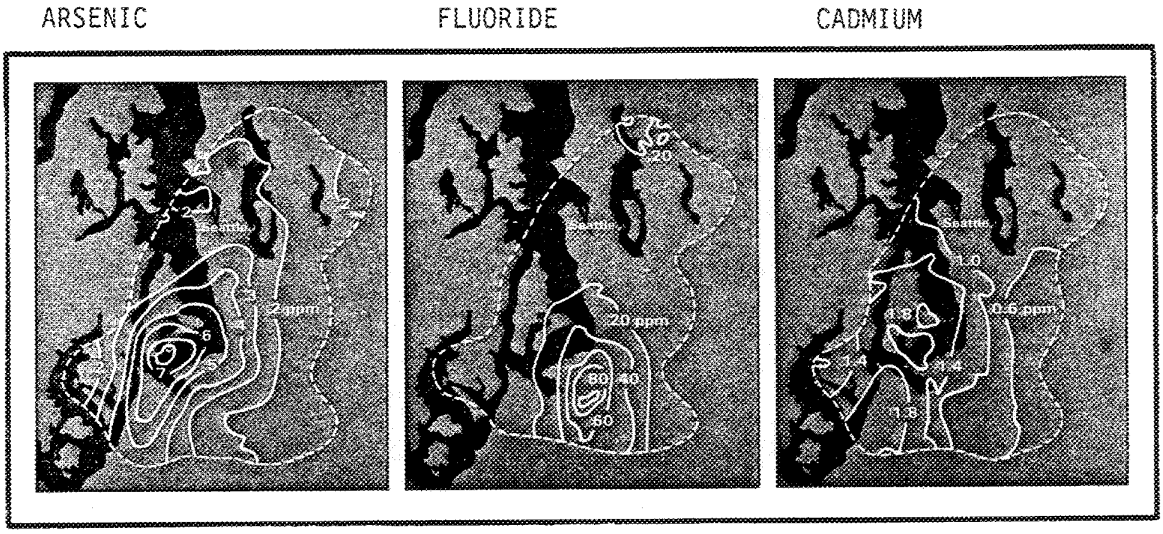

FIGURE 7.22. Kriging Estimates (dashed lines) for Arsenic, Fluoride, and Cadmium in Honeybees Used to Map Areas of Contamination in Puget Sound, Washington (For arsenic, the error cutoff point was limited to 50%, for fluoride, 75%, and for cadmium it was 60%. From Bromenshenk et al. 1985)

corroborated similar isopleth maps available from local regulatory agencies, which were based on measured soil concentrations and deposition calculated from atmospheric models. However, the agency maps described only a very small area of contamination, circumscribed by the 5-6 ppm arsenic isopleth shown in Figure 7.22. In contrast, the honeybee monitoring data enabled the mapping of both difficult locations, as well as a far more extensive area out to the isopleth for a 2-ppm arsenic concentration, as shown in the figure.

The approach was also explored on the Hanford Site, where foraging distance for the honeybees was 7.4 kilometers, similar to the 6.5 kilometer distance reported by Gary (1975). Hives were placed near radioactive waste areas. The bees collected pollen and nectar from nearby flowering plants. The collected pollen showed an enhanced concentration of ^{137}Cs as shown in Figure 7.23, although the honey did not. Honeydew from aphids, plant resins (for conversion into propolis, a sticky substance used in hive construction) and water were also collected. In this process, the bees act as tiny "dustmops," inadvertently picking up particles from the air and those deposited on foliar surfaces; hence the ^{137}Cs collected is of airborne origin. Measured concentrations of ^{137}Cs in the pollen of bees having access to waste zones ranged up to 623 pCi/g dry weight, while samples from hives in nonradioactive zones measured about 0.2 pCi/g. Unlike the heavy-metal example described earlier, the source of radiocesium contaminant was highly restricted, and only a few of the bee hives showed detectable pollen radioactivity.

Some insects are also useful for monitoring the fate of surface-buried wastes containing a "marker" chemical compound. Preliminary studies were conducted, for example, on harvester ants of the genus Pogonomyrmex. These ants are ubiquitous to the shrub-steppe region, and may move significant

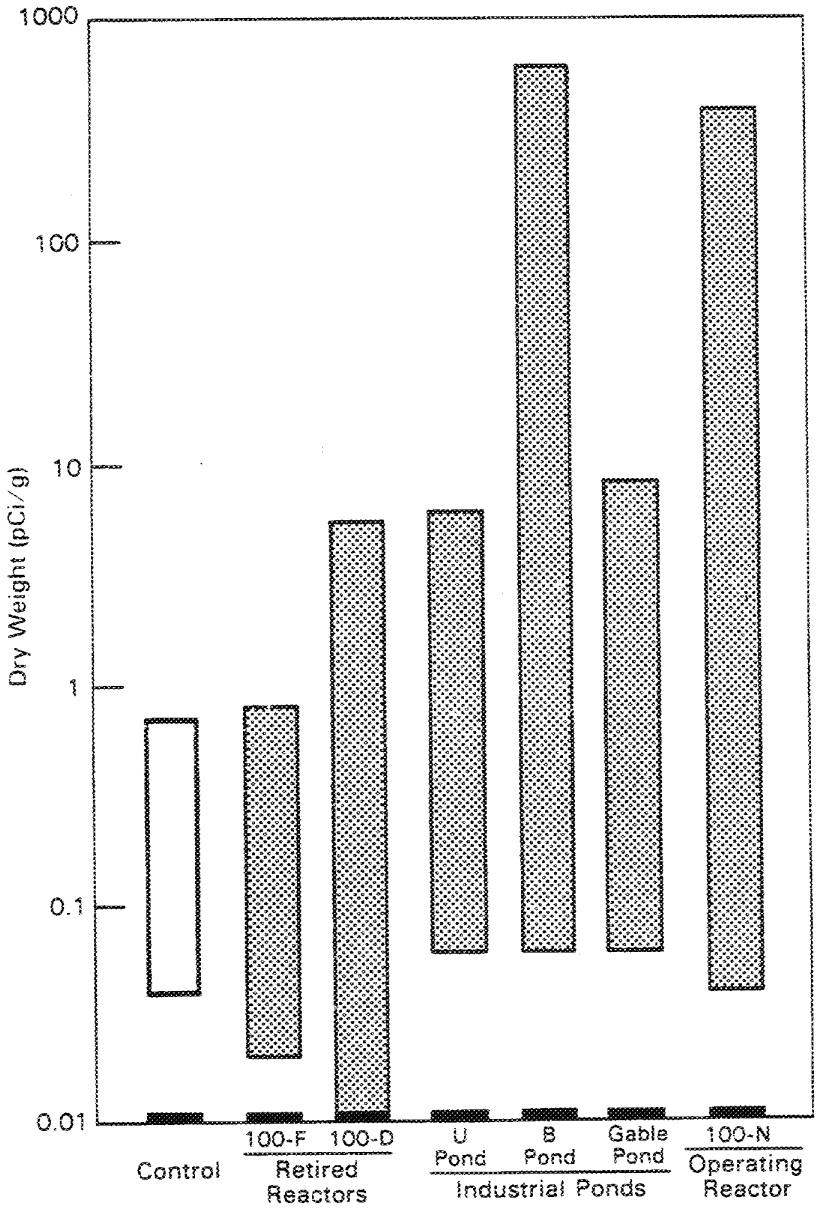

FIGURE 7.23. Radioactive Cesium (^{137}Cs) in Honeybee Pollen Collected at Retired and Operating Reactor Areas and Industrial Ponds on the Hanford Site (The bars show the range of values.)

quantities of soil. For typical colonies, the amounts of soil moved per hectare are roughly equivalent to the weight of an average man per year.

