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DISSERTATION

**CARBON DIOXIDE EXCHANGE RATES AND PLANT-SOIL RESPONSES TO
SOIL LOSS ON SHORTGRASS PRAIRIE AND SAGEBRUSH STEPPE SITES**

Submitted by

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In partial fulfillment of the requirements

For the Degree of Doctorate of Philosophy

Colorado State University

Fort Collins, Colorado

Fall 2002

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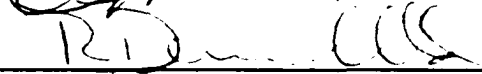
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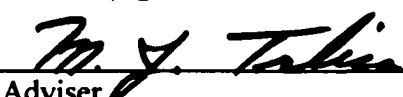
**WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED
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PHILOSOPHY.**


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ABSTRACT OF DISSERTATION

CARBON DIOXIDE EXCHANGE RATES AND PLANT-SOIL RESPONSES TO SOIL LOSS ON SHORTGRASS PRAIRIE AND SAGEBRUSH STEPPE SITES

The purpose of this study was to determine the effects of 3 different levels of soil loss on the CO₂ exchange rates of 2 rangeland ecosystems in northern Colorado, the shortgrass prairie and the sagebrush steppe. The experimental design was a split-plot, randomized block, with a factorial arrangement of 3 levels of soil removal (0, 11.2, and 22.4 t ha⁻¹). At the shortgrass site, net photosynthesis in western wheatgrass and blue grama was greater ($P < 0.10$) in the 11.2 and 22.4 t ha⁻¹ soil removal treatments than in the control (0 t ha⁻¹). This response was coupled to a significant ($P < 0.10$) increase in nitrogen use efficiency (NUE) and a decrease in inter-cellular CO₂ concentration (C_i). The consistency and similarity of the responses of net photosynthesis, NUE, and C_i for these 2 species suggests that it was driven by a common physiological process.

While total soil respiration at the shortgrass site increased significantly ($P < 0.10$) as soil removal level increased, bare soil respiration did not vary ($P > 0.10$) among the 3 treatments. Plant respiration rates generally increased as soil removal level increased, but this response was controlled by environmental factors that influenced plant productivity.

The photosynthetic rates of big sagebrush were unaffected ($P > 0.10$) by the soil removal treatments at the sagebrush site. However, while the net photosynthetic rates of

bluebunch wheatgrass did not vary ($P > 0.10$) between the 0 and 11.2 t ha^{-1} soil removal levels, they decreased ($P < 0.10$) at the 22.4 t ha^{-1} level. The photosynthetic response in bluebunch wheatgrass may have been confounded by the droughty conditions at the sagebrush site. Total, bare soil, and plant respiration rates at the sagebrush site varied little ($P > 0.10$) among the 3 soil removal treatments.

Results from this study suggest that the effect of soil loss on photosynthetic rates is: 1) the same regardless of the physiology of the plant indicating that the response occurs within a common physiological process; and 2) affects grasses more than Wyoming big sagebrush indicating that where soil loss is severe, this shrub might have a competitive advantage.

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For granting me the patience, strength, and courage to persevere, I give thanks and praise to God. I also want to acknowledge the sacrifice of those who have served and died honorably for this nation, granting us the freedom to pursue endeavors that shed light on the created beauty of our world. May God protect them for eternity,....Semper Fi.

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**for
Jackie, Chris, and Tyler
who have been ever patient and unwavering in their support,
who sacrificed much and gave love unconditionally
so that this could be....**

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CHAPTER I

INTRODUCTION TO STUDY

Rangelands comprise anywhere from 40 to 70% of the earth's 13.8 billion ha of land surface depending on how they are defined (Branson et al. 1981a, Holechek et al. 1989a). More than 80% of the world's rangelands occur in arid and semi-arid regions (Branson et al. 1981a) with less than 500 mm of precipitation per year. In the United States approximately 80% of the 400 million ha of rangelands occur in the 17 western states (Child and Pearson 1995). The rangeland ecosystems in the western United States provide important sources of food, fuel, fiber, wildlife habitat, recreation, and water (Branson et al. 1981a, Holechek et al. 1989a, Child and Pearson 1995).

The shortgrass prairie and sagebrush steppe are 2 very important rangeland ecosystems in the semi-arid western United States (USA). The shortgrass prairie is the third most important rangeland type for livestock production in the USA and covers 20 million ha across parts of Wyoming, Colorado, Nebraska, Kansas, Oklahoma, Texas and New Mexico, (Holechek et al. 1989b). The sagebrush steppe is 1 of the more extensive rangeland ecosystems, covering about 39 million ha across 11 western states including large areas of Nevada, Idaho, Wyoming, Oregon, Washington, and Colorado (Holechek et al. 1989b). Nearly 65% of the sagebrush steppe is under federal control (Holechek et

al.1989b). Because of its vastness, accessibility, and productivity, the sagebrush steppe is important for livestock production, wildlife habitat, watershed values, and a wide variety of recreational activities (Blaisdell et al. 1982).

Average annual precipitation for both the shortgrass prairie and sagebrush steppe ecosystems varies between 200 mm and 500 mm depending on location (Holechek et al. 1989b). Though the annual precipitation received for both ecosystems is similar, the timing of precipitation events differ. On the shortgrass prairie, 60 to 70% of the precipitation occurs during the growing season (Holechek et al. 1989b). In contrast, about 60% of the precipitation is received as snow during the winter within the sagebrush steppe. The 2 ecosystems support different plant communities because of these differences. Grasses, including blue grama [*Bouteloua gracilis* (Kunth) Lag. ex Steud.], buffalograss [*Buchloë dactyloides* (Nutt.) Englem.], and western wheatgrass [*Pascopyrium smithii* (Rydb.) A. Love] dominate plant communities on the shortgrass prairie (Brown and Trlica 1977, Kemp and Williams 1980, Monson et al. 1982, 1986, Milchunas et al. 1989). Conversely, sagebrush (*Artemisia* spp.) dominates the landscape of the sagebrush steppe (Holechek et al. 1989b). Grasses such as bluebunch wheatgrass [*Pseudoroegneria spicata* (Prush) A. Love], western wheatgrass, Idaho fescue (*Festuca idahoensis* Elmer), and sheep fescue (*Festuca ovina* L.) are a few among many species that are important in the understory of the sagebrush steppe (Blaisdell et al. 1982).

Cultivation of most rangelands is usually precluded because they are too dry, or steep, or are otherwise too nonproductive. Citing sparse vegetative cover, steep topography, and low infiltration rates as contributing factors, Renard (1980) suggested

that sediment yields from many rangelands in the western United States were larger than expected given their associated low annual precipitation levels. Soil loss on non-cultivated, native rangeland may be highest in areas with annual precipitation between 250 and 380 mm (Branson et al. 1981b, Wight and Siddoway 1982). Insignificant erosion occurs below 250 mm because of low runoff volume, while above 380 mm there is usually adequate vegetive cover to impede soil loss (Branson et al. 1981b, Wight and Siddoway 1982). Since much of the shortgrass and sagebrush steppe occur within the 250 to 380 mm precipitation zones, erosion potentials within these 2 rangeland ecosystems are high. The average rate of erosion on Colorado's 62 million ha of rangeland, of which the shortgrass prairie and sagebrush steppe comprise a substantial portion, is 6.2 metric tonnes $\text{ha}^{-1} \text{y}^{-1}$ (USDA 1980, Boone 1987).

Soil Erosion

Soil erosion is a process where wind and water act to remove soil from the landscape (Weltz et al. 1998). The erosion potential of any given site is a complex interaction between its physical characteristics (i.e. soil, vegetation, topography, and climate), and its use and management (Branson et al. 1981, Pierson et al. 1994, Weltz et al. 1998). Erosion occurs naturally in most ecosystems, but the rate of soil loss can be greatly influenced by different land uses and management practices (Weltz et al. 1998). Early researchers noted a direct correlation between accelerated erosion rates and management practices that caused a decline in vegetative cover on rangelands (Sampson

and Weyl 1918, Chapline 1929). For example, Chapline (1929) found that when vegetative cover decreased from 40 to 16%, soil loss increased by 56%.

Concern about the extent of accelerated soil erosion on western rangelands (Sampson and Weyl 1918, Chapline 1929, Weaver and Noll 1935) and croplands (Bennett and Lowdermilk 1938) have been expressed by investigators since the 1920's. Efforts by these early researchers led to the idea that there existed some level of tolerable soil loss beyond which site productivity could not be maintained (Schmidt et al. 1982). Formal development and application of a soil loss tolerance value (T-value) began in 1962 when the U.S. Soil Conservation Service determined T-values for most major United States soil types (Schmidt et al. 1982). The soil loss tolerance value has been defined as "the maximum level of soil erosion that will permit a high level of crop productivity to be sustained economically and indefinitely" (Wischmeier and Smith 1978). By 1982, T-values ranging from 4.5 to 11.2 metric tonnes ha^{-1} (t ha^{-1}) y^{-1} (2 to 5 tons acre^{-1} y^{-1}) had been assigned to all soils in the United States (Schmidt et al. 1982). Determination of these T-values was based on the Universal Soil Loss Equation that was developed for estimating annual erosion rates on cultivated lands (Weltz et al. 1998).

Despite suggestions by Blackburn (1980), Schmidt et al. (1982), and Wight and Siddoway (1982) that the T-value concepts and guidelines developed for croplands were not necessarily applicable to rangelands, little has been done to adjust the values that have been assigned to rangelands (Weltz et al. 1998). This is primarily because rangelands are, on a per unit area basis, of lower economic value than forest and cultivated lands and consequently do not receive comparable management and research inputs (Wight and

Siddoway 1982). The result of this lack of management and research effort is that current assumptions about the relationship between erosion and rangeland productivity and sustainability are based on concepts developed for cultivated lands nearly 40 years ago.

Current rangeland management guidelines suggest that if the T-value for a given range site is exceeded, rangeland plant productivity and sustainability will decline (SRM-Task Group 1995, Rasmussen et al. 1998). This potential loss of productivity and sustainability on rangelands where the erosion rates exceed the associated T-value is often the impetus for altering current uses and management strategies (SRM-Task Group 1995, Rasmussen et al. 1998). Recently however, Weltz et al. (1998) suggested that because research that directly measured erosion and its effects on plant productivity and sustainability of rangelands was lacking, the current concept of T-values for rangelands could not be validated. Weltz et al. (1998) provided research recommendations that would answer many of the questions about the relationship between erosion and rangeland plant productivity and sustainability. They further suggested that research should focus on collection of data on plant community characteristics (i.e. canopy cover, plant height, and productivity) based on their relationship to erosion, rather than as a forage resource.

Primary Productivity and Erosion

With accelerated erosion rates, many soil properties that promote plant growth are adversely affected. Erosion removes mineral particles, organic matter, and nutrients from the soil, reducing surface horizon thickness and water-holding capacity (Singer and

Munns 1991). The production of biomass in a plant community depends on the availability of resources, the ability of plants to assimilate essential resources, and the quantity of resources required to produce a given quantity of biomass (Bloom et al. 1985). Plants respond to resource limitations by increasing the efficiency of investment of the limiting resource into the production of new biomass (Bloom et al. 1985, Chapin et al. 1987), and a low resource investment often reflects low resource availability (Chapin 1989). Lower availability and quantity of essential resources induced by erosion may be reflected in the net photosynthetic rate of plants. For example, photosynthetic capacity (the maximum rate of carbon assimilation by a single leaf at light saturation and optimal conditions) is highly correlated with leaf organic nitrogen content (Chapin et al. 1987). Therefore, the loss of soil nitrogen through accelerated erosion rates may adversely impact net photosynthetic rates in plants. Net photosynthesis may also be influenced by the loss of water-holding capacity in the soil that can occur following erosion.

The degree to which net photosynthesis is affected by the decline in nitrogen and soil moisture may depend on the specific carbon assimilation pathway utilized by a plant. Plants that utilize the C_4 pathway generally exhibit higher water and nitrogen use efficiencies than plants that use the C_3 pathway (Caldwell et al. 1977, Brown and Trlica 1977, Wong 1979, Kemp and Williams 1980, Sala et al. 1982, Brown and Wilson 1983, Monson et al. 1986, Sage and Pearcy 1987, Carpenter and West 1987). Thus, under conditions of accelerated erosion, C_4 species may be better equipped to cope with increasing resource limitations than C_3 species. Currently however, it is unclear how

species using these 2 different photosynthetic pathways respond to the effects of soil loss at or greater than the established T-values (ranging between 4.5 and 11.2 t ha⁻¹).

Most rangeland ecosystems are populated by a mixture of C₃ and C₄ species. To determine if T-values that have been assigned to rangelands are valid, it is imperative that research efforts focus on responses of C₃ and C₄ species to soil loss levels that are at, or exceed, the established T-values for rangelands. Comparison of photosynthetic rates among C₃ and C₄ species at different levels of soil loss may also help explain the propensity for species composition to change with increasing erosion rates. Chapters II and III of this dissertation discuss investigations into the influence of soil loss on the photosynthetic rates of dominant C₃ and C₄ grasses of the shortgrass prairie and of the dominant shrub and grass component of a sagebrush steppe.

Soil Respiration and Erosion

Plant biomass is the major source of organic material for the soil carbon (C) pool (Klemmedson 1989). The accumulation of organic matter in a soil is the difference between the inputs of organic debris and the output of decay processes (Klemmedson 1989, Schlesinger 1997). Because plant biomass is the primary input of soil C, the character of vegetation is a major factor in determining the rate of decomposition (Swift et al. 1979) and the quality, quantity, and distribution of soil organic matter (Klemmedson 1989). Soil organic matter is concentrated primarily in the upper soil horizons in arid and semi-arid regions (Charley and West 1975, Klemmedson 1989). Progressing from grass to shrubby vegetation and to lower and less reliable precipitation,

soil organic matter often declines and is distributed more superficially (Charley and West 1975). Consequently, arid and semi-arid rangelands have a disproportionately higher risk of losing soil organic matter to erosion than more humid systems (Klemmedson 1989). Erosion therefore, may, through reductions in primary productivity and removing soil organic matter, have a large impact on carbon input and decomposition rates in rangeland soils.

Measurements of CO₂ efflux from soils provides information about belowground productivity (root respiration) and decomposition rates. For any system in steady state, the soil respiration rate averaged over a unit of time should equal the rate of C input to the soil over that period (Kirschbaum 1995, Schlesinger 1997). Consistent with this steady state relationship, Raich and Schlesinger (1992) showed a good linear correlation between annual soil respiration rate and net primary productivity. Since accelerated erosion disturbs steady state conditions, it would be expected that the relationship between net primary productivity and soil respiration would be altered with increasing soil loss. However, this assumption does not consider the influence of other important environmental variables (i.e. soil temperature, moisture, etc.) on soil CO₂ efflux.

Soil respiration rates are controlled directly and indirectly by soil temperature and moisture (Singh and Gupta 1977). Other factors that affect soil respiration rates include soil nutrient content, depth of soil organic matter, and cultural practices (Singh and Gupta 1977). With the exception of cultural practices, erosion can directly or indirectly influence each of these factors. For example, erosion can remove litter exposing more soil to direct sunlight resulting in higher temperatures in the first few centimeters of soil.

In general, as soil temperature increases soil respiration rate increases until some maximum is reached, beyond which CO₂ efflux begins to decrease again (Witkamp 1966, Wiant 1967, Reiners 1968, Witkamp 1969).

More important to soil respiration rate, however, may be the erosion induced loss of nutrients and organic matter along with reduced surface horizon thickness and water-holding capacity. Reduced nutrient availability in the soil profile may create greater competition between soil microbes and plants for increasingly limited resources. This may result in decreases in both root and microbial activity, and thus, lower soil respiration rates. Likewise, soil respiration rate may decline with loss of soil moisture and reduced surface horizon thickness. In a study on the Pawnee National Grassland, Clark and Coleman (1972) noted a several-fold increase in the rate of CO₂ efflux following a heavy rainfall event, suggesting that soil respiration rate was a function of soil moisture. Moreover, De Jong et al. (1974) found that a low moisture content of 5 to 10% by volume in the surface soil resulted in cessation of CO₂ production. These results may be particularly relevant in arid and semi-arid rangelands where most of the activity in the soil occurs in the upper surface horizon. For example, Clark and Coleman (1972) reported that 85% of the daily CO₂ efflux from a shortgrass prairie site (Pawnee National Grassland) occurred in the top 10 cm.

It can be postulated, given the evidence, that erosion induced losses in soil carbon and nutrients, surface horizon thickness, and water-holding capacity may all influence soil respiration rates on western rangelands. However, whether soil loss levels on rangelands that are within or exceed established T-values, invoke an increase, decrease or

a static response in CO₂ efflux rates has not been determined. Assuming a response, the directionality of that response could have important implications for the global carbon budget, given the extent of the world's rangelands that may be subjected to accelerated erosion (Wight and Siddoway 1982). Moreover, coupled with estimates of primary productivity, measurements of soil respiration may indicate whether eroded lands contribute CO₂ to the atmosphere or sequester C into plant material and soil organic matter. Either way, understanding how soil loss affects soil respiration on rangelands could provide valuable information regarding the global carbon budget, and may help determine the validity of T-values assigned to rangeland ecosystems. The results of a study of the response in soil respiration rates to soil loss on the shortgrass prairie and sagebrush steppe are detailed in Chapter IV.

The last chapter (V) of this dissertation provides a summery and integration of the findings in Chapters II, III, and IV. However, to better understand the impact of soil loss on rangelands, more research is needed. Thus, building on the results from the research in this dissertation, Chapter V also provides suggestions for additional research. These suggestions could be developed into new research hypotheses that would improve our understanding of the effects of soil loss on rangeland plant ecophysiology and CO₂ exchange rates.

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CHAPTER II

PHOTOSYNTHETIC RESPONSES OF BLUE GRAMA AND WESTERN WHEATGRASS TO SOIL LOSS

Introduction

The erosion potential for any given range site is a complex interaction between the site's physical characteristics (i.e. soil, vegetation, topography, and climate), and its use and management (Branson et al. 1981, Pierson et al. 1994, Weltz et al. 1998). Early researchers noted that accelerated erosion rates on rangelands were correlated with management practices that resulted in a decline in vegetative cover (Sampson and Weyl 1918, Chapline 1929, Weaver and Noll 1935, Bennett and Lowdermilk 1938). Chapline (1929), for example, found that soil loss increased by 56% when vegetative cover decreased from 40 to 16%. Results such as these led early researchers (Sampson and Weyl 1918, Chapline 1929, Weaver and Noll 1935, Bennett and Lowdermilk 1938) to suggest that some level of tolerable soil loss existed beyond which site productivity could not be maintained (Schmidt et al. 1982). By 1982, soil loss tolerance values (T-values) ranging from 4.5 to 11.2 metric tonnes ha^{-1} (t ha^{-1}) y^{-1} had been assigned to all soils in the United States (Schmidt et al. 1982). Determination of these T-values was based on the

Universal Soil Loss Equation that was developed to estimate annual erosion rates on cultivated lands (Weltz et al. 1998).

Current rangeland management guidelines suggest that if the T-value for a given range site is exceeded, rangeland productivity and sustainability will decline (SRM-Task Group 1995, Rasmussen et al. 1998). This potential loss of productivity and sustainability on rangelands where accelerated erosion rates exist is often the impetus for altering current land uses and management strategies (SRM-Task Group 1995, Rasmussen et al. 1998). However, rangeland research that has quantified the effects of erosion on plant productivity and sustainability is lacking. Thus, the current concept of T-values for rangelands may not be valid (Weltz et al. 1998). Indeed, early in the development of the T-values, Blackburn (1980), Schmidt et al. (1982), and Wight and Siddoway (1982) all suggested that the T-value concepts and guidelines developed for croplands could not necessarily be applied to rangelands. To alleviate the uncertainty surrounding rangeland T-values, Weltz et al. (1998) suggested that research should focus on the relationship of plant community characteristics (i.e. canopy cover, plant height, and productivity) to erosion, rather than as a forage resource.

Erosion removes mineral particles, organic matter, and nutrients from the soil, and in the process reduces the surface horizon thickness and water-holding capacity of the soil (Singer and Munns 1991). The production of biomass in a plant community depends on the availability and quantity of essential resources, and the ability of plants to assimilate those resources (Bloom et al. 1985). Plants respond to resource limitations by increasing the efficiency of investment of the limiting resource into the production of new biomass

(Bloom et al. 1985, Chapin et al. 1987), and a low resource investment often reflects low resource availability (Chapin et al. 1987). Lower quantity and availability of essential resources induced by erosion may be reflected in the net photosynthetic rate of plants. For example, photosynthetic capacity (the maximum rate of carbon assimilation by a single leaf at light saturation and optimal conditions) is highly correlated with leaf organic nitrogen (N) content (Chapin et al. 1987). Therefore, the loss of soil N through accelerated erosion rates may adversely impact net photosynthetic rates in plants. Net photosynthesis may also be influenced by the loss of water-holding capacity in the soil that can occur following erosion.

The degree to which net photosynthesis is affected by a decline in soil N and water content may depend on the specific carbon (C) assimilation pathway utilized by a plant. Plants that utilize the C₄ pathway generally exhibit higher water and nitrogen use efficiencies than plants that use the C₃ pathway (Caldwell et al. 1977, Wong 1979, Kemp and Williams 1980, Monson et al. 1986, Sage and Pearcy 1987). Thus, under conditions of accelerated erosion, C₄ species may be better adapted to cope with increasing resource limitations than are C₃ species. It is currently unclear, however, how species using these 2 different photosynthetic pathways respond to the effects of soil loss. Since many rangeland ecosystems are populated by a mixture of C₃ and C₄ species, it is imperative that research focus on differentiating between the responses of plants that have these 2 photosynthetic pathways to soil loss levels that are at, or exceed, the established T-values for rangelands. Comparison of photosynthetic rates among C₃ and C₄ species at different levels of soil loss may indicate whether or not rangeland T-values are valid and may also

establish a link between erosion and changes in the “kind, amount, and pattern” of vegetation in the community (SRM-Task Group 1995).

Objectives and Hypotheses The specific objective of this research was to determine the effects of 3 levels of soil loss (0, 11.2, and 22.4 t ha⁻¹) on net photosynthetic rates of western wheatgrass [*Pascopyrium smithii* (Rydb.) A. Love] and blue grama [*Bouteloua gracilis* (Kunth) Lag. ex Steud.], the dominant C₃ and C₄ grasses on a shortgrass prairie range site. Soil loss levels chosen for comparison represented no soil loss (0 t ha⁻¹), a soil loss level that is widely accepted to be the maximum allowable T-value (11.2 t ha⁻¹; Schmidt et al. 1982), and twice the maximum allowable T-value (22.4 t ha⁻¹). It was hypothesized that: a) photosynthetic rates of the C₃, western wheatgrass, would decrease with increasing soil removal level, and b) photosynthetic rates of the C₄, blue grama, would increase with increasing soil removal level. It was predicted that this differential response between the 2 species would result from differences in resource use efficiencies.

Materials and Methods

Study Site The shortgrass prairie research site was located at the USDA-Agricultural Research Service, Central Plains Experimental Range (CPER, 40°50' N latitude, 104°43' W longitude), a 6,280 ha research area in northeastern Colorado. The shortgrass prairie has a long history of grazing (Milchunas et al. 1992). Currently, CPER is moderately grazed by cattle during the growing season. The study site, however, was fenced in the spring of 1998 to protect it from livestock grazing.

Long-term (1939 - 1990) annual temperature at CPER averaged about 9 °C with an average annual precipitation of 321 mm (Lauenroth and Sala 1992). Soils at the research site were formed from calcareous sandy alluvial and eolian material and are classified as a Vona Sandy Loam, which are coarse-loamy, mixed, mesic Ustollic Haplargids (USDA 1982). The vegetation at the study site was representative of the shortgrass prairie ecosystem (Milchunas et al. 1989) and was dominated by blue grama and buffalograss [*Buchloë dactyloides* (Nutt.) Englem.]. Western wheatgrass is also an important component of the shortgrass ecosystem (Brown and Trlica 1977a, Kemp and Williams 1980, Monson et al. 1982, 1986) and was present at the study site.

Experimental Design The experimental design of the study was a split-plot, randomized block, with a factorial arrangement of treatments. Factor levels consisted of 2 range condition classes (NRCS 1997), good and fair, and 3 levels of soil removal (0, 11.2 and 22.4 t ha⁻¹), with 3 replications of each level (18 plots). Western wheatgrass did not occur frequently in the fair condition plots. Thus, comparison of all response variables between species was done only for plants in the good condition class. Conversely, comparison of all response variables between good and fair condition classes was done only for blue grama, since it occurred within both condition classes.

Treatments and Data Collection In the spring of 1998, nine (3 soil removal levels x 3 replications) permanent 0.6 x 2 m steel frame plots were randomly placed within both the good and fair condition class sites (18 total plots). Topsoil from all treatment plots was removed to the desired level using a vacuum and collection bag. Treatments were imposed during the summer of 1998. The removed soil was transported to Colorado

State University (CSU) for analysis of carbon (C) and nitrogen (N) content (mg g^{-1}) for each plot using a LECO CHN-1000 Analyzer.

Gravimetric water content (%) of study site soils was estimated from soil cores removed from the immediate vicinity of each plot at depths of 0-5 and 5-10 cm at weekly intervals during the 1999 and 2000 growing seasons. Total soil C and N content (mg g^{-1}) was determined for the 0-2.5, 2.5-5.0, and 5.0-10.0 cm depths from soil core samples removed from each plot at the end of the 1999 and 2000 growing seasons.

Net photosynthetic ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and transpiration rates ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), and inter-cellular CO_2 concentrations (C_i ; $\mu\text{mol CO}_2 \text{ mol air}^{-1}$) were measured on 5 leaves per species within each plot with a Li-Cor 6400 Portable Photosynthesis System.

Measurements were made at mid-day on weekly intervals during the 1999 and 2000 growing seasons. Leaf chamber conditions were maintained at ambient for atmospheric CO_2 , water vapor pressure, and air temperature. Photosynthetically active radiation (PAR) was maintained at $1500 \mu\text{mol PAR m}^{-2} \text{ s}^{-1}$ with a Li-Cor 6400 Light Source. Leaf areas (cm^2) of the sampled leaves were measured using a Li-Cor 3000 Portable Leaf Area Meter following the photosynthesis measurements. Sampled leaves were then bagged, cooled and transported to CSU for analysis of total leaf C and N content (mg g^{-1}) using a LECO CHN-1000 Analyzer. Water and nitrogen use efficiencies ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ and $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$, respectively) were calculated for each measurement of photosynthesis and transpiration. Leaf water potentials (MPa) were measured simultaneously with the photosynthesis measurements on 3 leaves per species

within each plot using a pressure chamber (Scholander et al. 1965, Waring and Cleary, 1967).

Statistical Analyses A repeated measures analysis of variance (ANOVA) procedure (Vonesh and Chinchilli 1997) was used to test for differences between western wheatgrass and blue grama, good and fair condition classes, among soil removal levels (0, 11.2, and 22.4 t ha⁻¹) across sample periods (week of year) within years, and between years (1999 and 2000) for net photosynthetic and transpiration rates, inter-cellular CO₂ concentration (C_i), leaf C and N content, leaf water potential, and water and nitrogen use efficiencies. Repeated measures ANOVA was also used to test for differences among sample depths (0-2.5, 2.5-5.0, and 5.0-10.0 cm) across sample periods (week of year) within years for soil water content and for total soil C and N among sample depths, soil removal levels, and years (Vonesh and Chinchilli 1997). Results were considered significant at $P \leq 0.10$, and Fisher's least significant difference was used to separate means when appropriate (Dowdy and Wearden 1991). All means (\bar{x}) are reported with their respective standard error (\pm SE) and sample size (n). Data, statistical outputs, and supporting material for this chapter are located in Appendix A.

Results

Soil Water, Carbon, and Nitrogen Content Gravimetric soil water content (%) varied ($P < 0.10$) by depth across sampling periods and years (Figure 2.1). Generally, the 5 to 10 cm soil depth had a higher soil water content than the 0 to 5 cm depth (Figure 2.1). The differences in soil water content observed among periods between 1999 and

2000 was explained by the differences in the timing of precipitation events as well as total amount received. Peak soil water content in both years followed precipitation events, but occurred at different times of the year (Figure 2.1). For example, in 1999, soil water content in the 5 to 10 cm depth varied from 6.5% (± 0.6 SE; $n = 18$) in week 30 to 12.8% (± 0.8 SE; $n = 18$) in week 32, while in the 0 to 5 cm depth, soil water content varied from 2.5% (± 0.2 ; $n = 18$) in week 25 to 12.5% (± 0.6 SE; $n = 18$) in week 34 (Figure 2-1). However in 2000, the lowest soil water content for both the 0 to 5 and 5 to 10 cm depths ($1.6\% \pm 0.1$ SE, $n = 18$; and $2.7\% \pm 0.3$ SE, $n = 18$, respectively) in week 32 was followed by the highest soil water content ($11.8\% \pm 0.6$ SE, $n = 18$; and $12.8\% \pm 0.6$ SE, $n = 18$, respectively) in week 33 (Figure 2-1) after a 94 mm precipitation event.

Total precipitation received at CPER in 1999 (419 mm) was approximately 29% greater than the long term average total annual precipitation of 321 mm (Lauenroth and Sala 1992). Conversely, in 2000 the total precipitation at CPER (240 mm) was about 26% below the long term average. This difference in total precipitation between years was reflected in the differences in average soil water content, which was approximately 28% lower in 2000 (6.1 ± 0.2 % SE, $n = 324$) than in 1999 (8.5 ± 0.2 % SE, $n = 324$).

Both soil C and N content (mg g^{-1}) decreased ($P < 0.10$) with depth (0-2.5, 2.5-5.0, and 5-10 cm) and this trend was consistent between condition classes (good and fair), among soil removal levels (0, 11.2, and 22.4 t ha^{-1}), and between years (1999 and 2000). There was a significant ($P < 0.10$) condition class by year interaction for soil C (Figure 2-2). Between 1999 and 2000, soil C increased ($P < 0.10$) in both fair and good condition classes, but was greater ($P < 0.10$) in the fair condition plots in both years (7.9 ± 0.4 and

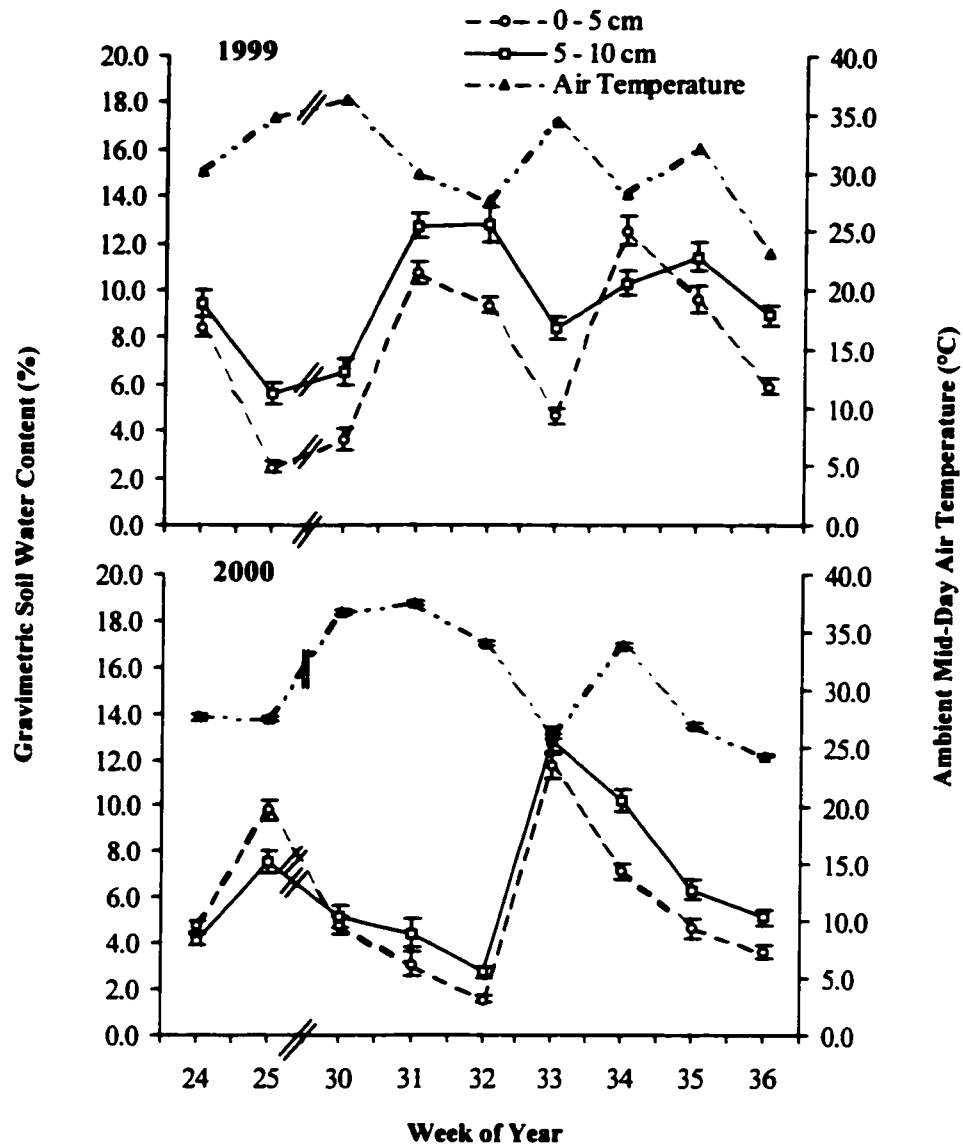


Figure 2-1. Weekly average (\pm SE) gravimetric soil water content (%; $n = 18$) for the 0 - 5 and 5 - 10 cm depths and ambient mid-day air temperatures ($^{\circ}\text{C}$; $n = 135$) at the Central Plains Experimental Range research area during the 1999 and 2000 growing seasons.

8.4 ± 0.3 mg g⁻¹, respectively; n = 54) than in the good condition plots (6.6 ± 0.3 and 7.9 ± 0.3 mg g⁻¹, respectively; n = 54). There was no difference (P > 0.10) in soil C among soil removal levels in the fair condition class, and this did not change between years (Figure 2-2). Within the good condition class however, soil C was greater (P < 0.10) in the 11.2 t ha⁻¹ soil removal level in 1999 and 2000 (7.5 ± 0.5 and 8.8 ± 0.6 mg g⁻¹, respectively; n = 18) than in either the 0 t ha⁻¹ (5.9 ± 0.6 and 7.6 ± 0.6 mg g⁻¹, respectively; n = 18) or 22.4 t ha⁻¹ (6.3 ± 0.5 and 7.3 ± 0.6 mg g⁻¹, respectively n = 18) levels (Figure 2-2).

Soil N content varied (P < 0.10) among soil removal levels but this was dependent on condition class and year (Figure 2-3). Within the fair condition class, differences in soil N among soil removal levels varied (P < 0.10) between 1999 and 2000 (Figure 2-3). Conversely, the relative differences in soil N among soil removal levels within the good condition class varied little (P > 0.10) between 1999 and 2000 (Figure 2-3). Soil N increased between 1999 and 2000 among all 3 soil removal levels within the fair condition plots (Figure 2-3) but, the largest increase in soil N was in the 22.4 t ha⁻¹ soil removal level (from 0.8 ± 0.04 to 1.0 ± 0.06 mg g⁻¹, respectively; n = 18). In the good condition class though, soil N was greater (P < 0.10) in the 11.2 t ha⁻¹ soil removal level in 1999 and 2000 (0.83 ± 0.03 and 0.98 ± 0.06 mg g⁻¹, respectively; n = 18) than in either the 0 t ha⁻¹ (0.68 ± 0.04 and 0.82 ± 0.05 mg g⁻¹, respectively; n = 18) or the 22.4 t ha⁻¹ (0.7 ± 0.04 and 0.74 ± 0.08 mg g⁻¹, respectively; n = 18) levels (Figure 2-3).