Typical mounds ("ant hills") contain an extensive system of belowground tunnels and chambers. The mounds are 1-2 decimeters in height and 3-4 decimeters in diameter. Although a mound usually consists of fine-textured soil, its surface is covered by small pebbles. The vegetation around the actual colonies is clipped by ants, and there is usually a bare zone around each mound. Burrowing depths between 2 and 3 meters have been reported for ants (Headlee and Dean 1908, Severin 1955, Willard 1964, Lavigne 1969, Erickson 1972, Rogers and Lavigne 1974). Wheeler and Wheeler (1963) observed increased numbers of ant colonies in pastures that were overgrazed. Ant colonies were observed by Fitzner et al. (1979) to be four times greater on the low-level radioactive waste burial grounds of the Hanford Site (195 colonies/ha) than in adjacent undisturbed sites (49 colonies/ha). It is not clear whether the preference for the waste burial site was a selection of open habitat or a reflection of a greater abundance of seed produced by the annual plants that had invaded the burial site.

Burrowing depths and calculated volumes of soil exhumed by five colonies of Pogonomyrmex owyheei are displayed in Table 7.23. On the average, 1800 cubic centimeters of soil was excavated, similar to the 2000 cubic centimeter volume reported for colonies in the meadow-steppe region of eastern Colorado (Rogers 1972). Approximately 11 percent of the soil moved was from depths greater than 1.5 meters.

Ants unexpectedly invaded an experimental soil column in an outdoor facility and burrowed 1 meter, the length of the column. Radioisotopes that had been placed in a thin (1 centimeter) soil layer 20 centimeters below the

TABLE 7.23. Maximum Depths of Volumes of Soil Excavated by Five *Pogonomyrmex owyheei* Colonies in Southeastern Washington

Colony	Amount (cm^3)	Maximum Depth (m)
1	2468	2.7
2	3147	2.5
3	1518	2.5
4	713	2.0
5	1027	1.7
$\bar{x}$ ± S.E.	1774 ± 453	2.3 ± 0.2

surface were detected at the bottom of the column after ants had burrowed from the surface. It is not known whether the ants themselves moved the isotopes downward through the soil column or whether it moved by gravity after the initial tunnels were made. Bohn et al. (1979) described a process by which soil particles break and fall from the walls of vertical cracks in soil, thereby moving soil from upper layers downward. Similar movements could have occurred in the tunnels made by the ants.

In the absence of ants, surface contamination was detected in a few of the soil columns described in the previous paragraph. Close visual observations of the soil surface revealed granular soil particles that were contaminated with radioactive isotopes. It was later confirmed that bees (*Agapostemon texanus*) had dug into the soil. Their tunnels were approximately 0.4 centimeters in diameter and ranged between 0.3 and 0.5 meters in depth. A comparison was made between the amount of isotope brought to the surface by the burrowing bees and that transported by plants through root-shoot pathways. Calculations showed that a single bee, while making a single tunnel, could transport to the surface a quantity of isotope located 20 centimeters below ground that was

equivalent to the amount that could be moved by the root-shoot pathway by one metric ton of barley growing in the same soil! Such activity certainly indicates a potential mechanism for contaminant transport.

BIRDS

Birds are well-recognized as useful indicators of both chemical and radionuclide contamination. Their foraging areas can be quantified, as shown in Figure 7.24, in such a way that in principle they may be used in much the same way as bees. Birds' biomagnification potential suggests a greater utility for tracing contaminants than has been realized in most monitoring practice. Hawks and owls that nest on the Hanford Site, for example, prey upon small mammals that in turn may have had direct access to various radionuclides associated with low-level radioactive waste disposal zones or with obsolete reactor buildings.

Several bird species on the Hanford Site have been examined as potential candidates for quantitative monitoring (Rickard et al. 1978, Fitzner et al. 1982, Rickard and Fitzner 1985). For example, Cadwell and Fitzner (1984) found that owl pellets collected within the Site boundaries had greater concentrations of radionuclides than pellets collected offsite (Table 7.24). This indicates that the prey animals on the Hanford Site have had access to radionuclides that were not available to them at the offsite locations. The data also show greater concentrations of radionuclides in barn owl pellets than in pellets of the great-horned owl, possibly because of different foraging areas or prey items for the different owl species.

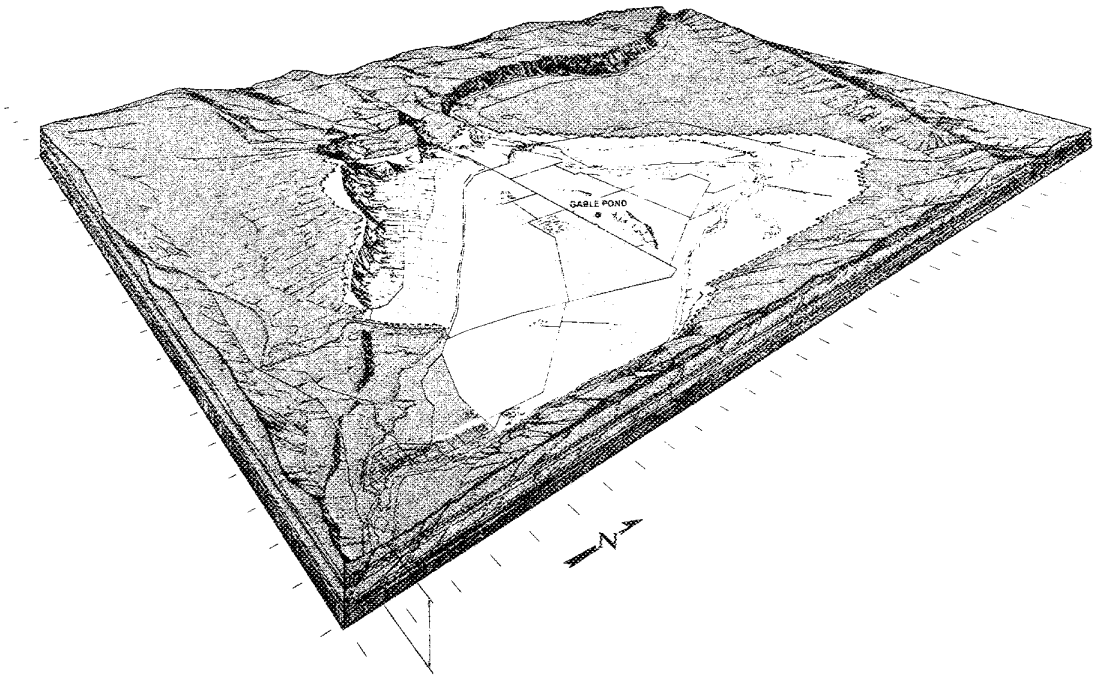

FIGURE 7.24. Foraging Ranges (shaded elipse) of Northern Harriers nesting on the Hanford Site (Foraging ranges are estimated at 300 km^2 for harriers, unusually large compared to 10 km^2 for other nesting hawks.)

TABLE 7.24. Selected Radionuclides (pCi/g dry wt.) in Regurgitated Pellets of Owls on and off the Hanford Site (Cadwell and Fitzner 1984)

	Hanford Site		Off Site
Radionuclide	Barn Owl	Great-Horned Owl	Barn Owl
^{137}Cs	6.0	1.7	ND
^{60}Co	9.0	0.41	ND
^{54}Mn	5.6	0.19	ND
^{155}Em	2.0	0.18	ND

ND = Not detected

The great blue heron has also been examined by chemical analysis of the debris cast from nests containing juveniles. On the Hanford Site, heavy metals (lead, cadmium and mercury) in the nest debris cast from the heron colony were present in lesser concentrations than they were in the nest debris collected at an urban-industrial area in western Washington and in a semi-wild area in northern Idaho (Table 7.25).