Leaf Carbon and Nitrogen Blue grama leaf C and N content did not vary (P > 0.10) between the good and fair condition classes, nor was there any significant interactions

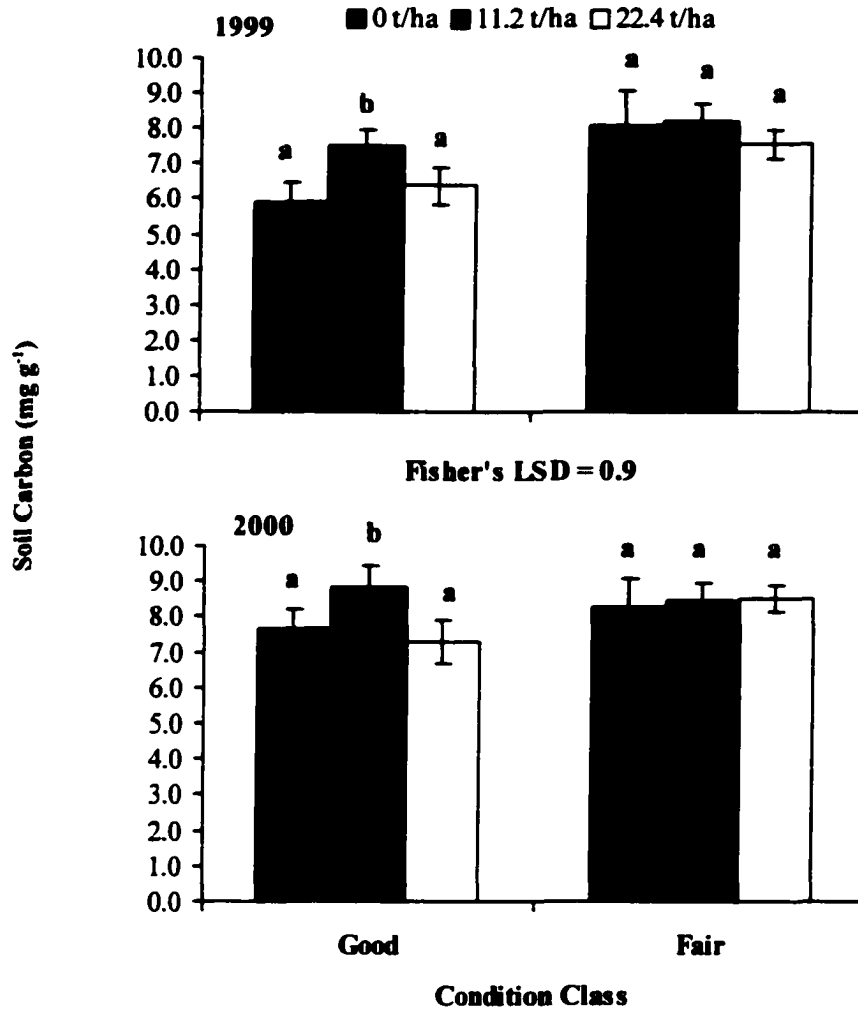


Figure 2-2. Average (\pm SE, $n = 18$) yearly soil carbon (mg g^{-1}) among the 0, 11.2, and 22.4 t ha^{-1} soil removal levels for the good and fair range condition classes at the Central Plains Experimental Range research area. Similar letters above bars within a range condition class and year are not significantly different ($P \leq 0.10$, Fisher's LSD = 0.9 mg g^{-1} ; $t = 1.65$, MSE = 0.027, $n = 18$).

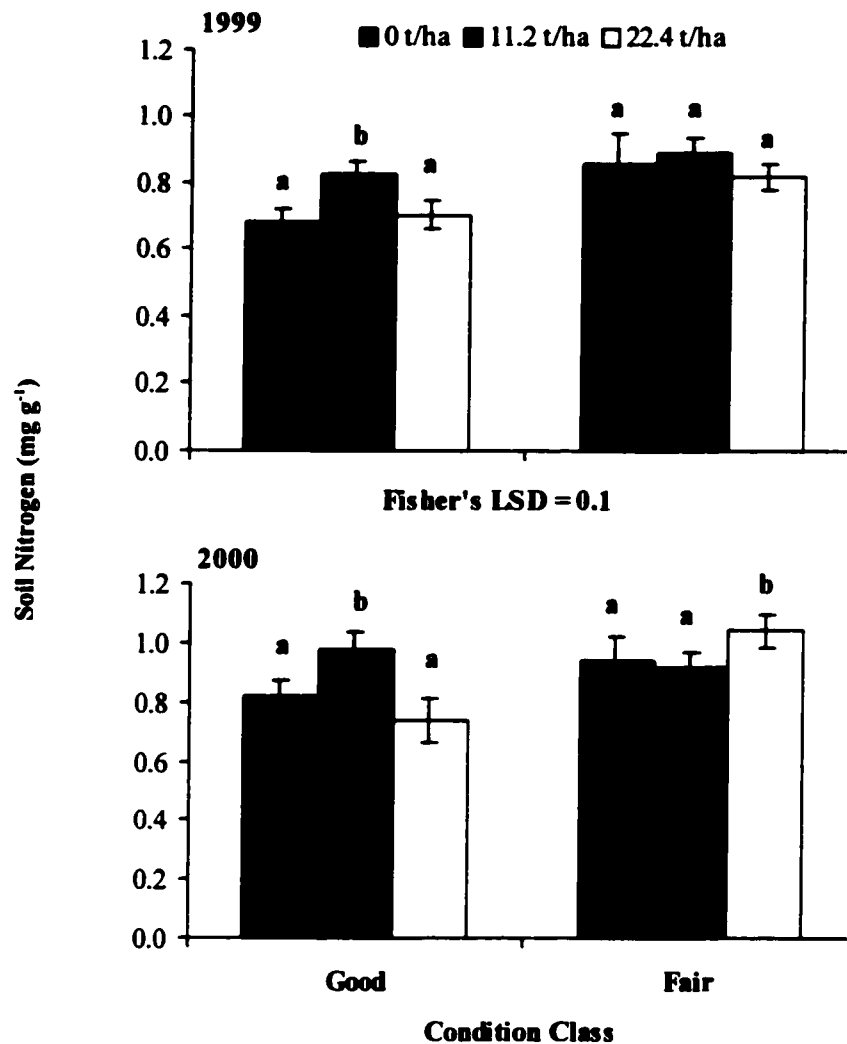


Figure 2-3. Average (\pm SE, $n = 18$) yearly soil nitrogen (mg g^{-1}) among the 0, 11.2, and 22.4 t ha^{-1} soil removal levels for the good and fair range condition classes at the Central Plains Experimental Range research area. Similar letters above bars within a range condition class and year are not significantly different ($P \leq 0.10$, Fisher's LSD = 0.1 mg g^{-1} ; $t = 1.65$, MSE = 0.006 , $n = 18$).

between years or sample periods with condition class. Differences in leaf C content of blue grama leaves among sample periods was dependent on year, but generally were greater earlier in the growing season than in later weeks (Table 2-1). Average leaf C content in blue grama was greater ($P < 0.10$) in 2000 ($434 \pm 2 \text{ mg g}^{-1}$, $n = 162$) than in 1999 ($425 \pm 1 \text{ mg g}^{-1}$, $n = 162$). Leaf N in blue grama also varied ($P < 0.10$) among sample periods and between years (Table 2-1). In 1999, blue grama leaf N varied between a low of $13.3 (\pm 0.4, n = 18) \text{ mg g}^{-1}$ during week 30 and a high of $16.8 (\pm 0.4, n = 18) \text{ mg g}^{-1}$ in week 32 (Table 2-1). Blue grama leaf N in 2000 was more variable however, ranging between a low of $11.6 (\pm 0.4, n = 18) \text{ mg g}^{-1}$ in week 25 and a high of $19.7 (\pm 1.0, n = 18) \text{ mg g}^{-1}$ in week 35 (Table 2-1). Average N content in blue grama leaves in 1999 ($14.9 \pm 0.2, n = 162$) was less ($P < 0.10$) than in 2000 ($15.6 \pm 0.3, n = 162$).

Soil removal level had little effect on blue grama leaf C content ($P > 0.10$). However, N content of blue grama leaves varied ($P < 0.10$) among soil removal levels across sample periods (Figure 2-4), and this response was not affected by year. In general, blue grama leaf N content tended to be less in the 11.2 t ha^{-1} soil removal level than in either the control (0 t ha^{-1}) or 22.4 t ha^{-1} removal level (Figure 2-4). Leaf N did not vary ($P > 0.10$) between the 0 and 22.4 t ha^{-1} soil removal levels. The largest separation between soil removal levels in leaf N content occurred late in the growing season (i.e. weeks 34, 35, and 36; Figure 2-4).

Within the good range condition class, differences in leaf C content between western wheatgrass and blue grama were not affected by sample week or year ($P > 0.10$). Leaf C in western wheatgrass ($454 \pm 1 \text{ mg g}^{-1}$, $n = 162$) was significantly greater than in

blue grama ($431 \pm 2 \text{ mg g}^{-1}$, $n = 162$), and this was consistent across soil removal levels. However, differences between western wheatgrass and blue grama in leaf N varied ($P < 0.10$) weekly during both 1999 and 2000 (Table 2-2). In both years, weekly leaf N levels in western wheatgrass were nearly always greater than in blue grama (Table 2-2). Thus, overall leaf N in western wheatgrass ($18.9 \pm 0.3 \text{ mg g}^{-1}$, $n = 162$) was greater than in blue grama ($15.6 \pm 0.2 \text{ mg g}^{-1}$, $n = 162$). Within each species, leaf N did not vary significantly ($P > 0.10$) between 1999 and 2000 (Table 2-2).

Table 2-1. Average weekly (\pm SE, $n = 18$) and yearly (\pm SE, $n = 162$) leaf carbon and nitrogen contents (mg g^{-1}) in blue grama within the good and fair range condition classes at the Central Plains Experimental Range research area during 1999 and 2000. Values are averaged across soil removal levels.

Year	Week of Year									Yearly Mean
	24	25	30	31	32	33	34	35	36	
----- Leaf Carbon ^{1,2} -----										
1999	438 ^d ± 2	434 ^{cd} ± 1	427 ^{bc} ± 3	428 ^{ab} ± 3	429 ^{cd} ± 3	416 ^a ± 3	414 ^a ± 2	419 ^{ab} ± 2	421 ^{ab} ± 2	425 [*] ± 1
2000	443 ^c ± 2	442 ^{bc} ± 4	423 ^a ± 2	434 ^{bc} ± 2	423 ^a ± 3	433 ^{bc} ± 2	437 ^{bc} ± 4	436 ^{bc} ± 3	439 ^{bc} ± 2	434 [*] ± 2
----- Leaf Nitrogen ^{3,4} -----										
1999	15.2 ^{bcd} ± 0.5	13.3 ^a ± 0.4	13.3 ^a ± 0.4	15.4 ^{cd} ± 0.5	16.8 ^e ± 0.4	15.2 ^{bcd} ± 0.4	15.5 ^d ± 0.6	14.5 ^b ± 0.6	14.6 ^{bcd} ± 0.5	14.9 [*] ± 0.2
2000	11.8 ^a ± 0.4	11.6 ^a ± 0.4	15.5 ^{bc} ± 0.7	16.1 ^c ± 0.5	14.4 ^b ± 0.5	14.7 ^b ± 0.5	18.2 ^d ± 0.8	19.7 ^e ± 1.0	18.6 ^d ± 0.9	15.6 [*] ± 0.3

¹Mean (\pm SE, $n = 18$) leaf carbon values in a row followed by the same letter were not significantly different ($P > 0.10$, LSD = 10 mg g^{-1} ; $t = 1.66$, MSE = 3.5, $n = 18$).

²Yearly mean (\pm SE, $n = 162$) leaf carbon values followed by * were significantly different ($P < 0.10$) between years.

³Mean (\pm SE, $n = 18$) leaf nitrogen values in a row followed by the same letter were not significantly different ($P > 0.10$, LSD = 0.9 mg g^{-1} ; $t = 1.66$, MSE = 0.028, $n = 18$).

⁴Yearly mean (\pm SE, $n = 162$) leaf nitrogen values followed by * were significantly different ($P < 0.10$) between years.

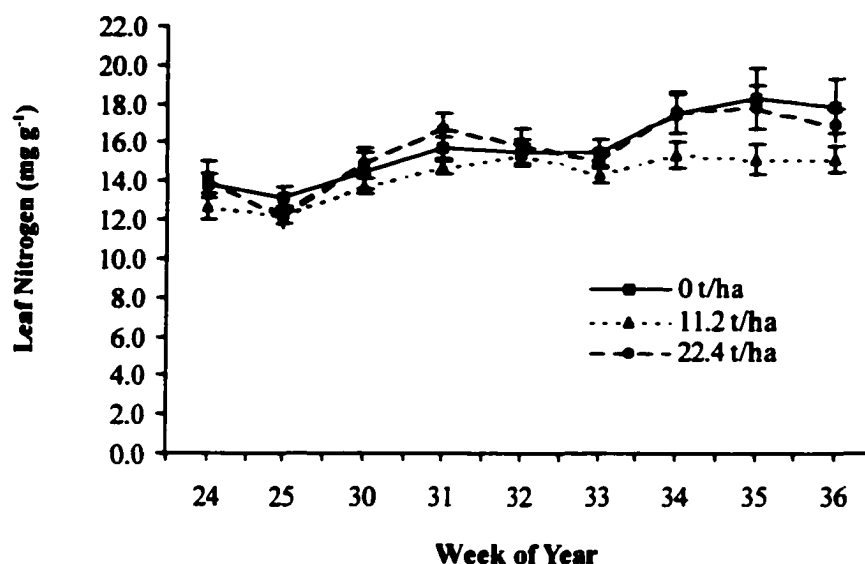


Figure 2-4. Weekly average (\pm SE, $n = 18$) leaf nitrogen content in blue grama among the 0, 11.2, and 22.4 t ha⁻¹ soil removal levels at the Central Plains Experimental Range research area.

Leaf N did not respond to soil removal for either western wheatgrass or blue grama ($P > 0.10$), but varied between years (Figure 2-5). In 1999, leaf N in the 0 (16.8 ± 0.4 mg g⁻¹, $n = 54$) and 11.2 t ha⁻¹ (16.7 ± 0.4 mg g⁻¹, $n = 54$) soil removal treatments were similar (LSD = 0.5 mg g⁻¹; $t = 1.66$, MSE = 0.028), but were significantly less than that found in the 22.4 t ha⁻¹ (17.6 ± 0.4 mg g⁻¹, $n = 54$) soil removal level (Figure 2-5). In 2000 though, leaf N levels among the 3 soil removal levels were all significantly different (LSD = 0.5 mg g⁻¹; $t = 1.66$, MSE = 0.028) from each other. With the exception of the 11.2 t ha⁻¹ treatment, leaf N increased ($P < 0.10$) in 2000 over that found in 1999. The greatest amount of leaf N in 2000 was in grasses from the 22.4 t ha⁻¹ soil removal treatment (18.6 ± 0.7 mg g⁻¹, $n = 54$), while the least was in grasses from the 11.2 t ha⁻¹ (16.1 ± 0.6 mg g⁻¹, $n = 54$) soil removal level (Figure 2-5).

Table 2-2. Average weekly (\pm SE, $n = 9$) and yearly (\pm SE, $n = 162$) leaf nitrogen content (mg g^{-1}) in western wheatgrass and blue grama within the good range condition class at the Central Plains Experimental Range research area during 1999 and 2000. Values are averaged across soil removal levels.

Year	Week of Year									Yearly Mean ²
	24	25	30	31	32	33	34	35	36	
----- Western Wheatgrass ¹ -----										
1999	17.4 ^c ± 0.6	16.8 ^{bc} ± 0.4	14.7 ^a ± 0.7	16.0 ^b ± 0.6	19.4 ^d ± 0.7	20.1 ^{de} ± 0.8	20.9 ^c ± 0.6	22.0 ^e ± 0.6	20.9 ^c ± 0.7	18.7 ± 0.3
2000	16.4 ^b ± 0.5	14.8 ^a ± 0.6	17.1 ^{bc} ± 0.8	19.1 ^d ± 0.7	17.2 ^{bc} ± 0.7	17.7 ^c ± 0.9	21.6 ^e ± 1.2	23.1 ^f ± 1.0	24.8 ^g ± 0.7	19.1 ± 0.4
----- Blue Grama ¹ -----										
1999	15.6 ^{bc} ± 0.7	13.8 ^a ± 0.6	13.7 ^a ± 0.5	16.3 ^{cd} ± 0.8	16.8 ^d ± 0.6	15.7 ^{bcd} ± 0.5	16.1 ^{cd} ± 0.8	15.3 ^{bc} ± 1.0	14.8 ^{ab} ± 0.7	15.3 ± 0.2
2000	12.5 ^a ± 0.4	11.9 ^a ± 0.5	16.1 ^{de} ± 1.0	17.0 ^{ef} ± 0.8	15.5 ^{cd} ± 0.8	14.9 ^{bc} ± 0.7	17.5 ^f ± 0.7	20.0 ^g ± 1.0	17.7 ^f ± 0.9	15.9 ± 0.4

¹Mean (\pm SE, $n = 9$) leaf nitrogen values in a row followed by the same letter are not different ($P > 0.10$, LSD = 1.2 mg g^{-1} ; $t = 1.66$, MSE = 0.024, $n = 9$).

²Yearly mean (\pm SE, $n = 162$) leaf nitrogen values within each species are not different ($P > 0.10$) between 1999 and 2000.

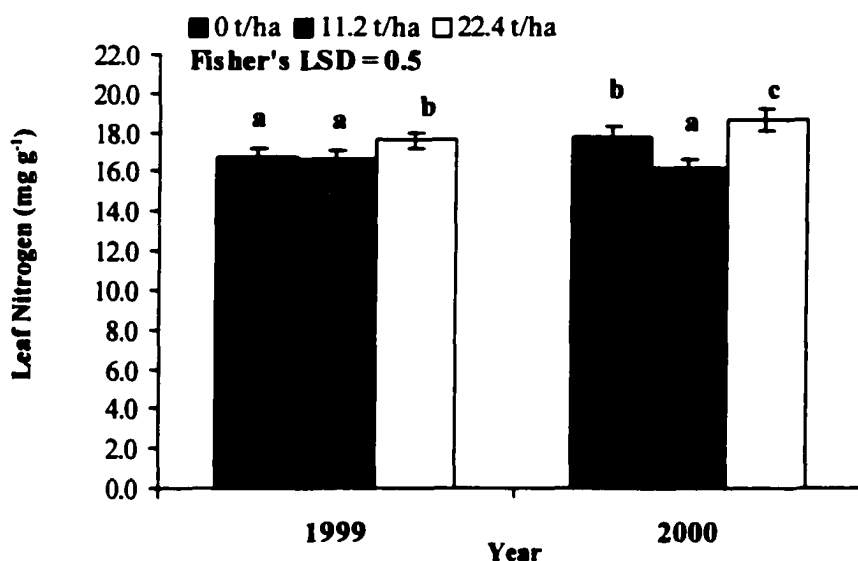


Figure 2-5. Yearly average (\pm SE, $n = 54$) leaf nitrogen (mg g^{-1}) among the 0, 11.2, and 22.4 t ha^{-1} soil removal levels at the Central Plains Experimental Range Research Area. Similar letters over bars within a year are not significantly different ($P > 0.10$, Fisher's LSD = 0.5 mg g^{-1} ; $t = 1.66$, MSE = 0.028, $n = 54$).

Photosynthesis, Transpiration, C_i , LWP, NUE, and WUE Net photosynthetic rates, WUE, and NUE, in blue grama leaves within the good and fair condition classes were different ($P < 0.10$) between years and across sample periods. However, despite weekly variations in net photosynthetic rates and NUE of blue grama, the values for these responses were generally greater in plants from the fair condition class than those in the good condition class, and were consistently higher in 1999 than in 2000 (Table 2-3). For example, in 1999 the average yearly net photosynthetic rate of blue grama in the fair condition class was 10% greater ($P < 0.10$) than in the good condition class (Table 2-3). Even though there was an overall reduction in net photosynthesis between 1999 and 2000, photosynthetic rates in blue grama remained higher for plants in the fair condition class than in the good condition class (Table 2-3). There was a significant 3-way interaction for C_i in blue grama leaves between condition classes, week of year, and year. Although transpiration rates in blue grama leaves varied across sampling periods within years ($P < 0.10$), there was no consistent trend between classes within year, or among sample periods. Leaf water potential of blue grama leaves varied ($P < 0.10$) between the good and fair condition classes, but this was dependent separately on year (Table 2-3) and sample period. Similarly, WUE in blue grama leaves showed no consistent trend between condition classes across years (Table 2-3).

Soil removal level did not affect ($P > 0.10$) WUE, NUE, leaf water potential or transpiration rates in blue grama leaves when data for the good and fair condition classes were compared. However, the net photosynthetic rate of blue grama increased ($P < 0.10$)

with increasing soil removal (Figure 2- 6). This response was consistent between condition classes, years and among sample periods.

The response of C_i in blue grama leaves to the soil removal treatments was dependent on condition class. In the good condition class, C_i was significantly lower (Fisher's LSD = $18 \mu\text{mol CO}_2 \text{ mol air}^{-1}$, $t = 1.782$, $n = 270$, $\text{MSE} = 13,727$) in the 11.2 and 22.4 t ha^{-1} treatments (120 ± 5 and $129 \pm 6 \mu\text{mol CO}_2 \text{ mol air}^{-1}$, respectively) than in the control ($151 \pm 8 \mu\text{mol CO}_2 \text{ mol air}^{-1}$). However, C_i varied little (Fisher's LSD = $18 \mu\text{mol CO}_2 \text{ mol air}^{-1}$, $t = 1.782$, $n = 270$, $\text{MSE} = 13,727$) among the soil removal treatments within the fair condition class and averaged $133 \pm 4 \mu\text{mol CO}_2 \text{ mol air}^{-1}$.

Table 2-3. Average (\pm SE) net photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $n = 405$), transpiration ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, $n = 405$), leaf water potential (MPa, $n = 243$), water use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, $n = 405$) and nitrogen use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$, $n = 405$) for blue grama leaves in the good and fair range condition classes at the Central Plains Experimental Range research area in 1999 and 2000.

Condition Class	Photosynthesis	Transpiration	Leaf Water Potential	Water Use Efficiency	Nitrogen Use Efficiency
----- 1999 -----					
Good	17.7 ± 0.5	4.6 ± 0.1	-2.7 ± 0.04	4.1 ± 0.1	$0.11 \pm 0.003^*$
Fair	19.6 ± 0.5	5.3 ± 0.1	-2.7 ± 0.04	4.1 ± 0.1	$0.12 \pm 0.003^*$
Average	$18.7 \pm 0.4^{**}$	4.9 ± 0.1	-2.7 ± 0.03	4.1 ± 0.1	$0.12 \pm 0.002^{**}$
----- 2000 -----					
Good	15.9 ± 0.4	4.8 ± 0.1	-3.2 ± 0.06	4.0 ± 0.1	$0.09 \pm 0.002^*$
Fair	16.5 ± 0.4	5.2 ± 0.2	-3.4 ± 0.07	3.8 ± 0.1	$0.10 \pm 0.003^*$
Average	$16.5 \pm 0.3^{**}$	5.0 ± 0.1	-3.3 ± 0.07	3.9 ± 0.1	$0.10 \pm 0.001^{**}$

*values were different ($P < 0.10$, $\text{LSD} = 0.1$, $t = 1.782$, $\text{MSE} = 0.0125$) between classes within year.

**values were different between 1999 and 2000 ($P < 0.10$).

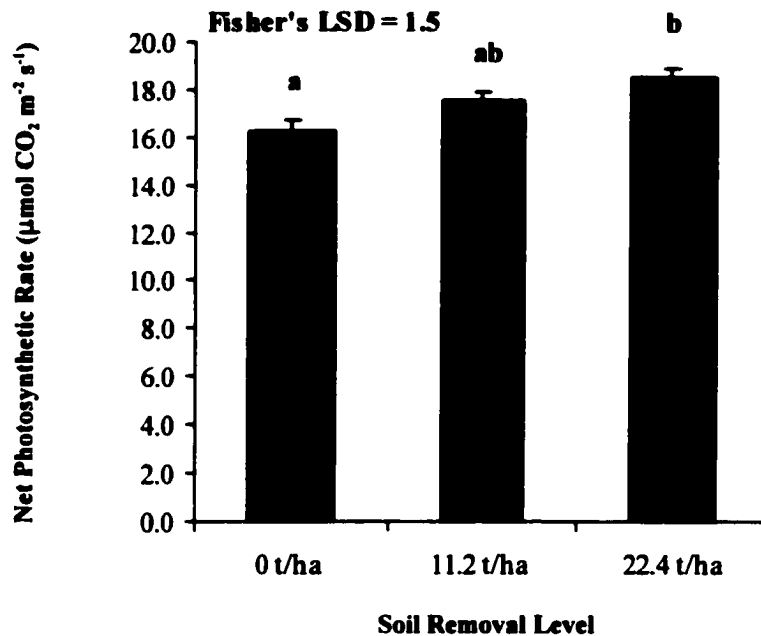


Figure 2-6. Average (\pm SE, $n = 540$) net photosynthetic rate of blue grama leaves among the 0, 11.2, and 22.4 t ha⁻¹ soil removal levels at the Central Plains Experimental Range research area (Fisher's LSD = 1.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $t = 1.782$, MSE = 194.9, $n = 540$).

Within the good range condition class there was a significant interaction ($P < 0.10$) between the species of grass, sample period, and year for net photosynthesis, C_i , leaf water potential, NUE, and WUE. While photosynthesis was generally higher in western wheatgrass than in blue grama in both years, there was considerable variation in the net photosynthetic rates of both species across sample periods (Figure 2-7). On average though, the net photosynthetic rates of western wheatgrass and blue grama were greater in 1999 (19.2 ± 0.4 and $17.7 \pm 0.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively, $n = 405$) than in 2000 (18.1 ± 0.3 and $15.9 \pm 0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively, $n = 405$). Greater ($P < 0.10$) weekly transpiration rates in western wheatgrass than in blue grama, resulted in

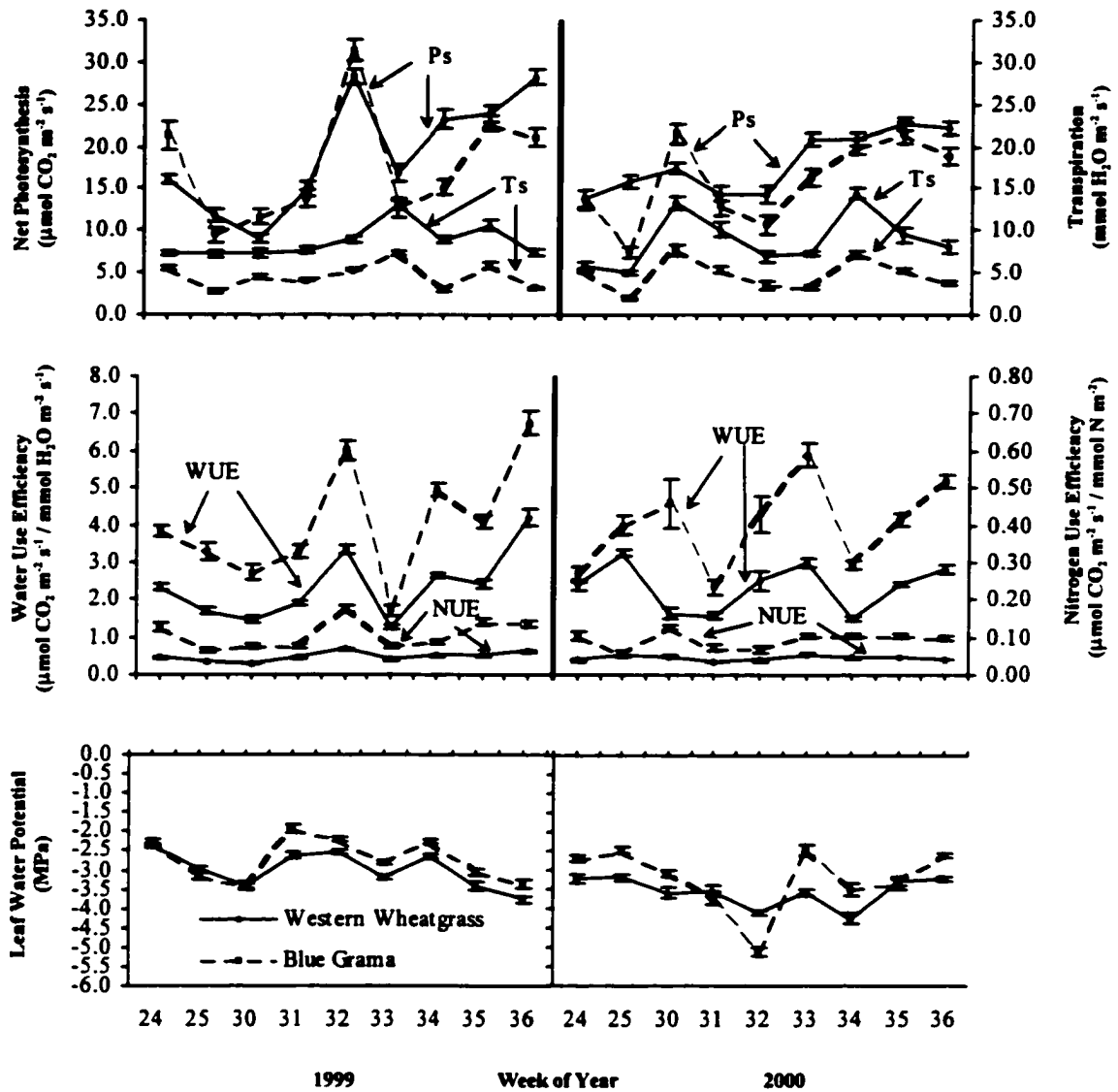


Figure 2-7. Weekly average (\pm SE) net photosynthetic rates (Ps, n = 45), transpiration rates (Ts, n = 45), water use efficiencies (WUE, n = 45), nitrogen use efficiencies (NUE, n = 45), and leaf water potentials (n = 27) for western wheatgrass and blue grama in the good range condition class at the Central Plains Experimental Range research area during 1999 and 2000.

consistently lower WUE for western wheatgrass relative to blue grama in both years (Figure 2-7). Weekly nitrogen use efficiencies in 1999 and 2000 were also consistently higher in blue grama than in western wheatgrass (Figure 2-7). With a few exceptions in 2000, weekly leaf water potentials tended to be higher (less negative) in blue grama than in western wheatgrass (Figure 2-7). Inter-cellular CO₂ concentrations varied among weekly samples, but on average were higher in 1999 ($184 \pm 3 \mu\text{mol CO}_2 \text{ mol air}^{-1}$, $n = 810$) than in 2000 ($178 \pm 4 \mu\text{mol CO}_2 \text{ mol air}^{-1}$, $n = 810$). Between species, C_i was approximately 60% greater ($P < 0.10$) in western wheatgrass ($229 \pm 1 \mu\text{mol CO}_2 \text{ mol air}^{-1}$, $n = 810$) than in blue grama ($133 \pm 4 \mu\text{mol CO}_2 \text{ mol air}^{-1}$, $n = 810$).

Soil removal level within the good range condition class affected ($P < 0.10$) net photosynthesis and NUE in much the same way (Figure 2-8). The net photosynthetic rate was significantly higher (Fisher's LSD = $2.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $t = 1.782$, MSE = 340.33, $n = 540$) in the 11.2 ($19.3 \pm 0.38 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $n = 540$) and 22.4 ($18.2 \pm 0.36 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $n = 540$) t ha⁻¹ soil removal levels than in the control ($15.7 \pm 0.35 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $n = 540$). NUE was significantly higher (Fisher's LSD = $0.013 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$, $t = 1.782$, MSE = 0.0147, $n = 540$) in the 11.2 t ha⁻¹ ($0.081 \pm 0.002 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$, $n = 540$) soil removal level than in the 22.4 ($0.071 \pm 0.002 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$, $n = 540$) or 0 ($0.064 \pm 0.002 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$, $n = 540$) t ha⁻¹ levels. The response of net photosynthesis and NUE to the different soil removal levels was consistent between blue grama and western wheatgrass, across sample periods, and between years.

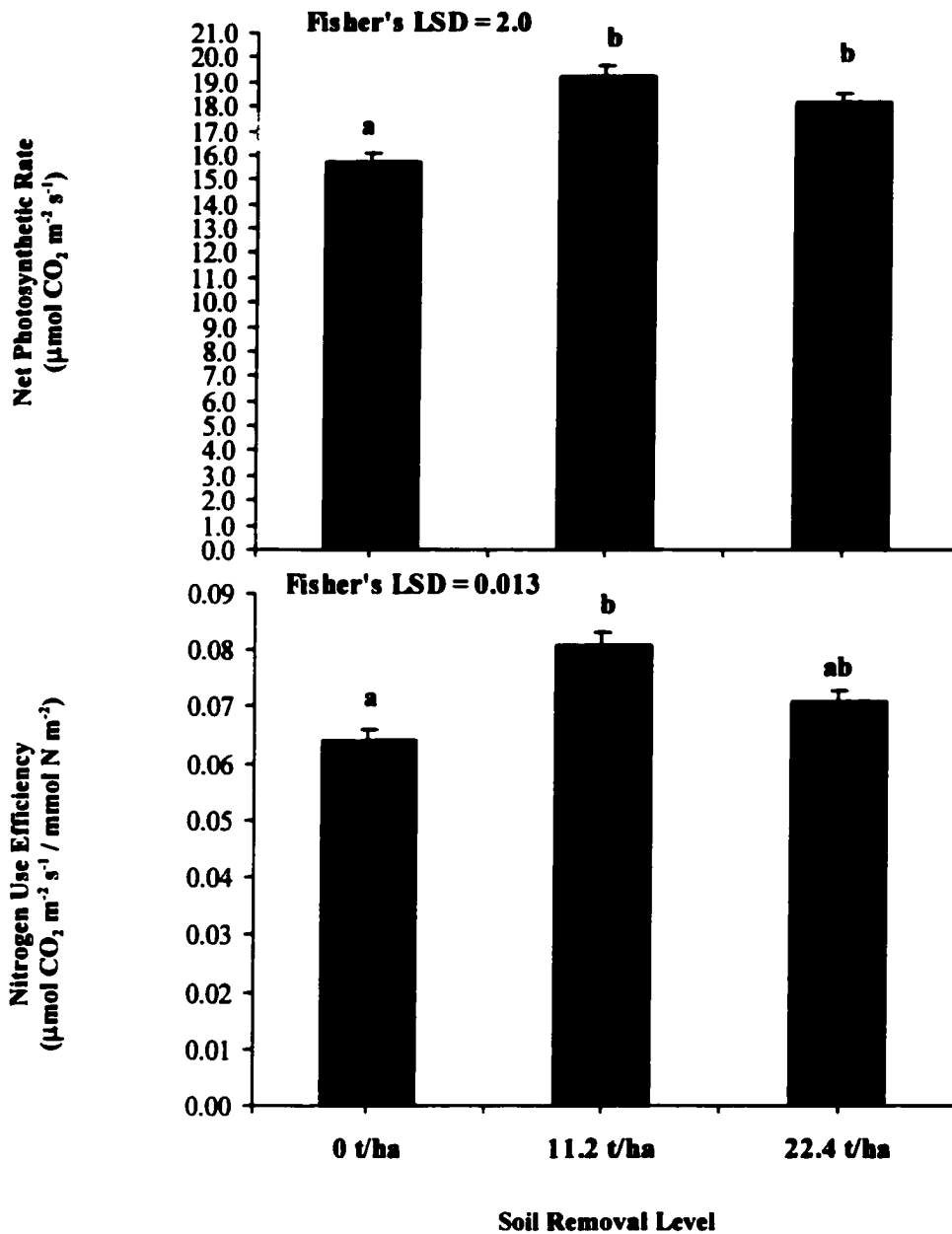


Figure 2-8. Average (\pm SE, $n = 540$) net photosynthetic rates and nitrogen use efficiencies of western wheatgrass and blue grama plants in the 0, 11.2, and 22.4 t/ha soil removal levels in the good condition class at the Central Plains Experimental Range research area (Fisher's LSD = $2.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $0.013 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$; $t = 1.782$, $n = 540$, $\text{MSE} = 340.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $0.015 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$, respectively).

Similar to net photosynthesis and NUE, the response of C_i to the soil removal treatments was consistent ($P > 0.10$) between blue grama and western wheatgrass, among sample periods, and between years. However, while photosynthesis and NUE tended to increase with increasing soil removal level, C_i tended to decrease. Inter-cellular CO_2 concentration was significantly higher (Fisher's LSD = $11 \mu\text{mol } CO_2 \text{ mol air}^{-1}$, $t = 1.782$, $n = 540$, $MSE = 10,325$) in the control plants ($191 \pm 4 \mu\text{mol } CO_2 \text{ mol air}^{-1}$), than in plants from either the 11.2 ($175 \pm 4 \mu\text{mol } CO_2 \text{ mol air}^{-1}$) or 22.4 ($177 \pm 4 \mu\text{mol } CO_2 \text{ mol air}^{-1}$) $t \text{ ha}^{-1}$ soil removal treatments, that were not significantly different from each other. Transpiration rates and WUEs of western wheatgrass and blue grama were not different ($P > 0.10$) among soil removal levels.