Such debris was used by Rickard et al. (1978) to determine quantities of ^{137}Cs that may have been injested by the herons nesting on the Hanford Site. Heron nests occur at well-defined, semi-permanent locations. Parent birds collect fish from the Columbia River and nearby lakes and ponds and bring them back to the nests to feed their young. These fish contain varying amounts of ^{137}Cs, depending on their habitat, i.e., industrial ponds, Columbia River or the seep lakes associated with offsite irrigation canals. By collecting the feces and debris cast from active heron nests, an indication was obtained of the concentrations of ^{137}Cs present in heron foods brought to different nests in the colony. Rickard and Fitzner found that some of the heron nests received more ^{137}Cs than others (nests 1 and 5 in Table 7.26), suggesting that the parent herons at these particular nests were foraging in places inhabited by fish with greater concentrations of ^{137}Cs. The industrial ponds

TABLE 7.25. Average Lead, Cadmium and Mercury Content (ppm ± standard error) in Debris Cast from Heron Nests at Colonies in Washington and Idaho (Fitzner et al. 1982)

Location	Lead	Cadmium	Mecury
Lake Chatcolet, Idaho	46 ± 7.4	1.8 ± 0.08	0.28 ± 0.011
Tacoma, Washington	29 ± 5.3	0.19 ± 0.020	0.17 ± 0.019
Hanford Site	3.3 ± 0.35	0.45 ± 0.040	0.10 ± 0.007

on the Hanford Site are known to contain fish with enhanced concentrations of ^{137}Cs (Rickard et al. 1981), and these could be the origin of the enhanced levels of ^{137}Cs detected in the debris cast from some of the heron nests. However, one of the unknown features of nesting herons on the Hanford Site is the distance at which parent herons forage from their nests in search of food. The lower levels of radiocesium in the debris of certain nests in the same colony probably represent background concentrations that have been introduced to the environment as worldwide fallout from nuclear weapons testing.

Habitat destruction, a dramatic change in historic habitat, or excessive commercial exploitation are the usual reasons given for the extirpation and extinction of bird species on a worldwide basis. However, in recent years, releases of synthetic and naturally occurring toxic chemicals into the surface environment from various industrial processes and commercial uses have caused death and impaired reproductive success in high-trophic-level birds. The recognition of potentially harmful toxic chemical buildup in the surface environment has prompted studies of "wildlife toxicology" and awareness of a need for sensitive environmental monitoring programs.

TABLE 7.26. Radioactive Cesium (^{137}Cs)[a] in Debris Cast from Heron Nests on the Hanford Site (Rickard et al. 1978)

	Nest Identification Number							
Collection Period	1	2	3	4	5	6	7	Avg.
18 Apr to 9 May	36	5.4	3.9	13	18	23	11	16.8
10 May to 30 May	47	9.0	2.9	15	70	15	13	24.6
31 May to 20 June	25	4.7	2.9	11	30	11	5.7	12.9
AVERAGE	36	6.4	3.2	13	39	16	9.9	18.1

(a) ^{137}Cs pCi/g dry wt.

Chemical pesticides used in agriculture, such as endrin, are toxic to local populations of game birds as well as the target rodents. For example, death and impairment of reproduction in a nesting Canada goose population along the Columbia River in eastern Oregon occurred when field-foraging geese ate grain treated with heptachlor, an organic insecticide used to prevent wireworm damage to germinating wheat (Blus et al. 1979). To remedy this harmful effect to an important wildlife resource, different kinds of insecticides with less potential for toxicity to wildlife are being used by area wheat farmers.

Controlled releases of radioactive materials from Hanford Site facilities have never been observed to accumulate in the tissues of wild birds to the point where they could be expected to be harmful to health or reproduction; nevertheless, surveillance programs that include wild birds in the sampling protocols provide information on the biological availability of radionuclides that is obtainable only by sampling the biotic components of the environment.

MOBILE ANIMALS

It is extremely difficult to correlate the release of environmental contaminants from a limited or local source with accumulation of these contaminants in the bodies of animals and plants. The task is even more difficult when the sample involves mobile animals. The accumulation of contaminants by animals is usually a gradual process, requiring weeks or months before the animal tissues reach their maximum concentrations, and generally, there is no way of assessing how long an animal has used a contaminated area prior to its collection for sampling purposes. For example, concentrations of ^{137}Cs in muscle tissue of American coots collected from a contaminated industrial waste

pond ranged from nearly zero to more than 2000 pCi/g-dry weight (Cadwell et al. 1979). The range of concentrations indicated that some of the coots sampled were probably new arrivals that had not yet accumulated ^{137}Cs in their muscles, while other coots had resided on the pond for sufficient periods of time to accumulate a body burden of ^{137}Cs. Similar inconsistencies have been found in deer sampled for monitoring purposes at Hanford and elsewhere. In these situations, radiotelemetry becomes a valuable tool for obtaining the necessary quantitative parameters of home range and residence time.

In situations like those indicated above, residence time and home range or foraging range become critical parameters for the quantitative development of monitoring observations. Despite frequent use of mule deer (Odocoileus hemionus) in monitoring studies (Price et al. 1985), surprisingly little information has been available on their movement patterns and activities, even when they have been equipped with radio-transmitters. However, home range and residence patterns for mule deer were recently established by conducting radio-telemetry studies of 37 deer living within approximately 1200 square kilometers on the Hanford Site (Eberhardt et al. 1984). As shown in Figure 7.25, the home range of Hanford deer was established at 39.3 ± 4.6 km2 (±95% elliptical confidence limit). This home range is quite small relative to the area of the Site as a whole. Other data obtained at the same time by this procedure included activity patterns and detection of periodic "trips" away from the home range area.

The telemeter approach was subsequently applied to the evaluation of radionuclide concentration data for deer exposed to an area containing low-level ^{90}Sr contamination (Eberhardt and Cadwell 1984). Residence history was

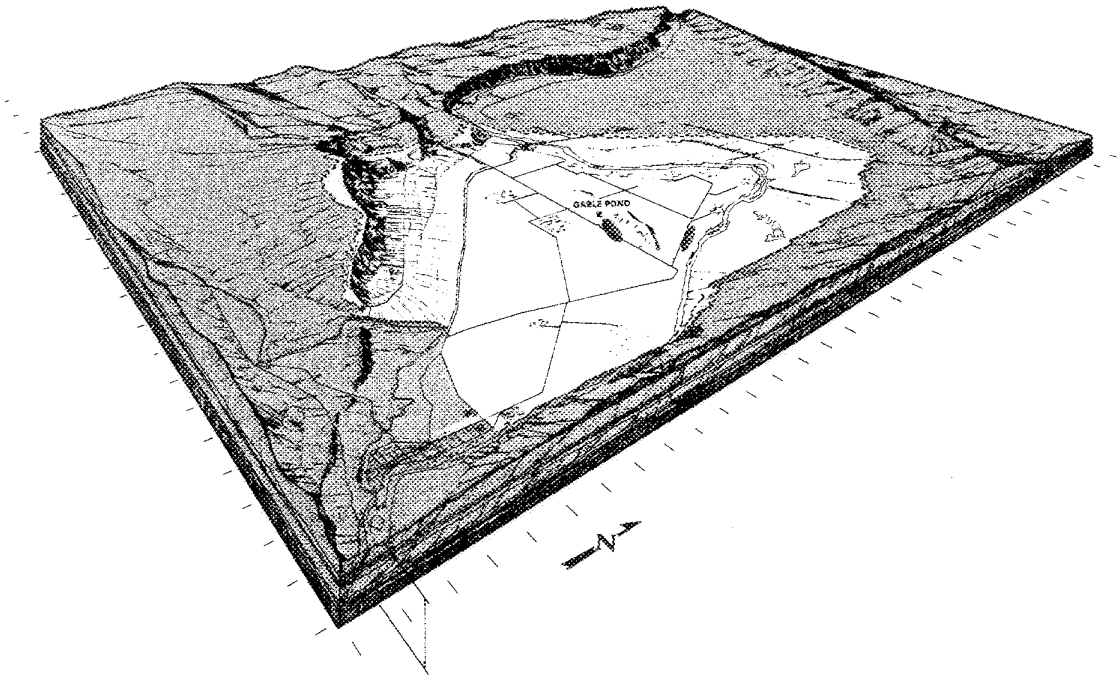

FIGURE 7.25. Home Range of Mule Deer (shaded ellipses) at the Hanford Site in Relation to the Columbia River and Ponds within the Site. The home range was 39.2 ± 4.6 km^2 (95% confidence limits); the Site area is 1400 km^2.

established for 17 instrumented deer, both near and isolated from a once active waste pond on the Site. The data showed clearly that animals with home ranges remote from the contaminated site did not frequent the area and therefore did not accumulate any 90Sr in their bones. As shown in Figure 7.26, animals whose average distance from the pond to center of their home range exceeded approximately 4 kilometers showed minimal ^{90}Sr concentrations in bone, characteristic of world-wide fallout levels. The pond was subsequently deactivated.