Discussion

Seasonal Responses The seasonal responses of net photosynthesis, C_i , transpiration, water use efficiency, and nitrogen use efficiency in western wheatgrass and blue grama in this study were similar to the range of values reported in other studies on the same species (Williams 1974, Brown and Trlica 1977a, 1977b, Kemp and Williams 1980, Painter and Detling 1981, Monson et al. 1982, 1983, 1986) and for other C_3 and C_4 plants (Caldwell et al. 1977, Brown and Wilson 1983, Nowak and Caldwell 1984, Percy and Ehleringer 1984, Sage and Percy 1987, Evans 1989, Polley 1997). Fluctuations in the rates of photosynthesis and transpiration, C_i , WUE, and NUE are usually observed within and between growing seasons, and are typically driven by temporal variations in environmental conditions (Williams 1974, Brown and Trlica 1977a, 1977b, Kemp and

Williams 1980, Monson et al. 1982, 1983, 1986). In the present study however, the decrease in photosynthesis between 1999 and 2000 observed in both species was not accompanied by concomitant changes in the transpiration rate, WUE, and C_i . The similarity in these factors between 1999 and 2000, coupled with fairly similar ambient temperatures for both years, indicated that the lower average photosynthetic rates in 2000, relative to 1999, were not the result of differences in atmospheric conditions that typically influence photosynthesis (i.e. relative humidity, temperature, vapor pressure deficit, etc.; Williams 1974, Brown and Trlica 1977a, 1977b, Kemp and Williams 1980, Monson et al. 1983, 1986, Pearcy and Ehleringer 1984, Brown 1995, Coyne et al. 1995). What did change between 1999 and 2000, however, was the amount of precipitation.

The Central Plains Experimental Range received 29% more precipitation than normal in 1999, but in 2000 received only 74% of the average total annual precipitation (321 mm). This large variation in precipitation between 1999 and 2000 was reflected in the average soil water content at the study site, which decreased, from 8 to 6 % in the top 5 cm and from 10 to 7% at 10 cm depth between the 2 years of study. The decrease in photosynthetic rates with lower soil water contents in 2000 compared with 1999 was also linked to a large decline in leaf water potential (LWP) for western wheatgrass and blue grama over the same period. Since there was not a difference in atmospheric demand for water between years, the decrease in LWP probably resulted from lower water availability in 2000, and thus, was an indication of greater plant water stress in 2000 than in 1999. It appears therefore, that the decline in the photosynthetic rates of western

wheatgrass and blue grama between years was primarily a function of soil water availability.

The influence of plant water stress on photosynthetic rates of western wheatgrass and blue grama (Brown and Trlica 1977a, 1977b, Kemp and Williams 1980, Monson et al. 1986) and other species has been thoroughly studied (Deput and Caldwell 1975, Caldwell et al. 1977, Percy and Ehleringer 1984, Ehleringer 1984). For example, Kemp and Williams (1980) found in a greenhouse study that, at a given leaf temperature (i.e. 25°C), photosynthesis in western wheatgrass and blue grama decreased exponentially from a high of approximately $31 \mu\text{mol m}^{-2} \text{s}^{-1}$ to less than $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ as LWP decreased from -1 to -5 MPa. In that study however, Kemp and Williams (1980) noted no significant difference between the response curves relating photosynthesis with LWP for western wheatgrass and blue grama. This led them to conclude that the individual responses of western wheatgrass and blue grama to seasonal moisture gradients was not as an important parameter in defining their niches as was the seasonal temperature gradient (Kemp and Williams 1980). In the field however, seasonal variability in temperatures and soil water content may cause the photosynthesis-leaf water potential response curves of western wheatgrass and blue grama to shift differentially, resulting in their widely different water use patterns (Monson et al. 1986). For example, photosynthesis, transpiration, LWP, and WUE responded differently in western wheatgrass than in blue grama between weeks 24 and 25, and weeks 32 through 34 of 2000 depending on changes in temperature and soil water content (Figure 2-7).

Between weeks 24 and 25 there was little change in air temperature (28° C), but soil water content was higher during week 25 than in week 24 (Figure 2-1). While the net photosynthetic rates of western wheatgrass and blue grama were similar in week 24, in week 25 photosynthesis in blue grama had declined to less than half of the rate observed in western wheatgrass which changed little between weeks (Figure 2-7). Despite this differential photosynthetic response, LWP and WUE increased between weeks 24 and 25 for both species (Figure 2-7). Why western wheatgrass and blue grama exhibited this differential photosynthetic response between weeks 24 and 25, when soil water content, LWP, and WUE increased, is not entirely clear. However, Kemp and Williams (1980) noted in their study that the temperature response of net photosynthesis in blue grama and western wheatgrass was strongly influenced by pretreatment temperature. Thus, the prolonged exposure to relatively cool temperatures in June of 2000 may have induced the differential response in photosynthesis, LWP and WUE observed in western wheatgrass and blue grama during weeks 24 and 25 (Kemp and Williams 1980, Monson et al. 1986). This suggests that during the early portion of the growing season in the shortgrass steppe, temperature, rather than soil water availability, may be more significant in defining the differences in net photosynthetic rates and water use patterns between blue grama and western wheatgrass.

By mid-summer (weeks 30-33) the combined influence of temperature and soil water content may have become more significant in controlling the photosynthetic rate and water use of western wheatgrass and blue grama than in the early portion of the season. Photosynthesis in western wheatgrass and blue grama for example, increased

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between weeks 32 and 33 of 2000 (Figure 2-7) following a large precipitation event where soil water content went from less than 3% to as high as 13% in the 5-10 cm depth and temperature declined from 34 to 26° C (Figure 2-1). At the same time, and because of the cooler temperatures and greater available soil moisture, LWP increased for both western wheatgrass and blue grama, but did not result in an increases in their respective transpiration rates (Figure 2-7). Consequently, WUE in both species increased between weeks 32 and 33. Notably however, the increases in LWP and WUE were proportionately greater in blue grama than in western wheatgrass (Figure 2-7). In contrast, between weeks 33 and 34 in 2000, the increase in temperature (26 - 34°C, respectively) and decrease in soil water content (i.e. 13 - 10%, 5-10 cm depth, respectively) led to a differential response in photosynthesis between western wheatgrass and blue grama, but, unlike the differences observed between weeks 32 and 33, resulted in a 2-fold decrease in LWP, a doubling of the transpiration rate, and a 50% decrease in WUE for both species (Figure 2-1 and 2-7).

The different physiological responses observed in western wheatgrass and blue grama, between weeks 32 through 34 of 2000, suggested that later in the season, temperature and soil water availability combined to differentially shift the photosynthesis-leaf water potential response curves for each species. This temperature and soil water content dependent shift in the photosynthesis-leaf water potential response curve may, therefore, be responsible for the different water use patterns commonly observed between western wheatgrass and blue grama (Williams 1974, Brown and Trlica 1977a, 1977b, Kemp and Williams 1980, Monson et al. 1982, 1983, 1986). However,

additional field research is needed to separate the effects of temperature and soil water availability on the water use patterns in western wheatgrass and blue grama. Such research will become increasingly important to the management of the shortgrass ecosystem if climatic changes (ie. global warming) occur (Polley 1997).

Effects of Soil Loss Even though there were seasonal and yearly differences in net photosynthesis, NUE, and C_i between western wheatgrass and blue grama, their response to the soil removal treatments were similar (Figure 2-6 and 2-8). In both western wheatgrass and blue grama, increasing the level of soil removal resulted in increases in the net photosynthetic rate and NUE, and decreases in C_i . This response was likely not dependent on soil water availability, since the transpiration rates and WUEs of both species did not vary among the soil removal levels. These results, coupled with the concomitant increase in NUE and decrease in C_i with photosynthesis, suggests that the increase in productivity observed in the 11.2 and 22.4 t ha⁻¹ soil removal treatments relative to the control, was a function of differential allocation of nitrogen by both species among plants in the 3 soil removal treatments.

Increasing soil N supply has been shown to increase production of C_3 and C_4 plants, like western wheatgrass and blue grama (Brown and Wilson 1983; Sage and Pearcy 1987, Lajtha and Whitford 1989; Doescher et al. 1990; Coyne et al. 1995). However, greater N supply does not necessarily influence the capacity of plants to capture N (Hodge et al. 2000). In this study it was found that the distribution of soil N among the soil removal treatments was inconsistent with the distribution of leaf N levels (Figures 2-3 and 2-5). Additionally, the distribution of leaf N levels among the soil

removal treatments was different between years and was not consistent with the increases observed in the net photosynthetic rates of western wheatgrass and blue grama leaves (Figure 2-5). For example, even though soil N was higher in the 11.2 t ha⁻¹ soil removal level than in the control in 1999, leaf N levels did not vary between the control and the 11.2 t ha⁻¹ treatment (Figures 2-3 and 2-5). Thus, it is unlikely that differences in soil N among the soil removal levels (Figure 2-3) contributed to the higher photosynthetic rates observed in the 11.2 and 22.4 t ha⁻¹ treatments than in the control. Consequently, it may be the way that western wheatgrass and blue grama allocated the N within the plant that brought about the higher photosynthetic rates in plants within the 11.2 and 22.4 t ha⁻¹ soil removal treatments than in the control.

Plants allocate N into 2 major categories of proteins that have a direct influence on photosynthesis (Evans 1989, Coyne et al. 1995, Larcher 1995). The first are proteins associated with the thylakoid membranes of the chloroplasts and consist of the pigment-protein complexes, photosystem reaction centers, components of the electron transport chain, and ATP synthase (Evans 1989, Coyne et al. 1995, Larcher 1995). The majority (60 -85%) of N in thylakoid membranes is found in the light harvesting proteins of the pigment-protein complexes and the photosystem reaction centers (Evans 1989). The allocation of more or less plant N to light harvesting proteins is often dependent on the light environment of the plant or leaf (Evans 1989, von Caemmerer and Farquhar 1991). In environments where light may be otherwise limiting to photosynthesis, plants generally allocate more N to proteins of the pigment-protein complexes and the photosystem reaction centers, thereby increasing their photosynthetic capacity through

increased light absorption (Evans 1989, Coyne et al. 1995, Larcher 1995). In the shortgrass prairie however, western wheatgrass and blue grama do not exist in a light limited environment. Thus, it is unlikely that increasing the allocation of N into the light harvesting proteins would increase their relative photosynthetic rates.

The second major fraction of proteins that directly influence photosynthesis, all soluble, include primarily, the enzyme ribulose 1,5-bisphosphate carboxylase (Rubisco) among other Calvin cycle enzymes, and photorespiratory enzymes in the mitochondria and peroxisomes (Evans 1989, Coyne et al. 1995, Larcher 1995). The enzyme Rubisco is responsible for the carboxylation of ribulose 1,5-bisphosphate (RuBP), the first reaction in the Calvin cycle, which is the only pathway in plants (i.e. the Calvin cycle is present in both C₃ and C₄ plants) that can catalyze the net fixation of CO₂ (Salisbury and Ross 1992, Coyne et al. 1995, Larcher 1995, Bowyer and Leegood 1997). Higher relative photosynthetic rates in western wheatgrass and blue grama could be achieved by either increasing the absolute quantity of Rubisco or by increasing the enzyme's relative activity level (Evans 1989, von Caemmerer and Farquhar 1991, Coyne et al. 1995, Larcher 1995, Bowyer and Leegood 1997). Increasing either the quantity or activity level of Rubisco, independently or together, would result in a higher turnover of the Calvin cycle and therefore, higher apparent rates of net photosynthesis. In most plants, the quantity of Rubisco is highly correlated with total leaf N (Evans 1989). While the leaf N levels within the 0, 11.2, and 22.4 t ha⁻¹ soil removal levels did not necessarily vary with respect to the photosynthetic rates, the relative proportion of N allocated between thylakoid membrane proteins and Rubisco within the treatment groups may have been different. In

a review of the literature, Evans (1989) noted several cases where leaf N content remained constant, but apparent Rubisco quantity and activity changed.

The activity level of Rubisco is regulated, during light periods, by Rubisco activase, a protein that catalyzes the carbamylation of Rubisco and requires adenosine triphosphate (ATP) and RuBP for maximum activity (Salisbury and Ross 1992, Coyne et al. 1995, Larcher 1995, Bowyer and Leegood 1997). The photophosphorylation of ATP is regulated by ATP synthase, a thylakoid membrane protein (Salisbury and Ross 1992, Coyne et al. 1995, Bowyer and Leegood 1997). By allocating more N to ATP synthase, plants can raise the level of Rubisco activase activity, increasing the rate of carbamylation of Rubisco and thereby increase the rate of turnover in the Calvin cycle.

Evidence that western wheatgrass and blue grama differentially allocated N to increase the quantity or activity level of Rubisco, or both, in the 11.2 and 22.4 t ha⁻¹ treatments relative to the control is not straight forward. However, it is significant that while photosynthesis and NUE increased with the soil removal treatments, C_i decreased. Typically, increasing intercellular CO₂ concentrations are associated with increasing photosynthetic rates up to some maximum level of C_i, where Rubisco becomes saturated (von Caemmerer and Farquhar 1991, Coyne et al. 1995, Larcher 1995, Bowyer and Leegood 1997). Photosynthesis continually removes CO₂ from the intercellular space, which is constantly replenished from CO₂ outside the leaf by diffusion through stomates and the cuticle. Thus, the level of C_i is dependent, in part, on the supply of CO₂ outside the leaf (atmospheric CO₂, C_a) and on the photosynthetic demand for CO₂ inside the leaf. Theoretically, at a given constant supply of C_a (i.e. ambient C_a = 360 μmol CO₂ m⁻² s⁻¹),

and a constant photosynthetic rate under equal conditions, there should be no difference in C_i among plants of the same species. If however, while C_a and all other environmental conditions remain relatively constant and the photosynthetic demand for CO_2 increases, then C_i should decrease. In this study, leaf chamber conditions were held constant with respect to C_a , temperature, relative humidity, and PAR during the CO_2 exchange measurements within a given week. Thus, there were no fluctuations in chamber conditions that would have changed the supply or demand for CO_2 . It is possible therefore, that the lower C_i in the 11.2 and 22.4 t ha⁻¹ treatments relative to the control were an indication of increased photosynthetic demand for CO_2 , resulting from a more rapid turnover of the Calvin cycle and brought about by a higher quantity or greater activity level of Rubisco, or both.

The results of this study in more than one way support this suggested link between the observed photosynthetic rates, NUE, C_i and the differential distribution of N to Rubisco production or activity. Since the photosynthetic rates of western wheatgrass and blue grama among the soil removal treatments were measured under the same chamber conditions, it was expected that the grasses would differ in their responses. However, despite the differences between the C_3 and C_4 physiologies, and although photosynthesis, NUE, and C_i in western wheatgrass and blue grama varied in magnitude as expected, they unexpectedly responded in the same manner to the soil removal treatments. Moreover, because of the constant chamber conditions, plant N status and soil water content were the only remaining sources of observable variation that could have influenced photosynthetic rates. As it has been shown, soil water content was not

important in determining the photosynthetic response of western wheatgrass and blue grama among the soil removal treatments. Nitrogen use however, provides both a significant (Figure 2-8) and plausible explanation for the observed photosynthetic responses of both western wheatgrass and blue grama. Taken as a whole, these results suggest that the mutual, differential photosynthetic responses observed among the soil removal treatments for both western wheatgrass and blue grama occurred because of similar metabolic changes within the Calvin cycle, a metabolic pathway common to both species (Salisbury and Ross 1992, Coyne et al. 1995, Larcher 1995, Bowyer and Leegood 1997). If this were not true and by chance the physiological site of influence brought about by the soil removal treatments were different between the 2 species, then the responses of photosynthesis, NUE, and C, would more than likely also have been different. However, this was not the case, and in fact, 2 species that typically differ in their individual responses to environmental conditions because of their different physiologies, responded similarly to increasing soil removal.

It is not readily apparent why soil removal would stimulate western wheatgrass and blue grama to allocate N such that photosynthesis would increase. Part of the answer for this apparent compensatory response may be indicated by the increased plant respiration rates observed as soil removal level increased (Chapter IV). Plant respiration rates typically become elevated in response to increased need of metabolic energy for growth, ion uptake and transport, or stress (Chapin et al. 1987, Coyne et al. 1995, Larcher 1995). The increase in plant respiration rates may have been a result of increased root growth and ion uptake and transport, or stress caused by the soil removal treatments.

For many plants, roots account for a significant portion (50-80%) of the annual dry matter production, and only through continual growth can the roots explore enough soil volume to meet the nutritional needs of the plant (Chapin et al. 1987). It is possible that the removal of soil in the 11.2 and 22.4 t ha⁻¹ treatments altered 1 or more soil properties that generally supports plant growth (i.e. soil nutrient and organic matter content, water-holding capacity, surface horizon thickness; Singer and Munns 1991). If alteration of these soil properties was not severe, but sufficient enough to create a deficiency within the rooting zone, then more C might be allocated for root growth to maintain plant function (Ares 1976, Bloom et al. 1985, Chapin et al. 1987). Bloom et al. (1985) suggested that plants reduce inconsistencies in C and nutrient supplies by increasing their capacity to acquire the most limiting resource. The soil N content of the study site soils, measured at the end of each season, did not vary among soil removal levels. However, this does not mean that plant available N did not vary among the treatments over the course of the 1999 and 2000 growing seasons. Thus, if soil N became more readily deficient (but not limiting) within the rooting zones of the 11.2 and 22.4 t ha⁻¹ treatments than in the control, then western wheatgrass and blue grama may have responded by increasing root production to compensate for the increased aboveground demand for N (Bloom et al. 1985, Sage and Percy 1987, Chapin et al. 1987). This would account for the increased plant respiration (Chapter IV) and photosynthetic rates observed for plants in the 11.2 and 22.4 t ha⁻¹ soil removal levels relative to the control. In addition, the increased root growth would have allowed western wheatgrass and blue grama plants within the 11.2 and 22.4 t ha⁻¹ soil removal treatments to maintain leaf N

levels similar to those in the control. Consequently, any potential deficiencies in N would have been masked.

Summary and Conclusions

The purpose of this study was to determine the effects of 3 levels of soil loss at 0, 11.2 and 22.4 t ha⁻¹ on net photosynthetic rates of the dominant C₃ (western wheatgrass), and C₄ (blue grama) grasses on a shortgrass prairie site. The soil loss levels chosen for comparison represented no soil loss (0 t ha⁻¹), a soil loss level that is widely accepted to be the maximum allowable T-value (11.2 t ha⁻¹; Schmidt et al. 1982), and twice the maximum allowable T-value (22.4 t ha⁻¹). Two hypotheses were formulated to test the effects of the soil removal treatments. First, that the photosynthetic rates of western wheatgrass would decrease with increasing soil removal level and second, that the photosynthetic rates of blue grama would increase with increasing soil removal level. It was predicted that this differential response between western wheatgrass and blue grama would be associated with differences in their respective resource (water and nitrogen) use efficiencies. The net photosynthetic rates of both western wheatgrass and blue grama leaves in the 11.2 and 22.4 t ha⁻¹ soil removal levels were significantly higher than in the control (0 t ha⁻¹). Therefore, the hypothesis that the photosynthetic rates of western wheatgrass would decrease with an increase in soil removal was rejected. However, this study failed to reject the hypothesis that photosynthesis in blue grama would increase as soil removal level increased.

The seasonal variation in net photosynthetic rates of western wheatgrass and blue grama appeared to have been defined more by factors that affected their water use patterns than their nitrogen status. Despite differences in magnitude, water use in both western wheatgrass and blue grama had similar trends through the growing seasons in 1999 and 2000. Moreover, water use in both species appeared to be tightly coupled with seasonal fluctuations in air temperature and soil water content. Even though the air temperature and soil water content fluctuated widely through both the 1999 and 2000 seasons, the range among the weekly photosynthetic rates of both western wheatgrass and blue grama were comparable to the range of variation reported in the literature (Williams 1974, Brown and Trlica 1977a, 1977b, Kemp and Williams 1980, Painter and Detling 1981, Monson et al. 1982, 1983, 1986).

Amid the seasonal variation in photosynthesis, transpiration, leaf nitrogen content, and C_i observed for both western wheatgrass and blue grama, the similarity in the photosynthetic and NUE response exhibited among the soil removal levels by both species was striking. An increase in photosynthesis with increasing soil removal for these 2 physiologically different species was coupled with an increase in NUE and a decrease in C_i . This suggested that the response was driven by a common physiological process in both species. It is proposed, therefore, that western wheatgrass and blue grama plants within the 11.2 and 22.4 t ha⁻¹ soil removal treatments allocated more nitrogen into production of Rubisco or increasing this enzymes activity than did the plants within the control. The consequence of having a higher quantity of Rubisco, or more active Rubisco, would be a faster turnover of the carbon in the Calvin cycle and an increase in

the apparent photosynthetic rate. The decrease in C_i with increasing soil removal, at a constant C_a , may be a result of a more rapid turnover of the Calvin cycle.

Of special interest is that plant respiration rates also increased in the 11.2 and 22.4 t ha⁻¹ treatments relative to plants in the control (Chapter IV). This increase in belowground plant respiration would be consistent with plants allocating more photosynthate into root production in an effort to overcome some deficiency within the soil. What that deficiency was is not certain, but it may have been linked to soil N availability and seems to have brought about a compensatory physiological response among western wheatgrass and blue grama plants within the 11.2 and 22.4 t ha⁻¹ soil removal treatments.

The increase in photosynthesis observed for both western wheatgrass and blue grama in the 11.2 and 22.4 t ha⁻¹ soil removal treatments suggests that these 2 grasses are relatively resistant to these levels of soil loss. Where these species are dominant, such as on the shortgrass prairie, range sites that experience a onetime soil loss of less than 22.4 t ha⁻¹ will likely not lose short-term productivity nor change in species composition. It appears therefore, that shortgrass prairie rangelands where western wheatgrass and blue grama occur may be capable of maintaining range condition even if a single soil loss event exceeds the 11.2 t ha⁻¹ y⁻¹ T-value.

These results may also suggest that the soil loss tolerance value (T-value) of 11.2 t ha⁻¹ y⁻¹ that is commonly assigned to rangelands is conservative. However, caution is needed here for 2 reasons. First, the soil removal treatments in this study were conducted only once at the beginning of the study. Consequently, the responses that was observed

in the 11.2 and 22.4 t ha⁻¹ soil removal levels may not be directly related to the responses that might occur when soil is lost continually through time and over an extended period. The second reason for caution is that the soil removal levels used in this study may not be considered severe by some authors. For example, Singer and Munns (1991) suggested that erosion damage was severe at 34 t ha⁻¹. Therefore, research is still needed to develop a better understanding of the ecophysiological responses of range plants to erosion. Future research should focus on determining if the photosynthetic response of C₃ and C₄ species, such as western wheatgrass and blue grama, are affected by soil loss levels more severe than those imposed in this study. Such research should also include soil removal treatments that are repeated through time.

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CHAPTER III

PHOTOSYNTHETIC RESPONSES OF WYOMING BIG SAGEBRUSH AND BLUEBUNCH WHEATGRASS TO SOIL LOSS

Introduction

The erosion potential for any given range site is a complex interaction between its physical characteristics (i.e. soil, vegetation, topography, and climate) and its use and management (Pierson et al. 1994, Weltz et al. 1998). Erosion occurs naturally in most ecosystems, but the rate of soil loss can be greatly influenced by different land uses and management practices (Weltz et al. 1998). Early researchers suggested that accelerated erosion rates on rangelands were correlated with management practices that resulted in a decline in vegetation cover (Sampson and Weyl 1918, Chapline 1929, Weaver and Noll 1935, Bennett and Lowdermilk 1938). Chapline (1929) for example, found that soil loss increased by 56% when vegetative cover decreased from 40 to 16%. Results such as these led early researchers (Sampson and Weyl 1918, Chapline 1929, Weaver and Noll 1935, Bennett and Lowdermilk 1938) to suggest that some level of tolerable soil loss existed, beyond which site productivity could not be maintained (Schmidt et al. 1982). Soil loss tolerance values (T-values) ranging from 4.5 to 11.2 metric tonnes (t) ha⁻¹ y⁻¹ had been assigned to all soils in the United States (USA) by 1982 (Schmidt et al. 1982).

Determination of these T-values was based on the Universal Soil Loss Equation that was developed to estimate annual erosion rates on cultivated lands (Weltz et al. 1998).

Current rangeland management guidelines suggest that if the T-value for a given range site is exceeded, rangeland productivity and sustainability will decline (SRM-Task Group 1995, Rasmussen et al. 1998). This potential loss of productivity and sustainability on rangelands where accelerated erosion rates exist is often the impetus to alter current uses and management strategies (SRM-Task Group 1995, Rasmussen et al. 1998). However, because research that has directly measured erosion and its effects on rangeland plant productivity and sustainability is lacking, the current concept of T-values for rangelands may not be valid (Weltz et al. 1998). Indeed, in the development of the T-values Blackburn (1980), Schmidt et al. (1982), and Wight and Siddoway (1982) all suggested that T-value concepts and guidelines developed for croplands could not necessarily be applied to rangelands. To reduce the uncertainty that surrounds rangeland T-values, Weltz et al. (1998) suggested that research should focus on the relationship of plant community characteristics (i.e. canopy cover, plant height, and productivity) to erosion, rather than as a forage resource.

Erosion removes mineral particles, organic matter, and nutrients from the soil, and in the process reduces the surface horizon thickness and water-holding capacity of the soil (Singer and Munns 1991). The production of biomass in a plant community depends on the availability and quantity of essential resources and the ability of plants to assimilate those resources (Bloom et al. 1985). Plants respond to resource limitations by increasing the efficiency of investment of the limiting resource into the production of new biomass

(Bloom et al. 1985, Chapin et al. 1987), and a low resource investment typically reflects low resource availability (Chapin et al. 1987). Lower availability and quantity of essential resources induced by erosion may be reflected in the net photosynthetic rate of plants. For example, photosynthetic capacity (the maximum rate of carbon assimilation by a single leaf at light saturation and optimal conditions) is highly correlated with leaf organic nitrogen (N) content (Chapin et al. 1987). Therefore, the loss of soil N through accelerated erosion rates may adversely impact net photosynthetic rates in plants. Net photosynthesis may also be influenced by the loss of soil water holding capacity that can occur following erosion.

The degree to which net photosynthesis is affected by a decline in soil N and water content may depend on the physiological and morphological characteristics of the plant. In a previous study (Chapter II), how soil loss affected 2 grasses with either the C₃ or C₄ physiology was investigated. It was found that photosynthesis increased with increasing soil removal level regardless of the carbon (C) assimilation pathway of the plant (Chapter II). Moreover, increased plant respiration rates with increasing soil loss (Chapter IV) suggested that these grasses had increased root production. Increased root production would allow plants to exploit a larger volume of soil and compensate for deficiencies in N and soil water content. Therefore, the way plants exploit the soil environment to acquire resources, such as N and water, may also be important to define their productivity and survivability following a large erosion event. Since erosion alters soil structure at the surface, deeper rooted plants may be more tolerant of high erosion

rates than are shallow rooted plants. Additionally, the relative growth rate of roots may also be a significant factor in a plants' ability to tolerate soil loss. For example, plants with relatively fast root growth would be able to exploit more soil volume than plants with slower root growth during times when conditions were adequate for growth.

Objectives and Hypotheses The sagebrush steppe represents an ecosystem where physiologically and morphologically different plant species exploit soil resources differently (Charley and West 1975, Deputit and Caldwell 1975, Sturges 1977, Doescher et al. 1990). These species may therefore, respond differently to soil loss. The specific objective of this research was to determine the effects of 3 levels of soil loss (0, 11.2, and 22.4 t ha⁻¹) on net photosynthetic rates of Wyoming big sagebrush [*Artemisia tridentata* ssp. *wyomingensis* (Beetle and Young) Welsh] and bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh)A. Love] on a sagebrush steppe range site. The soil loss levels chosen for comparison represented no soil loss (0 t ha⁻¹), a soil loss level that is widely accepted to be the maximum allowable T-value (11.2 t ha⁻¹; Schmidt et al. 1982), and twice the maximum allowable T-value (22.4 t ha⁻¹). It was hypothesized that: a) the photosynthetic rates of the C₃ shrub, Wyoming big sagebrush, would remain constant as soil removal level increased, and b) the photosynthetic rates of the C₃ grass, bluebunch wheatgrass, would decrease with increasing soil removal level. It was predicted that this differential response between the 2 species would result from differences in physiological and morphological characteristics that define how each acquires limiting resources (i.e. deep rooting depth and low resource use efficiencies). Water and nitrogen were considered to be the most important resources for this study.

Materials and Methods

Study Site The sagebrush steppe site was located within the 10,000 ha Arapaho National Wildlife Refuge (ANWR) 15 km south of Walden, Colorado (40°38' N latitude, 106°17' W longitude). The refuge is managed by the U.S. Fish and Wildlife Service as a bird sanctuary and has been protected from livestock grazing since 1967. However, between 200 and 500 head of elk (*Cervus elaphus nelsoni* Nelson) graze ANWR ranges annually in the winter (Lanier 1999). The sagebrush research site was fenced to exclude livestock and wildlife grazing during the project.

The study site at ANWR was located on a dry exposure range site representative of a sagebrush steppe. Soils at this research site were formed in gravelly alluvium and were classified as a cabin sandy loam, which are fine-loamy over sandy or sandy-skeletal, mixed Argic Cryoborolls (USDA 1981). Wyoming big sagebrush was the dominant shrub component, with numerous C₃ grass species, including western wheatgrass [*Pascopyrium smithii* (Rydb.) A. Love], bluebunch wheatgrass, and sheep fescue (*Festuca ovina* L.) in the understory. Average annual temperature at Walden is 3°C with a mean annual precipitation of 275 mm (Western Regional Climate Center 2001).

Experimental Design, Treatments and Data Collection The experimental design was a split-plot, randomized block, with a factorial arrangement of treatments. Factor levels consisted of 2 species and 3 levels of soil removal (0, 11.2 and 22.4 t ha⁻¹), with 3 replications of each level (9 plots). In the spring of 1999, nine (3 soil removal levels x 3 replications) permanent, 0.6 x 2 m steel frame plots were randomly placed within the study site.

Top soil from all treatment plots was removed to the desired level using a vacuum and collection bag. Treatments were imposed during the early summer of 1999 following snow melt. Sampling of the plots for photosynthesis, transpiration, and other factors did not begin until the summer of 2000.

Gravimetric water content (%) of study site soils was estimated from soil cores removed from the immediate vicinity of each plot at depths of 0-5 and 5-10 cm at weekly intervals. Total soil C and N content (mg g^{-1}) was determined for the 0-2.5, 2.5-5.0, and 5.0-10.0 cm depths from soil core samples removed from each plot at the end 2000 growing season. The removed soil from each plot was transported to Colorado State University (CSU) for analysis of carbon (C) and nitrogen (N) content (mg g^{-1}) using a LECO CHN-1000 Analyzer.

Net photosynthetic ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and transpiration ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) rates, and inter-cellular CO_2 concentrations (C_i) were measured on 5 leaves per species from each plot with a Li-Cor 6400 Portable Photosynthesis System. Measurements were made at mid-day on weekly intervals during the 2000 growing season. Leaf chamber conditions were maintained at ambient for atmospheric CO_2 (C_a), water vapor pressure, and air temperature. Photosynthetically active radiation (PAR) was maintained at $1500 \mu\text{mol PAR m}^{-2} \text{ s}^{-1}$ with a Li-Cor 6400 Light Source. Leaf areas (cm^2) of the sampled leaves were measured using a Li-Cor 3000 Portable Leaf Area Meter following the photosynthesis measurements. Sampled leaves were then bagged, cooled and transported to CSU for analysis of total leaf C and N content (mg g^{-1}) using a LECO CHN-1000 Analyzer. Water and nitrogen use efficiencies ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ and

$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$, respectively) were calculated for each measurement of photosynthesis and transpiration made. Leaf water potentials (MPa) were measured simultaneously with the photosynthesis measurements on 3 leaves for each species within each plot using a pressure chamber (Scholander et al. 1965, Waring and Cleary 1967). Because of severe water stress in 2000, the growing season for bluebunch wheatgrass ended at about week 31 but measurements continued until mid-September for big sagebrush (i.e. week 36).

Statistical Analyses Changes in relative humidity and air temperature accounted for a significant ($P < 0.10$) portion of the seasonal (weeks 23 - 31) variability in net photosynthesis, C_i , and nitrogen use efficiency (NUE). Thus, a repeated measures analysis of covariance (ANCOVA) procedure (Vonesh and Chinchilli 1997) was used to test for differences between big sagebrush and bluebunch wheatgrass and among soil removal levels (0, 11.2, and 22.4 t ha⁻¹) across sample periods (week of year) for net photosynthesis, C_i , and NUE. A repeated measures analysis of variance (ANOVA) procedure (Vonesh and Chinchilli 1997) was used to test for differences between species and among soil removal levels across sample periods for transpiration rates, leaf C and N content, leaf water potential (LWP), and water use efficiency (WUE). Because of the longer growing season for sagebrush relative to that of bluebunch wheatgrass, a separate ANOVA, that incorporated the additional sampling periods, was conducted to test for treatment and weekly differences in photosynthesis, transpiration, C_i , NUE, WUE, LWP, and leaf C and N content for sagebrush. In this separate analysis for big sagebrush, relative humidity and air temperature were not significant ($P > 0.10$) covariates.

Repeated measures ANOVA was also used to test for differences among sample depths (0-2.5, 2.5-5.0, and 5.0-10.0 cm) across sample weeks for soil water content and for total soil C and N (mg g^{-1}) among sample depths and soil removal levels (Vonesh and Chinchilli 1997). All results were considered significant at $P \leq 0.10$. When ANOVA results were significant, Fisher's Least Significant Difference (LSD) was used to separate means (Dowdy and Wearden 1991). Separation of mean values when ANCOVA indicated significance was done on covariate-adjusted means using a procedure described by Dowdy and Wearden (1991). All means (\bar{x}) reported are true means (i.e. unadjusted) with their respective standard error (\pm SE) and sample size (n). Data, statistical outputs, and supporting material for this chapter are located in Appendix B.

Results

Soil Water, Carbon, and Nitrogen Content In 2000, the Arapaho National Wildlife Refuge (ANWR) received approximately 290 mm of precipitation, approximately 5% more than the long-term annual average of 275 mm (Western Regional Climate Center 2001). Of the 290 mm of precipitation received at the ANWR site, 44% occurred between June and September of 2000. However, June and July precipitation accounted for only 29 mm of the 128 mm received between June and September of 2000. Most of the precipitation events that occurred during the 4 months of observation at ANWR were short duration, low intensity storms that produced less than 2.5 mm of precipitation and consequently were not large enough to recharge the soil profile. The low frequency and low intensity of precipitation events that occurred at ANWR between June and September

of 2000 resulted in droughty soils low in water content. In fact, the gravimetric soil water content (%) only varied by 1 or 2 % for both depths and never exceeded 5% of the total soil mass (Figure 3-1). Nevertheless, gravimetric soil water content varied significantly ($P < 0.10$) between depths and across sampling periods. Soil water content in the 5-10 cm depth was generally greater than in the 0-5 cm depth and was also less variable between weeks (Figure 3-1). Greater weekly variation in the 0-5 cm depth likely resulted from higher evaporative losses in the upper 5 cm of the soil than in the 5-10 cm depth (Figure 3-1). For example, significant losses in soil water content in the 0-5 cm depth were observed from week 26 through week 29, but in the 5-10 cm depth the soil moisture did not decrease significantly until week 29.

Both soil C and N content (mg g^{-1}) decreased ($P < 0.10$) with soil depth (0-2.5, 2.5-5.0, and 5.0-10.0 cm). Soil C and N was highest in the upper 2.5 cm of soil (14.3 ± 1.5 and $1.36 \pm 0.11 \text{ mg g}^{-1}$, respectively, $n = 18$), but decreased significantly ($P < 0.10$) in the 2.5-5.0 cm (12.3 ± 0.6 and $1.18 \pm 0.04 \text{ mg g}^{-1}$, respectively, $n = 18$) and the 5.0-10.0 cm (11.1 ± 0.5 and $1.07 \pm 0.05 \text{ mg g}^{-1}$, respectively, $n = 18$) depths. The decrease in soil C and N with depth was consistent among the 3 soil removal levels (0, 11.2, and 22.4 t ha^{-1}). There was no difference ($P > 0.10$) in soil C or N content between the soil removal levels.