The examples described above show strong promise in placing biological monitoring effort on a firm quantitative basis. Further extension of these and related concepts has permitted predictive modeling of radionuclide movement

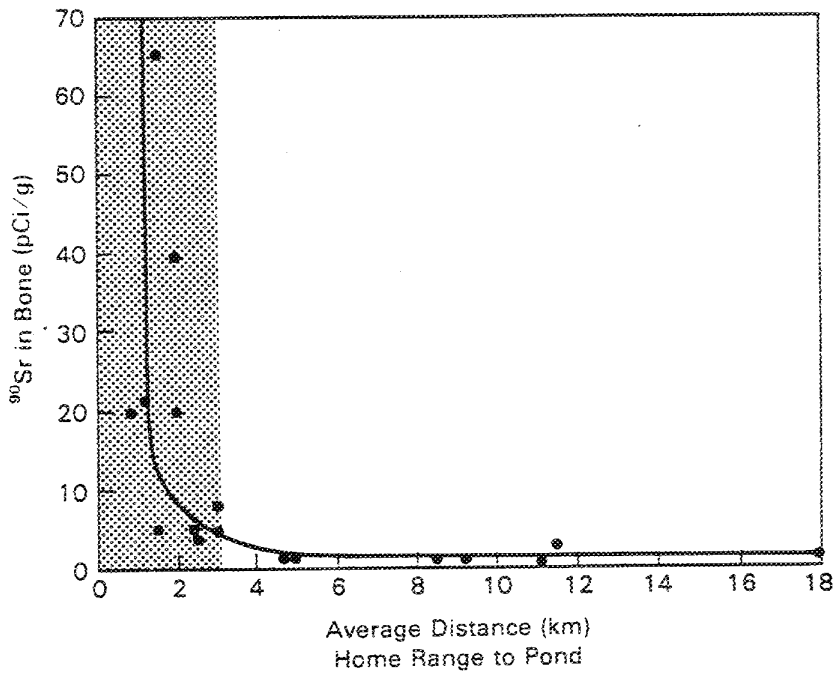

FIGURE 7.26. Bone Concentrations of ^{90}Sr in Mule Deer as a Function of Proximity to a Contaminated Site (Values in the shaded area exceed bone concentrations attributable to world-wide fallout.)

under the combined effects of biotic vectors, both animal and vegetational, acting over hundred-year intervals (Kennedy et al. 1985).

Dramatic expansion in types and volumes of toxic waste products generated over the past several decades increases the probability that those materials will become redistributed in the environment. Along with the continually increasing quantities of hazardous materials is a growing capability to detect very small quantities. This ability, coupled with a growing feeling that detriment to human health has no "threshold," means that even small releases of toxic materials may generate concern for the health and well-being of humans and other living organisms.

Compared to sampling of air or water, biological monitoring is advantageous in these circumstances, because of inherent features of biomagnification and bioconcentration (depending on trophic relationships of the species selected). There is, however, a need to develop a quantitative basis for biological monitoring. Such development evidently has not proceeded very far, judging from either health physics or ecological literature. Nevertheless, the advances discussed in this section show the feasibility of quantitatively accounting for such behavioral variables as mobility and preference. With foraging range and activity patterns of animal vectors quantitatively established, it is possible to determine the food chain availability of contaminants on a quantitative rather than anecdotal basis, and the data obtained become useful for modeling purposes.

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Chapter 8. THEORETICAL PERSPECTIVE ON ECOSYSTEM DISTURBANCE AND RECOVERY

P. A. Beedlow, P. Van Voris, L. E. Rogers

For more than 150 years, arid and semi-arid lands of the western United States have been subjected to increasingly severe human-induced perturbations associated with westward settlement and, concomitantly, with mineral and energy exploitation. On the basis of observational data, it is apparent that these ecosystems are fragile, that they need long time periods for recovery, and that long-term use of arid and semi-arid lands requires implementation of intelligent ecosystem management strategies. Such strategies must be based on sound ecological information in order to avoid potentially catastrophic irreversible environmental degradation (Smathers et.al 1983). Fundamental to long-term ecosystem management is the ability to predict, with some degree of certainty, the responses of both biotic and abiotic components of the ecosystems to various acute and chronic perturbations.

The information presented in earlier chapters provides a conceptual basis for identifying and quantifying the various mechanisms of shrub-steppe ecosystem response and recovery. In this chapter, we discuss the theoretical basis for understanding how shrub-steppe ecosystems respond to perturbation, and the role of research in understanding and then applying that knowledge to predict shrub-steppe responses to human-induced disturbances. Our emphasis is on the functional characteristics of the ecosystem rather than the classic diversity of species composition. However, if those who are responsible for managing these systems understand the basic mechanisms of ecological recovery, they can predict more effectively the most likely response of the ecosystems to various kinds of human activities, and the

long-term consequences of such activities. Ultimately, without such understanding and subsequent action, degradation of arid and semi-arid ecosystems could result in socioeconomic losses due to decreased productivity and diversity, decreased esthetic value of the land, and the increased likelihood of transport of toxic compounds.

Various land uses are associated with human activities in the arid and semi-arid regions of the West. Besides livestock grazing, farming, mining, and urbanization, these include the production of energy by hydropower, wind, geothermal, nuclear and fossil fuels, along with waste disposal from each of the above. Mechanical disruption of the ecosystem is one form of disturbance that has a severe impact and results in lengthy recovery processes. Another is the introduction of toxic materials to soils and waterways. The adverse effects of energy production are of particular concern because the impacts can extend for great distances as well as decades.

Section I. Concepts of Response and Recovery

An ecosystem can be considered a self-ordering biotic-abiotic system. Over time, it has developed a stable configuration and can be considered from the perspective of an individual organism or holistically as a web of interacting biotic and abiotic components (Shugart 1984, Loucks 1985, Johnson 1981, Patten and Odum 1981, Godron and Forman 1983). Conceptually, an ecosystem is an integrated set of processes that function synchronistically and are somewhat independent of particular species composition. However, the complexity of organization and interactions among the biotic and abiotic components seems to be a key element in the homeostatic response to

perturbations (Conrad 1976, Van Voris et al. 1980). Ecosystem productivity, for example, is not typically dependent upon particular species (Mooney and Gulmon 1983). Ecosystem change through time (i.e., short-term biotic fluctuations, succession, or evolution) is caused by very similar and fundamental processes, regardless of the time scale (MacMahon 1980). Similarly, the same basic processes occur in different ecosystems, but the rates of individual processes will vary from system to system. However, these processes are all controlled by common abiotic forcing functions such as light, temperature, water and natural mineral content of the substrate.

O'Neill and Waide (1981) visualized an ecosystem as a biogeochemical system, driven by solar energy, that transforms low-energy inorganic compounds into high-energy organic compounds. The efficiency of conversion of solar energy captured by the primary producers of the ecosystem is a critical function. Water, nutrients and temperature are the driving forces of primary production, which, in turn, affects the ability of the ecosystem to support primary and secondary consumers, including humans. Typically, ecologists and land managers have been slow to recognize holistic behavior or attributes. They have for the most part focused on the biological component at the population or community level of ecological hierarchical organization. This narrow scope has resulted in a reductionist viewpoint, with focus on components rather than on the overall functioning of the ecosystem. Measurements of the attributes of a given component have been shown to vary widely when extracted from the system. Schindler et al. (1980) noted that the variance of a component, when it is measured in isolation from the system, limits our

ability to predict the response of the whole. Therefore, the main objective of ecosystem studies should be to understand the "state of the whole" before any attempts are made to fractionate the system.

In a thermodynamic sense, ecosystems impose order through biologically-mediated processes (Godron and Forman 1983). Simon (1973) referred to this networking as "loose vertical coupling" among hierarchical levels in order to stabilize the system. Maintaining order requires the controlled flow of energy through a loosely structured system. A disturbance may affect the structure and functioning and, thus, the order by which control is maintained. Reordering the flow of energy in response to natural and human-induced perturbations results in an increased stability. Thus, the flow of energy and matter, controlled primarily by the biotic components, can be viewed as a prime function of an ordered ecosystem.

THE STABLE SYSTEM

An ecosystem that is able to control the flow of energy and materials through time when subjected to environmental change can be considered stable (O'Neill and Reichle 1980). This concept gives rise to a hypothesis that under a given set of climatic and edaphic and biochemical conditions, and in the presence of a particular disturbance regime, a stable system will ultimately develop for optimal energy capture. A stable ecosystem can be considered to be in dynamic equilibrium, but fluctuating through time within bounds between particular recurrent states (Botkin 1980). If we take into consideration ecosystem succession, both long-term and short-term dynamics must be considered. Operationally, dynamic equilibrium can be characterized by some degree of biotic control over nutrients and water movement within

the ecosystem through expenditure of carbon. During movement towards "climatic stability," the capturing of energy is at least the same as that lost through its total metabolic processes. Thus, fixed carbon functions as the "cash" that controls the flow of the commodities of nutrients and water. However, at any single point in time, the system may be less efficient at capturing energy and fixing carbon than is optimal, and movement towards a different stable equilibrium point may occur.

Stability can be interpreted as the capacity of an ecosystem to return to a functional equilibrium point from which it has been displaced (resilience), or as the ability of a system to maintain its function when subjected to perturbations (resistance) (Webster et al. 1975, DeAngelis 1980). Van Voris et al. (1980) presented experimental evidence that indicated an apparent relationship between system complexity in the functional sense and short-term ecosystem stability, which has both resistance and resilience components. Through ecosystem succession an ecosystem faced with recurring disturbance can develop a tolerance through colonization by more resistant species, through adaptations in the resident species (increasing the complexity of carbon and nutrient flow patterns within the system), or through use of abiotic sinks. The amount of variability in the environment during the development of an ecosystem affects its ability to resist or adjust to similar kinds of perturbations (Holling 1978, Preston and Lauenroth 1984). At the ecosystem level, "resistance" is the ability to control the flow of energy, nutrients and water. "Resilience" is defined as the ability of a system to adjust to changes and yet persist in fundamentally the same general functional and structural form. For example, a grassland can exist in several different forms and still be considered a grassland (Preston and Lauenroth 1984).

Another example was illustrated in earlier chapters, where cheatgrass communities were shown to compete efficiently, with respect to sagebrush-bunchgrass communities, following various perturbations.

If disturbed beyond the bounds of its flexibility (i.e., dynamic equilibrium), the ecosystem can be displaced from its equilibrium state and change its level of entropy until it reaches a different state of equilibrium (Godron and Forman 1983). This new state may have lower entropy, which is an agraded state (increase in potential energy), or it may have higher entropy, a degraded state. If degraded, the system may retain some control over nutrient and water flows, but it does not use stored or newly captured energy as efficiently. Through time, the system may regain more efficient use of energy, provided that a suitable structure can be rebuilt. Recovery to the initial state of equilibrium may be slow if degradation has resulted in the loss of significant amounts of the potential energy contained within the system. However, time for recovery from perturbation is not a critical factor when viewed from the ecosystem; time is only important when human concerns are involved.

THE RECOVERY PROCESS

Recovery may be defined as the process by which a system returns to a preexisting or new stable state following perturbation. The rate of recovery of an ecosystem is determined by its resilience, which is dependent upon the rate of energy flux and of nutrient cycling; the faster the system's recovery (turnover rate), the greater its resilience (DeAngelis 1980). A disturbed system, having lost control of energy capture and storage, water conservation,

and retention of nutrients, can regain direction of these flows by re-establishing the biotically mediated processes of control; however, this biotic control cannot be exercised without the proper abiotic conditions of climate or soil. Therefore, the rate at which control is regained is a measure of the system's rate of recovery with respect to biotic modification of abiotic conditions, and it is a measure of its resilience to any given perturbation. O'Neill and Waide (1981), Van Voris et al. (1980), and Loucks (1985) all provide evidence that the nature of the perturbation, such as fire, erosion, or the spill of a recalcitrant toxic chemical, clearly governs the rates of ecosystem recovery. Additionally, there is evidence that the timing, frequency, duration, and intensity of the perturbation are governing factors with regard to recovery.

A system can be said to have recovered from a disturbance when its previously existing rate of energy capture has been regained, nutrient export has been minimized, and control of water-use efficiency has been realized. The recovery of an ecosystem can be characterized by (1) regaining biological control of water and nutrients, and (2) regaining its energy capture efficiency.

Recovery differs from <u>succession</u> in that the <u>recovery</u> process involves regaining control of vital energy and material flows, while succession is the process by which a system's structure and function are optimized. Recovery, then, is the process by which control is regained; succession takes place after control of limiting resources has been established, and its occurrence generally implies increasing energy capture efficiency.

A simple model describing the relationships between disturbance characteristics, internal ecosystem processes, inputs to the system and

subsequent ecological responses is represented in Figure 8.1. This model shows precipitation, nutrients and solar energy as inputs, and the interactions among producers, consumers, decomposers and abiotic components. Disturbances are translated through the system by way of processes associated with the functioning of the major components, and various responses are produced. The complexity of these functional interactions within the ecosystem influences recovery (Van Voris et al. 1980).

The responses shown in Figure 8.1 refer to the kinds of ecological endpoints that ecologists normally measure in trying to determine whether changes are associated with a particular disturbance. These changes may

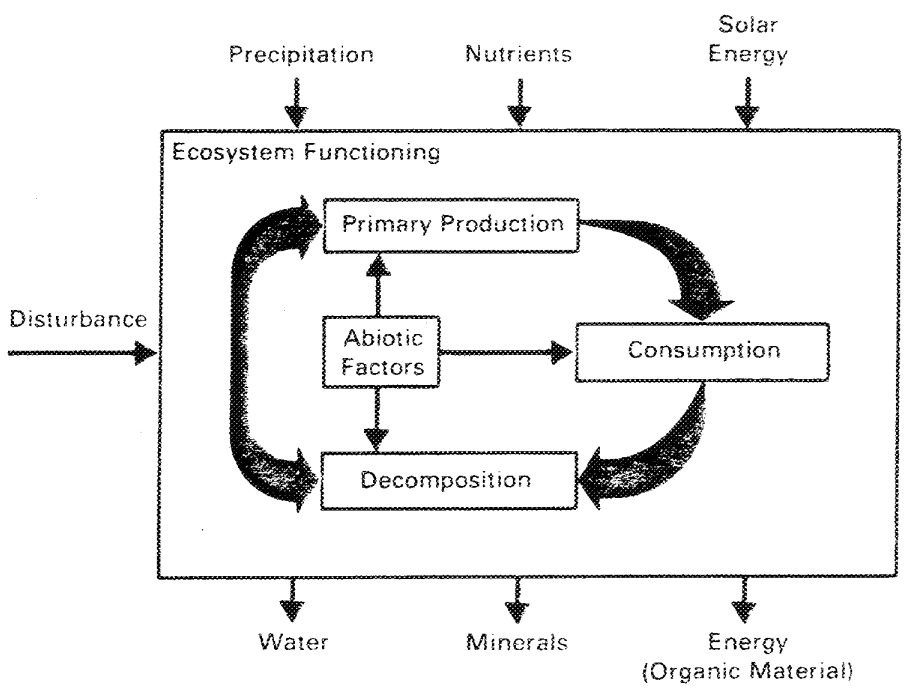

FIGURE 8.1. Relationships Between Disturbance, Ecosystem Functions and Ecological Responses