Leaf Carbon and Nitrogen Leaf C content was greater ($P < 0.10$) in big sagebrush than in bluebunch wheatgrass, but the relative differences between the 2 species were dependent ($P < 0.10$) on the week of year (Figure 3-2). In big sagebrush, leaf C content

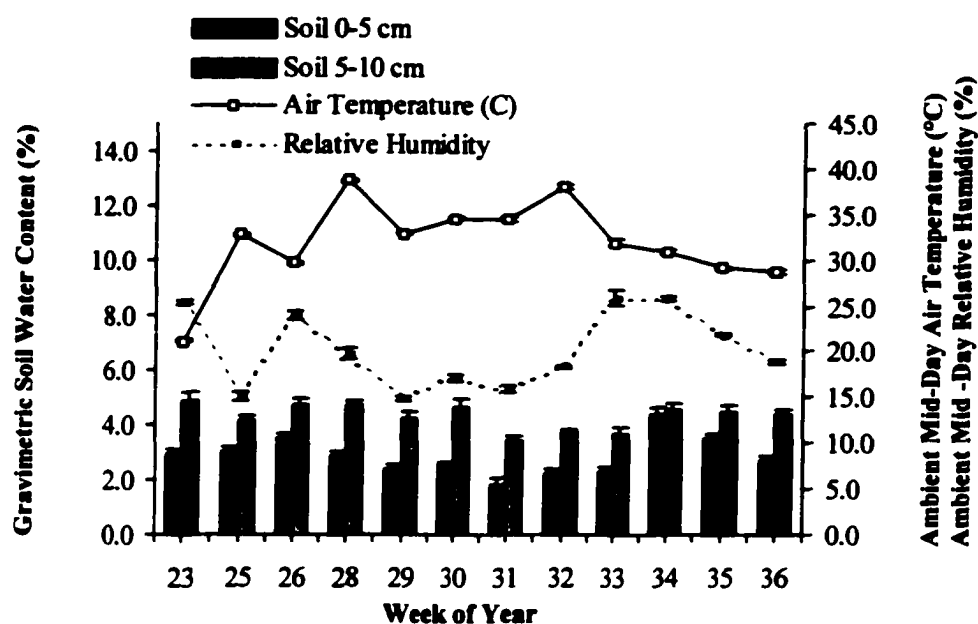


Figure 3-1. Weekly average (\pm SE) gravimetric soil water content (%), $n = 9$ and ambient mid-day air temperature and relative humidity ($^{\circ}$ C and %, respectively, $n = 90$, weeks 23-31, $n = 45$ weeks 32-36) at the Arapaho National Wildlife Refuge research area during the 2000 growing season.

generally increased throughout the growing season (Figure 3-2). The C content of bluebunch wheatgrass leaves was more variable with a general increase across the growing season, but punctuated by brief periods of declining leaf C content (Figure 3-2). Between weeks 23 and 31, leaf C content did not vary ($P > 0.10$) among the soil removal levels and this was consistent between species and across sample weeks. In a separate analysis for big sagebrush over weeks 23 through 36, leaf C content varied significantly ($P < 0.10$) by sample week among the soil removal levels, but the differences were not consistent and mainly occurred following week 31.

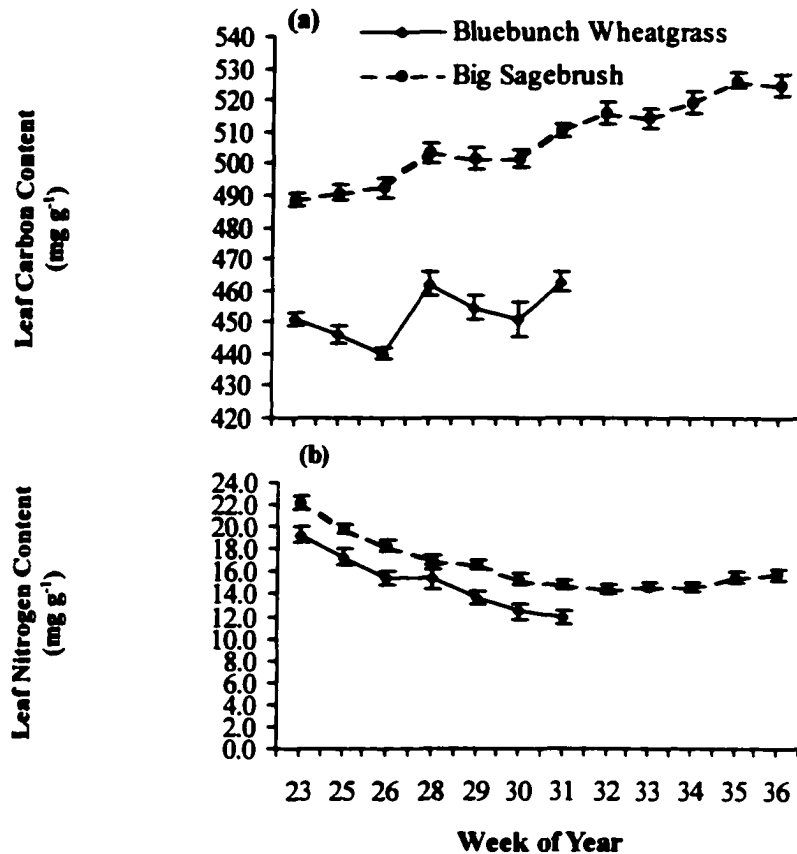


Figure 3-2. Weekly average (\pm SE, $n = 9$) leaf carbon (a) and nitrogen (b) content (mg g^{-1}) in bluebunch wheatgrass and big sagebrush during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Leaf N levels in big sagebrush leaves were consistently greater ($P < 0.10$) than in bluebunch wheatgrass (Figure 3-2). There was a significant ($P < 0.10$) decline in leaf N over the growing season for both species (Figure 3-2). Leaf N varied ($P < 0.10$) among the soil removal levels between weeks 23 and 31, but showed no consistent trend among the treatments. In a separate analysis for big sagebrush, leaf N content was significantly different among the soil removal levels, but was dependent on the sample week. As with

leaf C, most of the differences in N among the treatments for big sagebrush leaves occurred after week 31.

Plant Responses Net photosynthesis, transpiration, C_i , LWP, and NUE in big sagebrush and bluebunch wheatgrass varied significantly ($P < 0.10$) among sample weeks (Figure 3-3). However, while differences in C_i and LWP between big sagebrush and bluebunch wheatgrass were dependent on the sample week, differences between the 2 species in photosynthesis, transpiration, and NUE were consistent across weeks (Figure 3-3). Averaged across weeks 23 and 31, net photosynthetic and transpiration rates were approximately 70% greater ($P < 0.10$) in big sagebrush ($9.7 \pm 0.3 \mu\text{mol CO}_2 \text{ m}^{-1} \text{ s}^{-1}$ and $6.3 \pm 0.2 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, respectively; $n = 315$) than in bluebunch wheatgrass ($5.3 \pm 0.3 \mu\text{mol CO}_2 \text{ m}^{-1} \text{ s}^{-1}$ and $3.4 \pm 0.1 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, respectively; $n = 315$). Over the same period though, NUE in bluebunch wheatgrass ($0.02 \pm 0.001 \mu\text{mol CO}_2 \text{ m}^{-1} \text{ s}^{-1} / \text{mmol N m}^{-2}$, $n = 315$) was twice as high as that observed in big sagebrush ($0.01 \pm 0.0003 \mu\text{mol CO}_2 \text{ m}^{-1} \text{ s}^{-1} / \text{mmol N m}^{-2}$, $n = 315$).

Photosynthesis, transpiration, C_i , and LWP in big sagebrush tended to decrease as the growing season progressed from week 23 through week 36 (Figure 3-3). For example, net photosynthesis, transpiration, and C_i in big sagebrush were 39, 47, and 24% lower, respectively, at the end of the growing season (week 36) than at the beginning (week 23; Figure 3-3). In contrast, NUE and WUE in big sagebrush remained relatively constant throughout the growing season (Figure 3-3).

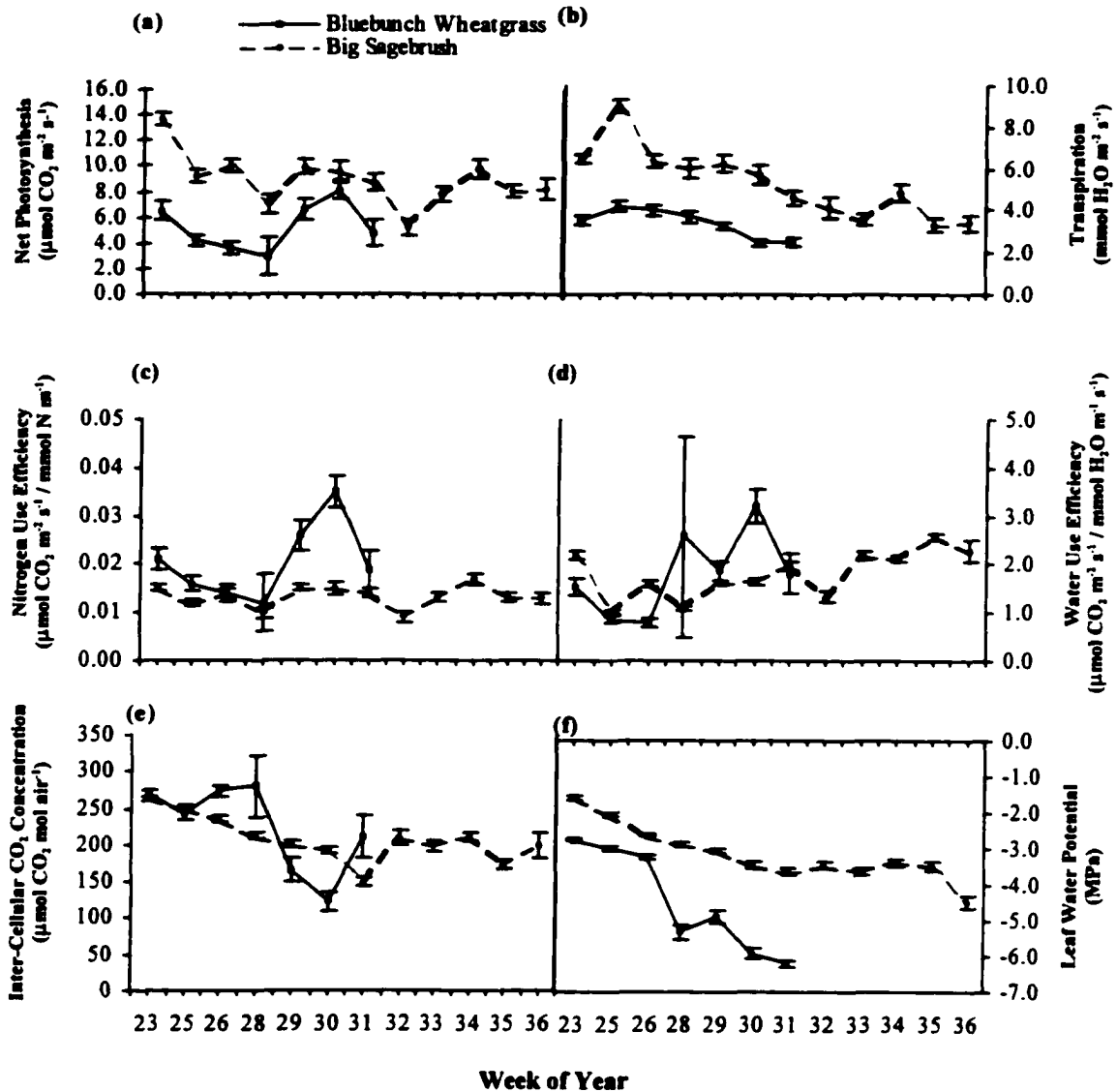


Figure 3-3. Weekly average (\pm SE) net photosynthetic rates (a; $n = 45$), transpiration rates (b; $n = 45$), nitrogen use efficiency (c; $n = 45$), water use efficiency (d; $n = 45$), inter-cellular CO_2 concentration (e; $n = 45$), and leaf water potential (f; $n = 27$) for bluebunch wheatgrass and Wyoming big sagebrush during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Water use efficiency did not vary ($P > 0.10$) between big sagebrush and bluebunch wheatgrass. Moreover, despite the weekly variation in photosynthesis and transpiration, WUE did not vary ($P > 0.10$) between sample weeks, nor was there a species by sample week interaction ($P > 0.10$). This indicated that water use in these 2 C_3 species changed proportionately to changes in the photosynthetic rate and suggests that water use was determined more by physiology (i.e. both C_3) than by growth form (i.e. shrub vs. grass). Between weeks 23 and 31 the average WUE for both big sagebrush and bluebunch wheatgrass was $1.9 (\pm 0.2, n = 630) \mu\text{mol CO}_2 \text{ m}^{-1} \text{ s}^{-1} / \text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$.

Soil removal level had little effect ($P > 0.10$) on net photosynthesis, NUE, transpiration, WUE, or LWP of big sagebrush. Soil removal level however, had a significant ($P < 0.10$) effect on bluebunch wheatgrass transpiration rates, and when adjusted for relative humidity and air temperature (significant covariates at $P < 0.10$), on net photosynthesis and NUE as well (Figure 3-4). Bluebunch wheatgrass transpiration rates were higher (Fisher's LSD = $0.48 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, $t = 1.943$, MSE = 3.188, $n = 105$) in the 11.2 and 22.4 (3.7 ± 0.1 and $3.5 \pm 0.2 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$, respectively) t ha^{-1} soil removal levels than in the control ($2.9 \pm 0.2 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$). Conversely, net photosynthetic rates and NUEs were greater in the 0 ($5.4 \pm 0.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $0.022 \pm 0.002, \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$, respectively, $n = 105$) and 11.2 ($6.2 \pm 0.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $0.024 \pm 0.002, \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$, respectively, $n = 105$) t ha^{-1} treatments than in the 22.4 ($4.3 \pm 0.6 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and $0.016 \pm 0.002, \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$, respectively, $n = 105$) t ha^{-1} soil removal level (Figure 3-4).

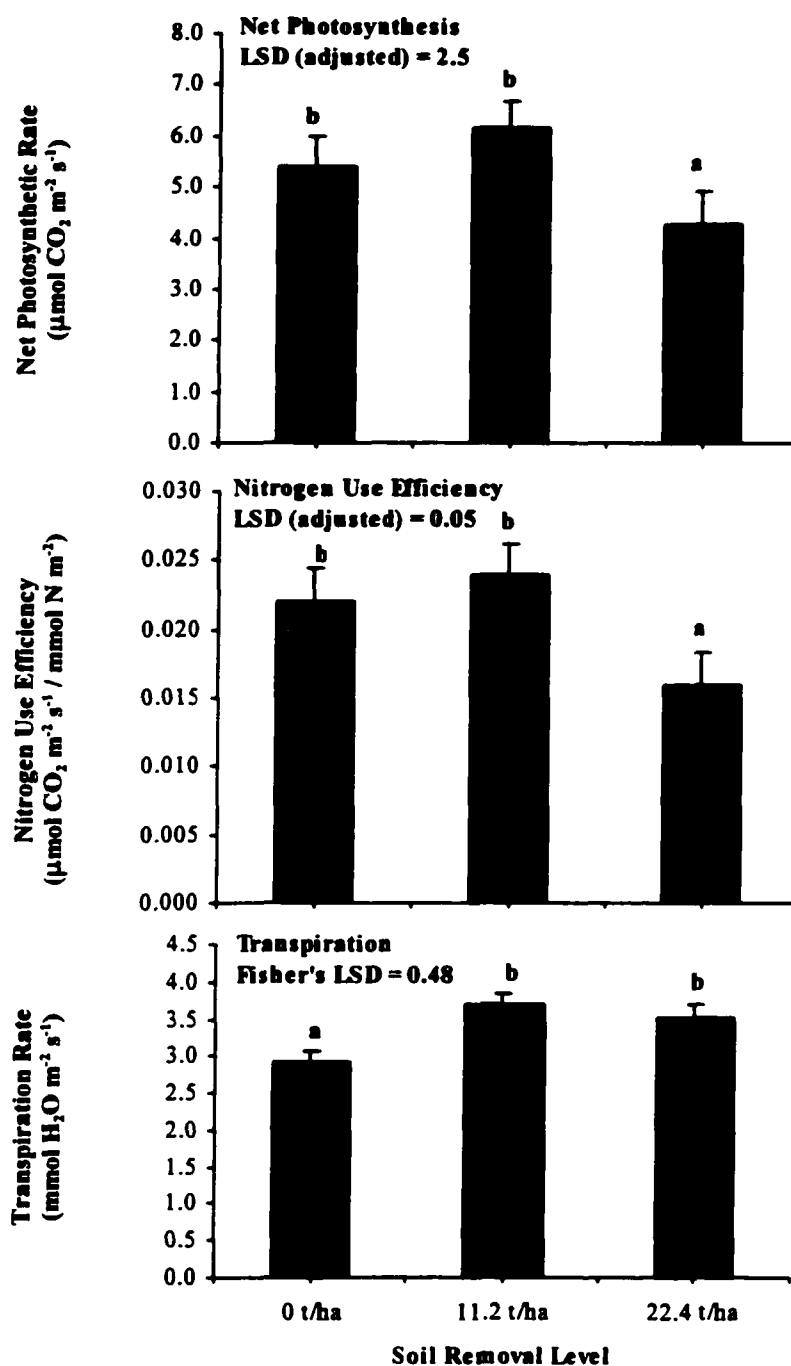


Figure 3-4. Average (\pm SE, $n = 105$) net photosynthesis, nitrogen use efficiency, and transpiration rate for bluebunch wheatgrass in the 0, 11.2, and 22.4 t/ha soil removal levels at the Arapaho National Wildlife research area during the 2000 growing season.

Water use efficiency in bluebunch wheatgrass was unaffected ($P > 0.10$) by the soil removal treatments. This may have been in part, because of the relatively higher variation in net photosynthesis, transpiration, and leaf water potential observed among the treatments from week 28 through 31 than in weeks 23 through 26 (Figure 3-5). This increase in variation in photosynthesis, transpiration, and leaf water potential following week 26 was accompanied by a change in the relationship among the treatment levels (Figure 3-5). Though only LWP had a significant ($P < 0.10$) treatment by week interaction, following week 28, the response of photosynthesis and transpiration in bluebunch wheatgrass plants among the soil removal levels was markedly different than in the previous 3 sample periods (Figure 3-5). This may have resulted from a change in phenology in bluebunch wheatgrass or it may have been brought about by extremely stressful environmental conditions. For example, between weeks 26 and 28 leaf water potential in bluebunch wheatgrass plants in the 22.4 t ha^{-1} soil removal level decreased from $-3.5 (\pm 0.1)$ to $-6.2 (\pm 0.3)$ MPa, respectively (Figure 3-5)

Intercellular CO_2 concentration varied ($P < 0.10$) between soil removal levels when adjusted for relative humidity and air temperature (significant covariates at $P < 0.10$). The response of C_i to the soil removal levels was consistent between both species. The C_i of big sagebrush and bluebunch wheatgrass plants in the 22.4 t ha^{-1} treatment ($230.4 \pm 8.3 \mu\text{mol CO}_2 \text{ mol air}^{-1}$) was greater (LSD (adjusted) = 47.4 and 30.6, respectively) than in either the 0 ($218.2 \pm 7.1 \mu\text{mol CO}_2 \text{ mol air}^{-1}$) or 11.2 ($209.2 \pm 7.9 \mu\text{mol CO}_2 \text{ mol air}^{-1}$) t ha^{-1} soil removal levels. However, when analyzed separately, C_i did not vary ($P > 0.10$) among the treatment levels for either species.