occur at one or more of the levels of organization within the ecosystem (Figure 8.2), i.e., at the organism, population, community or ecosystem level. Some response characteristics typically measured include those for identifying changes in ecological structure (density, biomass, taxonomic composition and diversity) and those for identifying changes in ecological processes (production, phenology, nutrient cycling rates, energy flow patterns, water balance regimes).

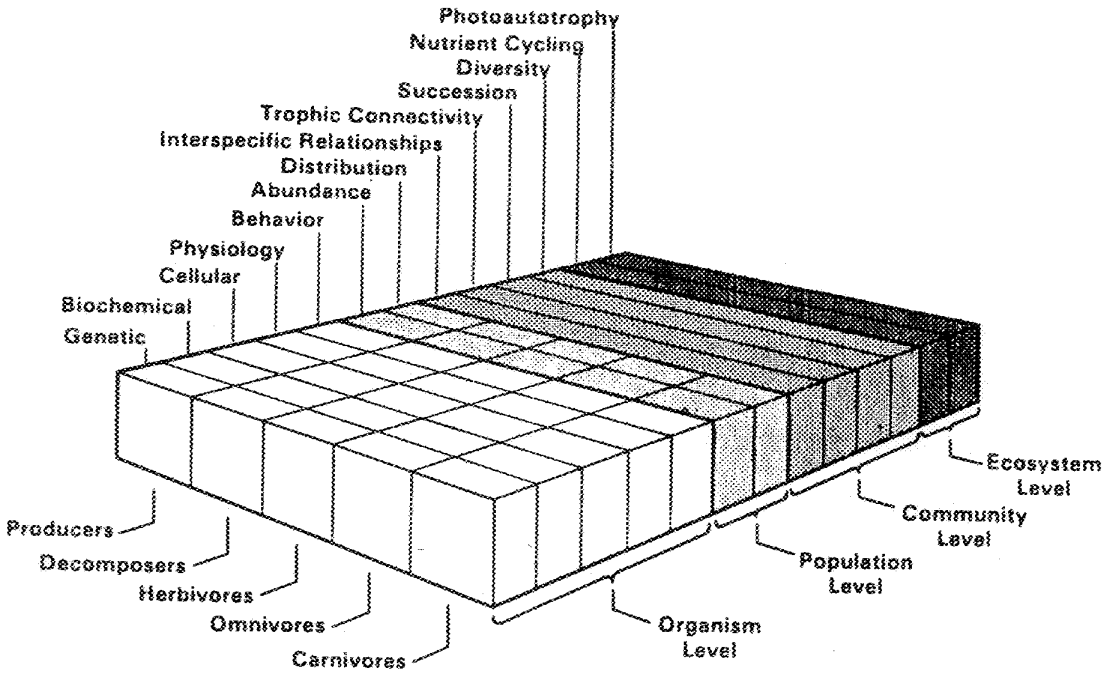

FIGURE 8.2. Levels of Ecological Organization and Their Attributes

Section II. Characterization of Disturbance and Stress in the Shrub-Steppe Ecosystem

The effects of human-induced disturbances on ecosystems are not necessarily distinct from the effects of natural disturbances. For example, human-induced fire is often difficult to distinguish from fire caused by lightening. Landslides can disturb the soil in a manner similar to construction activities, and intense grazing by wild animals can be similar to grazing by domestic animals.

Most studies concerning ecosystem response to disturbance have focused on particular types of disturbance such as fire, chemical, livestock grazing or harvesting. There are other characteristics associated with disturbances that also influence the kind of response that occurs. As noted earlier, such things as intensity, frequency of occurrence, seasonality of the event, duration, scale or uniqueness of the disturbance are all extremely important (Godron and Forman 1983, Cairns 1981).

A range of severities exists for both natural and human disturbances. In the shrub-steppe, a disturbance that breaks the soil surface alters the structure and functioning of the ecosystem more extensively than does the removal of aboveground biomass. For example, fire or grazing removes biomass; but in contrast to plowing, it has little long-term effect on species composition of the plant and animal communities, as has been demonstrated in Chapters 6 and 7. Shrub-steppe disturbances can be classified more appropriately into those that break the soil surface, such as farming, construction, or trampling by large grazing animals; those that remove or stress the vegetation without disturbing the soil, such as fire and moderate

livestock grazing; and finally those that are the result of the release of toxic or hazardous chemicals, such as pesticides or hazardous wastes.

Another measure of disturbance is its timing, both by season and by regularity of occurrence (Bazzaz 1983). For most types of shrub-steppe disturbances, the phenological timing is more or less constant. Fire usually occurs after the vegetation has dried in late summer; grazing is conducted during the spring months. Construction activities, however, are not so predictable and can occur at any time throughout the year.

A method of classifying disturbances that is based on the severity and periodicity of the disturbance is shown in Table 8.1. Here, the degree of soil disturbance and the regularity of occurrence form a matrix of disturbance types. The vertical axis represents the timing of the disturbance, from episodic to yearly, and the horizontal axis represents the degree to which the soil surface is broken. The four types of disturbances classified in the table represent the extremes of a two-dimensional continuum; a range of intermediate degrees is implied. For example, grazing could be less regular and/or involve more soil disturbance (as in those areas where cattle or sheep are held for long periods of time). Classifications of the magnitude of disturbance resulting from toxic chemical releases have not been entered into

TABLE 8.1. Classification of Disturbances Based on Periodicity of Occurrence and Severity of Soil Disturbance

	Severity of Soil Disturbance	
Periodicity	Low	High
Episodic	Wildfire	Construction
Regular	Grazing	Farming

Table 8.1 because of the scarcity of data available from semi-arid and arid ecosystem studies. However, we would anticipate that a range of "severity of disturbance" will in fact be evidenced depending on the chemical compound and the periodicity of the exposure.

WILDFIRE

Fire is a common disturbance on the shrub-steppe. It is caused naturally by lightening and also by human activities. Fire tends to be episodic and dependent on the amount of combustible material, its moisture content, weather conditions (especially wind), and the seasonal occurrence of lightening strikes. Another form of disturbance often associated with fire is fire suppression activities. The establishment of fire breaks by blading the soil surface causes a secondary disturbance that is often more severe than the fire.

Fire removes the aboveground biomass without damaging the belowground portions of the plants or destroying the seed stock resident in the soil. On the ALE Reserve, the most noticeable effect of fire has been the removal of sagebrush. Fire generally occurs in the late summer after the vegetation has cured, so damage to plants is minimal. Recovery of the semi-arid vegetation is rapid; new growth begins with the onset of the fall rains. Within the growing season, biomass of grass crowns and shoots is similar in the burned and unburned stands.

The effects of fire on bird species are mostly related to the elimination of sagebrush, which alters the physical structure of the community. Sage sparrows are the only passerine species that regularly use sagebrush for

nesting. It is not surprising, then, to find that they decline in number after a fire. Several fire-related studies on the ALE Reserve found no difference in the total density and biomass of breeding birds. The number of species was unaffected, but the relative abundance of bird species was changed; horned larks replaced sage sparrows as the dominant species.

Burrowing mammals are not affected by fire because of the protection afforded by their burrows. Fires usually occur in the dry season when most of these animals are inactive. By the time they emerge in the spring, vegetation has resumed growth, and sources of food are renewed.

No substantial differences in arthropod biomass were detected for the various trophic groups. As with birds, fire apparently changed the relative abundances of the arthropod trophic groups but had little effect on the overall biomass. Burning did not change the dominance of particular taxa. Invertebrate populations showed some effects immediately following the fire, but they recovered rapidly along with the vegetation.

LIVESTOCK GRAZING

Cattle and sheep grazing occurred on the ALE site for about 100 years. The area was moderately grazed, primarily by sheep, from the mid-1880s to 1940. With the exception of holding areas and trails, little or no evidence of grazing exists today. However, areas that were used for trails or holding sheep contain cheatgrass as the major plant species. This transition from bunchgrass dominance could have resulted from higher degrees of soil disturbance associated with the trails and holding areas relative to those areas that were only grazed.

In the study described in Chapter 6 concerning the effects of controlled grazing on vegetation (Rickard et al. 1975), cattle were grazed during the spring of each year for 3 years. Following the termination of grazing, the vegetation (as measured by mean peak biomass) recovered within a year to a level comparable to the control site. Production surpassed the control stand 2 years after release--an example of over-recovery. In the third year, it was again comparable to the control. The grazing produced no long-lasting effects on the vegetation, and the recovery was relatively rapid. However, there may have been a physical disturbance of the delicate cryptogamic crusts. An increase in shrub cover was noted for the grazed area.

The relationship between grazing density and increased abundance of invertebrates has been well documented. In general, heavy grazing has resulted in substantial increases in insect populations (Smith 1940, Hayes 1927). The reasons have not always been clear, but the changes in insect populations have been mostly related to changes in composition of vegetation species. Results from studies conducted at ALE failed to show any consistent differences in arthropod abundance after 3 years of moderate cattle grazing. Analysis by microhabitat did disclose substantially greater abundance of arthropods within bluebunch wheatgrass tussocks during two sample periods (April and May) of the study year. Analysis of taxonomic composition revealed that the Acari were primarily responsible for these differences. The Acari taxa involved (Glycerphagidae and Caligonellidae) are mostly detritus feeders and may have been responding to increased levels of detritus within tussocks resulting from the grazing activities of the cattle.

FARMING

Historically, cultivation of portions within the ALE Reserve consisted mostly of dry-land farming where the fields were tilled and left fallow, then planted to wheat/rye in alternate years. These farming practices were a chronic, annual disturbance. Such cultivation represents the most drastic form of disturbance to the native shrub-steppe system. The soil is mixed to 6 inches or more, the cryptogamic crusts are completely broken up, and all rooted plants are destroyed. After cultivation ceased on the ALE Reserve, cheatgrass quickly invaded the tilled sites. The present day old-field vegetation consists of generations of self-perpetuating cheatgrass.

Unfortunately, the impacts on native animal populations of the breakup of the virgin shrub-steppe lands were poorly documented. We do know that cultivation induced radical changes to the physical environment. In the shrub-steppe, plowing and the introduction of wheat resulted in a change in the vegetative structure from sparse, open stands to denser growth. This served to change the microclimate of the area by decreasing insolation and ventilation and increasing humidity for many microhabitats. The structure of the soil was also changed, which undoubtedly affected water penetration and soil temperatures with the soil profile. We do know that the opening of virgin steppe lands in Europe resulted in the immediate upset of insect populations (Cherepanov 1954). We see a similar response within the large stands of cheatgrass that developed on ALE lands following abandonment of wheat fields where cultivation reduced the abundance and species richness of small mammals. Undisturbed areas also contain more individuals and species

of birds than do the old-field areas. The lower density and diversity of birds seem related to the lack of structural diversity in the vegetation (Rotenberry 1978).

CONSTRUCTION

Construction activities result in removal of vegetation and disruption of the soil to various degrees. Construction activities on the ALE Reserve have been episodic, related to homesteading, road building, powerline construction, and operation of oil and gas wells. The most noticeable effect other than removing the vegetation has been the disruption of the cryptogamic crust. Research has shown that the vegetation recovered rapidly, but that the cryptogamic crust has not recovered after three decades (Jacques 1984). Where disturbance occurs but once, the vegetation goes through a form of succession where the invading annual species are replaced by perennial species. The cryptogamic crust, however, seems to have a very long recovery time.

The effects of construction activities on animal populations involve changes in the physical environment that are not dissimilar from farming. For the most part, any changes would probably be limited to the immediate area of disturbance and would not be expected to influence overall population levels.

Section III. Future Research Needs

On the basis of discussions in the previous sections of this chapter, we can define ecosystem functioning and, conversely, dysfunctioning, as the means by which the flows of energy and matter are controlled. Ecosystem functioning may be characterized by the way ecosystems use or process available resources such as light, water, and nutrients. Three major processes are involved in resource utilization within ecosystems: production, mineral cycling, and water dynamics. These processes primarily determine the patterns of energy, matter and water flows through ecosystems. A critical question remains unanswered: How does disturbance-induced change influence the major ecological processes within shrub-steppe ecosystems? This question is not merely academic; any environmental degradation that adversely affects human society (e.g., loss of productivity or contaminant transport) will largely be mediated through the ecological processes of productivity, mineral cycling and water dynamics.

An operational model describing how arid and semi-arid ecosystems respond to disturbance is shown in Figure 8.3. Focus is first directed to the "outputs" associated with the water dynamics, mineral dynamics and energy dynamics models in the overall, operational model. These "outputs" represent the critical information or questions to be answered concerning arid and semi-arid ecosystem responses to disturbance. For example, the water dynamics model identifies changes in groundwater recharge, overland flow (including sediment transport), and changes in water storage within the soil profile as critical ecosystem-level responses to disturbance. In the mineral dynamics

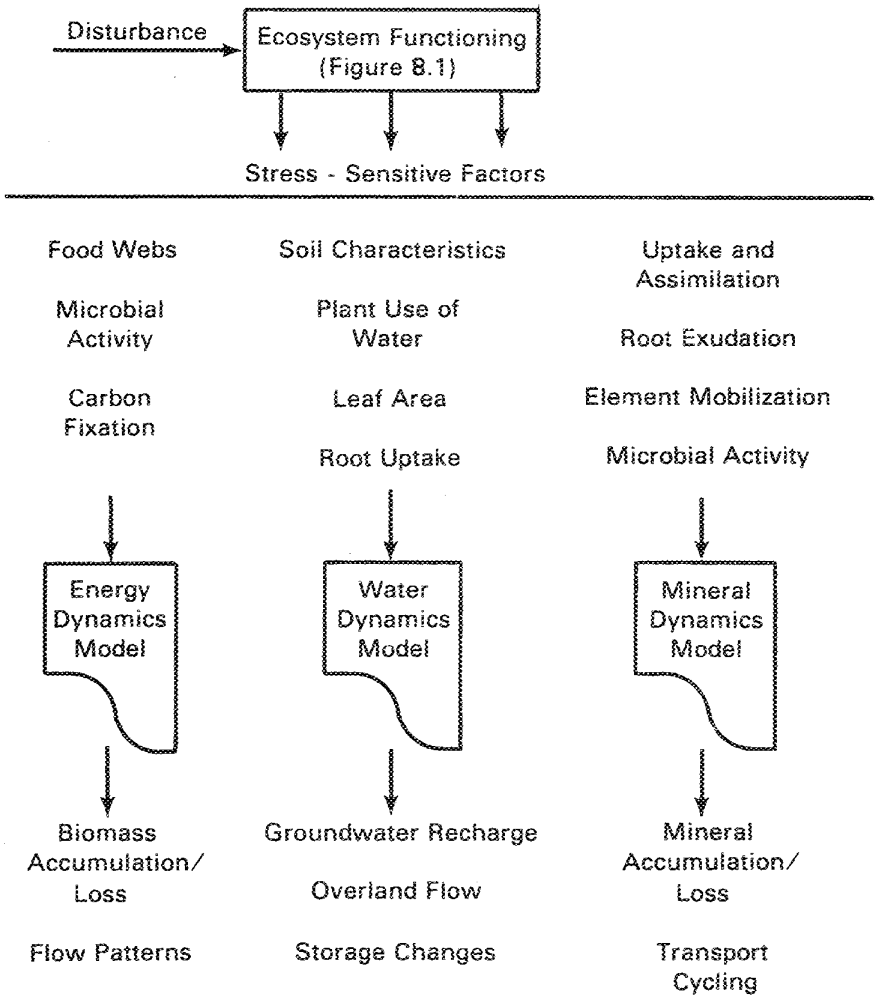

FIGURE 8.3. Some Effects of Disturbance on Biotic Components of Land Ecosystems: An Operational Model

model, the critical changes include rates of mineral losses, transport of contaminants, and mineral cycling. The energy flow model identifies biomass accumulation and loss, and also energy flow patterns, as critical changes.

The parameters required for predicting how these "outputs" might be influenced by disturbance are shown by the lists of stress-sensitive factors between the models and the box representing ecosystem functioning. For

example, a water dynamics model requires estimates of leaf area, phenology, root distributions, physical characteristics of the soil, and basic climatic data of the region. The mineral dynamics model requires estimates of parameters pertaining to mineral uptake and assimilation, the influence of root exudates on mineral availability, the mineralization activities of biota, the burrowing activities of animals, and leach rates associated with particular minerals. The energy flow model requires estimates of secondary production, microbial activity, consumption patterns (trophic relationships) and respiration rates. All of these parameters are derived from research concerning the impact of particular disturbances on the major processes shown in Figure 8.1.

Disturbance has an impact on the major processes of the ecosystem. It is expressed in terms of several characteristics: intensity, scale, duration, seasonality and type. Disturbance is often thought of simply as type (e.g., wildfire, toxic inputs, or mechanical); more realistically, as noted earlier, one should consider the characteristics of the entire disturbance regime recognizing that an ecological response is the sum of several factors (Godron and Forman 1983).

The characteristics of a particular disturbance will determine which of the numerous attributes of ecological functioning are affected directly. There are complex interrelationships among the basic attributes; for the sake of simplicity, these are not shown in Figure 8.2 or 8.3, although they provide the controlling mechanisms for many system-level responses. For example, a disturbance that results in a change in the gene pool (the kinds of plants present) could result in positive or negative feedback to demography, growth, standing crop, transpiration, and mineral absorption attributes. A

likely result would include changes of the parameters controlling major system responses in the form of soil water, mineral transport and cycling and energy flow patterns.

Much of the data in the earlier chapters describes current knowledge about the interrelationships between the feedback mechanisms in the shrub-steppe. However, much remains to be learned, and the critical need at the present time is to identify the interrelationships that govern the response and recovery patterns of arid and semi-arid ecosystems. These relationships must be understood before predictive capabilities and effective management strategies can be developed.

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EPILOG

L. E. Rogers and W. H. Rickard

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As we stated in the Preface, a principal aim of this book was to provide a summary and synthesis of the research conducted over the past 20 years concerning the structure and functioning of the shrub-steppe ecosystem. We hoped that as we worked to describe and synthesize past research, we would gain greater insight as to where future research efforts might be most profitably focused. In this respect, we exceeded our expectations.

We soon became aware that we currently have only a rudimentary understanding of the response and recovery mechanisms associated with stress in the shrub-steppe ecosystem. Before we can fully understand response and recovery, research efforts will need to build on the foundation provided by the existing data base to develop quantitative relationships that describe the functioning of the shrub-steppe ecosystem. "Ecosystem functioning," as used here, is defined as the means by which the flows of energy and matter are controlled, and it may be characterized by the way the shrub-steppe ecosystem uses available resources such as light, water, and nutrients. Three major processes clearly dominate ecosystem functioning: production, nutrient cycling, and water dynamics. These processes primarily determine the patterns of energy and matter flows through the system. This "process-function" perspective will guide our future research efforts, a contrast to the "structure-function" perspective that dominated the previous 20 years of ecological research at Hanford.

Specific research goals which have been identified as a result of this synthesis effort are identified below.

Energy Dynamics. The goal is to predict the influence of natural or human-related disturbances or stresses on productivity, detritus accumulation/depletion, and changes in energy flow patterns within the shrub-steppe ecosystem. Meeting this goal will require basic research on demography, growth rates, and standing crops of dominant consumer, producer, and decomposer groups. There are several areas for specific research: (1) determining the relationship between water and nutrient availability and primary productivity; (2) determining the relationship between changes in microbial activity patterns and biomass and detritus accumulation/depletion patterns; (3) quantifying climatic controls of plant growth and phenology; (4) quantifying detrital and grazing cycles; and (5) determining the role of major predators as regulators of energy and nutrient flows.

Nutrient Dynamics. This goal is focused on predicting the influence of natural or human-related disturbances on nutrient cycling patterns, contaminant transport, and rate of mineral losses from shrub-steppe ecosystems. Meeting this goal will require a basic understanding of those mechanisms and processes which control nutrient and contaminant solubility and cycling, and rates of input to the system. An integrated investigation of several tightly coupled processes will need to be conducted, including water transport, plant assimilation, organic matter decomposition, and the production of solubilizing and complexing ligands for nutrient mobilization. Specific research should be undertaken in the following areas: (1) defining the influence of biologically based rhizosphere processes on nutrient

cycling, solubility, retention and transport; (2) evaluating how rates of organic matter decomposition influence mineral cycling and mobilization; (3) identifying the role of canopy structure and density on nutrient and contaminant entrainment and input to the environment; (4) determining the effects of physical disturbances on mobilization and transport of minerals and organic components to ground and surface waters; (5) identifying nutrient sources and reservoirs within the system; and (6) determining the role of animals in the circulation and retention of nutrients.

Water Dynamics. The goal is to predict the influence of natural and human-related disturbances or stresses on ground-water recharge, overland flow patterns (including sediment transport), and storage changes within the soil column. Meeting this goal will require basic research to quantify the relations between soil characteristics, climatic variables and biologically-mediated processes, and their influence combined on water accretion and depletion patterns. Some areas for specific research: (1) quantifying the role of water in nutrient and organic export form arid ecosystems; (2) identifying the relationship of species composition to total leaf area and water use patterns in arid land plant communities; (3) defining the relationship between soil water potential and transpiration at the community level; (4) quantifying the effect of plant phenology on water use patterns; (5) determining water uptake parameters associated with root distribution patterns; and (6) determining the importance of periodic and seasonal water input to the system.

No attempt has been made here to identify which of the major processes listed above are the most critical to ecological functioning. Nevertheless, based on discussions in the earlier chapters, we believe that the most

critical short-term need is to identify and compare key processes that serve to control ecosystem functioning especially for the water balance and nutrient cycling processes. This can be accomplished by simultaneous conduct of both experimental manipulations and comparative studies of natural sites. An intermediate goal is to test the responses of key controlling processes to typical disturbance regimes. Two major questions would be addressed in this study phase: (1) How does the shrub-steppe ecosystem conserve and recover control over vital resources following disturbance? and (2) How do the processes controlling these resources affect the rate and patterns of recovery? As a long-term goal, we will test our ability to predict the response and recovery of ecosystems throughout the shrub-steppe region to various natural and human-related perturbations.