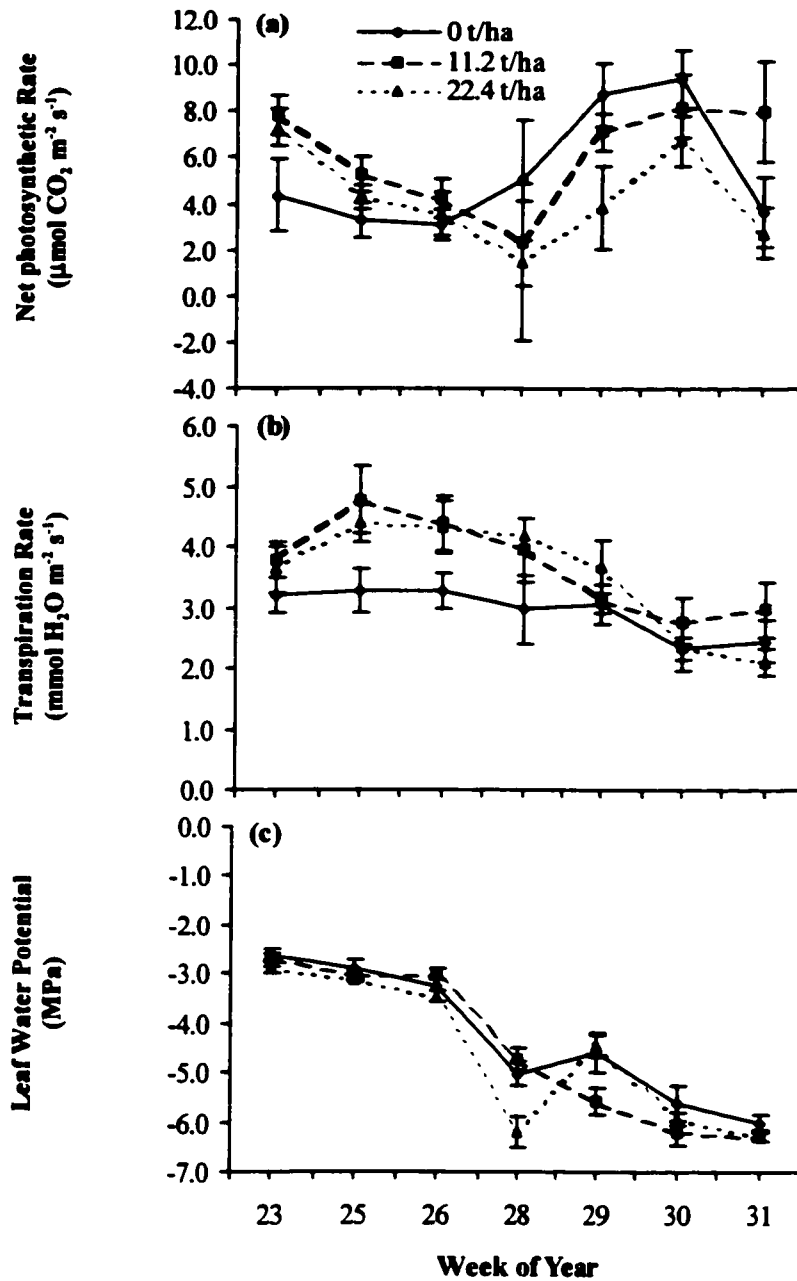


Figure 3-5. Weekly average (\pm SE, $n = 15$) net photosynthesis (a), transpiration rate (b), and leaf water potential (c) for bluebunch wheatgrass among the 0, 11.2, and 22.4 t/ha soil removal levels at the Arapaho National Wildlife Refuge research area during the 2000 growing season.

Discussion

Wyoming Big Sagebrush The seasonal fluctuations in net photosynthetic and transpiration rates, C_i , WUE, and NUE in Wyoming big sagebrush at the Arapaho National Wildlife Refuge were similar to the range of values reported in the literature (DePuit and Caldwell 1973, DePuit and Caldwell 1975, Knapp and Smith 1987, Miller 1988, Doescher et al. 1990, Evans and Black 1993). Seasonal variation in a plants' physiological processes are typically driven by temporal variation in environmental conditions (Williams 1974, Brown and Trlica 1977a, 1977b, Kemp and Williams 1980, Monson et al. 1982, 1983, 1986) and by phenological changes as the season progresses (DePuit and Caldwell 1973, 1975, Smith and Nobel 1977, Miller and Shultz 1987, Doescher et al. 1990, Evans and Black 1993). For example, DePuit and Caldwell (1973) found that while early in the growing season temperature and irradiation were the primary factors that limited net photosynthesis in big sagebrush, phenological changes and increased plant water stress were equally as important as temperature and irradiation during the mid- and late-summer period. Moreover, they determined that the optimal temperature for big sagebrush photosynthesis was lower in the spring (15 °C) than in the mid- and late-summer period (20 °C), with the latter representing the limit to acclimation.

Irradiation could not have been a limiting factor in our study, since it was held constant during sampling across all sample periods. However, ambient mid-day temperatures exceeded 20 °C on all sample dates and even reached nearly 40 °C on week 28 and 32 (Figure 3-1). Thus, the seasonal decline in net photosynthetic and transpiration rates, and C_i observed in big sagebrush at ANWR likely resulted from a

combination of high daily temperatures, increasing plant water stress, and phenological changes.

In Wyoming big sagebrush, net photosynthetic and transpiration rates, C_p , NUE, WUE, and LWP did not respond differently among the soil removal levels. Initially the soil removal treatments had the greatest potential effect on soil properties at the soil surface (Pierson et al. 1994). Thus, the lack of response to the soil removal treatments may have been in part, because of the capability of big sagebrush to develop a deep and broad root system (Branson et al. 1976, Sturges 1977). For example, Branson et al. (1976) found big sagebrush roots as deep as 1.8 m below the soil surface. Sturges (1977) noted that big sagebrush roots were capable of extending to a depth of over 2 m and laterally over 1 m depending on degree of intra-specific competition for space and resources, soil substrate characteristics (i.e. rock size and content), and soil water content. This large volume of soil exploited by big sagebrush roots likely buffers the plant, to some extent, from disturbances, such as erosion, that occur or alter conditions at the soil surface. Given enough time however, the loss of soil organic matter at the surface should be manifested deeper in the soil profile (Charley and West 1975). Therefore, a response to the soil removal treatments may develop in the Wyoming big sagebrush plants at ANWR given a sufficient amount of time between the treatments and measurements so that the altered soil conditions can be manifested at a depth where their roots are most active. This remains to be determined though.

Bluebunch Wheatgrass The net photosynthetic rates observed for bluebunch wheatgrass over the 2000 growing season at ANWR were somewhat lower than rates

previously reported for this species (DePuit and Caldwell 1975, Caldwell et al. 1983), and for other C₃ grasses (Williams 1974, Brown and Trlica 1977a, Kemp and Williams 1980, Painter and Detling 1981, Monson et al. 1982, 1983, 1986, Coyne et al. 1995). The seasonal response of bluebunch wheatgrass at ANWR was comprised of 2 apparently different periods (weeks 23-26 and weeks 28-31) marked by a large decrease in leaf water potential indicating a significant increase in plant water stress, and by large increases in the sample variation from week 28 through week 31 (Figure 3-3). The first period occurred between weeks 23 and 26 when net photosynthesis in bluebunch wheatgrass decreased from 6.5 (± 0.7 , n = 45) to 3.6 (± 0.5 , n = 45) $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ with very little variation between leaf samples (Figure 3-3). During this period, leaf water potential was moderately high, ranging from -2.7 (± 0.06 , n = 27) to -3.2 (± 0.07 , n = 27) MPa. The second period began with week 28 when the variation between samples doubled and net photosynthesis first increased from a low of 3 (± 1.5 , n = 45) $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ to a seasonal high of 8.1 (± 0.7 , n = 45) $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in week 30 before declining to 4.8 (± 1.0 , n = 45) $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in week 31. Leaf water potential during this period decreased to -5.3 (± 0.19 , n = 27) MPa in week 28 and then increased slightly in week 29 to -4.9 (± 0.19 , n = 27) MPa before decreasing again to a low of -6.2 (± 0.08 , n = 27) MPa in week 31 (Figure 3-3). The increases in bluebunch wheatgrass average net photosynthetic rate during this second period occurred following short duration precipitation events during weeks 29 and 31. However, it is apparent from the large degree of variability during this latter period (weeks 28-31) that not all bluebunch wheatgrass plants responded similarly to these precipitation events. DePuit and Caldwell

(1973) showed that bluebunch wheatgrass becomes photosynthetically dormant during periods of drought and high temperatures and suggested that they may use carbon reserves to complete their seasonal life cycles. It is possible that some of the bluebunch wheatgrass plants at ANWR became photosynthetically inactive during week 28, but that others, because of better micro-environments (Charley and West 1975, Doescher et al. 1984, Monson et al. 1986, Pierson et al. 1994), remained active and were able to respond to the precipitation events that occurred during weeks 29 and 31. This would account for the high variability observed in bluebunch wheatgrass physiological processes and simultaneously, the increase in net photosynthetic rate between weeks 29 and 31 (Figure 3-3).

Interestingly, bluebunch wheatgrass transpiration rates changed little over the entire 7 week period and only showed a significant decrease in weeks 30 and 31 (Figure 3-3). Moreover, aside from leaf water potential, transpiration was the only response measured that did not have a large increase in variability beginning in week 28 (Figure 3-3). This consistency in transpiration rates, even when plant water stress became extremely high after week 28, would suggest that bluebunch wheatgrass plants at ANWR exhibited a low degree of stomatal responsiveness to developing water deficits (Brown 1995). Dibble and Spomer (1987) showed that bluebunch wheatgrass plants have considerable potential to acclimate to developing water deficits through regulation of leaf osmotic potential, rigid cell walls, and changes in leaf size. Because of their rigid cell walls, acclimation to developing water deficits in bluebunch wheatgrass may begin before water stress levels become critical (Dibble and Spomer 1987) and may begin with

regulation of leaf osmotic potential. However, decreasing leaf area as soil water deficits increase over a growing season leads to a seasonally permanent relative reduction in water loss and maintenance of leaf turgor at lower water potentials (Dibble and Spomer 1987). Thus, despite increasing water deficits, bluebunch wheatgrass transpiration rates were likely maintained at relatively constant levels across the 2000 growing season through osmotic regulation and decreasing leaf area.

When adjusted for the seasonal variation in the relative humidity and temperature of the air, net photosynthesis and NUE in leaves of bluebunch wheatgrass were significantly different among the soil removal levels (Figure 3-4). The seasonal average net photosynthetic rate and NUE of bluebunch wheatgrass in the 0 and 11.2 t ha⁻¹ soil removal treatments were similar, but decreased significantly at the 22.4 t ha⁻¹ of soil removal level (Figure 3-4). This response in photosynthesis and NUE in bluebunch wheatgrass to the soil removal treatments would suggest that between 11.2 and 22.4 t ha⁻¹ of soil loss a threshold existed where plant productivity could not be maintained. Consequently, the seasonal average net photosynthetic rate and NUE of bluebunch wheatgrass plants in the 22.4 t ha⁻¹ soil loss treatments was significantly less than for plants in the 0 and 11.2 t ha⁻¹ soil removal levels.

In addition to being a function of the amount of soil loss, this potential threshold between the 11.2 and 22.4 t ha⁻¹ soil loss levels, may have had a temporal dimension as well. This temporal dimension was likely a function of increasing soil water deficits that developed at ANWR as the 2000 growing season progressed and is exemplified by the seasonal trend in bluebunch wheatgrass LWP (Figure 3-5). Thus, even though the soil

removal level by sample date interaction was not significant for net photosynthesis, transpiration, and NUE (data not shown), the response of these variables in bluebunch wheatgrass to soil loss can be separated into 2 distinct periods that are distinguished by differences in LWP (Figure 3-5). For example, early in the growing season when LWPs were relatively high (weeks 23 through 26), bluebunch wheatgrass net photosynthetic rates in the 11.2 and 22.4 t ha⁻¹ soil removal levels were generally greater than in the control (Figure 3-5). However, later in the growing season, when LWP decreased dramatically (weeks 28-31), the relationship in the response of bluebunch wheatgrass photosynthetic rates to the soil removal levels changed, with plants in the control treatment generally having higher photosynthetic rates than those in the 11.2 and 22.4 t ha⁻¹ soil loss levels (Figure 3-5).

The early season (weeks 23-26) response of photosynthesis and NUE in bluebunch wheatgrass to the soil removal treatments was similar to what was found in western wheatgrass and blue grama on the shortgrass prairie (Chapter II). However, the late season (weeks 28-31) response of bluebunch wheatgrass photosynthesis and NUE were unique to the ANWR site. During this late period several short duration precipitation events occurred. The increase in bluebunch wheatgrass photosynthesis among all 3 soil removal levels following week 28, despite the low LWPs, likely resulted from improved conditions caused by these precipitation events. Notably however, the rate and magnitude of the increases in photosynthesis following week 28 was nearly proportional to the level of soil removal and was greatest in the control and least in the 22.4 t ha⁻¹ soil removal level (Figure 3-5). Thus, increasing soil removal decreased the

ability of bluebunch wheatgrass to recover pre-drought (week 23) net photosynthetic rates. This would imply that the ability of bluebunch wheatgrass plants to acclimate to developing water stress through regulation of osmotic potential, rigid cell walls, and changes in leaf size (Dibble and Spomer 1987) declined with increasing soil loss.

Summary and Conclusions

The specific objective of this research was to determine the effects of 3 levels of soil loss (0, 11.2, and 22.4 t ha⁻¹) on the net photosynthetic rates of Wyoming big sagebrush and bluebunch wheatgrass on a sagebrush steppe range site. The soil loss levels chosen for comparison represented no soil loss (0 t ha⁻¹), a soil loss level that is widely accepted as the maximum allowable T-value (11.2 t ha⁻¹), and twice the maximum allowable T-value (22.4 t ha⁻¹). Two hypotheses were formulated to test the effects of these soil removal treatments on the photosynthetic rates of Wyoming big sagebrush and bluebunch wheatgrass. First, that the net photosynthetic rates of Wyoming big sagebrush would remain constant as soil removal level increased, and secondly, that the net photosynthetic rates of bluebunch wheatgrass would decline with increasing soil removal level. It was predicted that this differential response between the 2 species would result from differences in physiological and morphological characteristics that define how each acquires limiting resources.

The photosynthetic rates of Wyoming big sagebrush were unaffected by the soil removal treatments. Therefore, this study failed to reject the hypothesis that big sagebrush net photosynthetic rates would remain constant with increasing soil removal

level. The large volume of soil exploited by big sagebrush roots likely buffered the plants from any changes in soil properties caused by the soil removal treatments, since most of those changes occurred at the soil surface. The net photosynthetic rate of big sagebrush declined over the growing season in proportion to the seasonal decline in leaf nitrogen and transpiration rates. Therefore, the net photosynthetic rate of big sagebrush at ANWR was defined by the seasonal availability of soil water and nitrogen. These results suggest that big sagebrush is relatively resistant to disturbances, such as erosion, because of its ability to exploit large volumes of soil.

Net photosynthetic rates of bluebunch wheatgrass leaves did not decrease proportionately to the increase in soil removal. Thus, the hypothesis that bluebunch wheatgrass net photosynthetic rates would decrease with increasing soil removal was rejected. The net photosynthetic rate of bluebunch wheatgrass was similar between the 0 and 11.2 t ha⁻¹ soil removal levels, but decreased sharply at the 22.4 t ha⁻¹ soil removal level. This abrupt decrease in bluebunch wheatgrass net photosynthetic rates between the 11.2 and 22.4 t ha⁻¹ soil removal levels may be evidence of a soil loss tolerance threshold for this grass species. However, this potential threshold was defined not only by the amount of soil loss but also by seasonal trends in plant water stress.

The net photosynthetic response of bluebunch wheatgrass could be differentiated into 2 distinct periods. In the first period, the response of bluebunch wheatgrass photosynthesis was similar to that observed for western wheatgrass and blue grama on the shortgrass prairie (Chapter II). However, developing water stress in bluebunch wheatgrass limited this response, and by week 26 the photosynthetic rate of bluebunch

wheatgrass had decreased to very low levels. Beginning at week 28, short duration precipitation events stimulated bluebunch wheatgrass photosynthesis. Thus, the second period in the photosynthetic response of bluebunch wheatgrass to the soil removal levels was defined by a differential rate of recovery in pre-drought net photosynthetic rates among the soil removal treatments. As soil removal level increased, the ability of bluebunch wheatgrass to recover pre-drought net photosynthetic rates decreased. Therefore, it appears that increasing soil loss impaired the ability of bluebunch wheatgrass to acclimate to developing water stress.

These results suggest that severe soil loss on the sagebrush steppe could cause a decline in bluebunch wheatgrass productivity, especially when confounded with droughty conditions. Wyoming big sagebrush, on the other hand, would be unaffected by soil loss at the levels that were used in this study. Indeed, the lack of response in big sagebrush to the soil removal treatments may be an indication of why the species is so prevalent and persistent in the western United States.

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CHAPTER IV

SOIL CO₂ EFFLUX RESPONSES TO SOIL LOSS ON TWO RANGELAND ECOSYSTEMS

Introduction

Soil loss on Colorado agricultural lands is estimated to be 215 million metric tonnes (t) y⁻¹ (Boon 1987). In addition, erosion rates on 30% of these lands exceed the rate of soil formation. Hall et al. (1982) noted that if long-term productivity of rangelands was to be maintained, the rate of soil loss must be equal to or less than the rate of soil formation. The concept that some level erosion could be sustained without loss of productivity, led to the establishment of soil loss tolerance values (T-value) for all soils in the United States (Schmidt et al. 1982). Using the Universal Soil Loss Equation (USLE), the U.S. Natural Resource Conservation Service has assigned T-values ranging between 4.5 and 11.2 t ha⁻¹ y⁻¹ (2 to 5 tons acre⁻¹ y⁻¹) to all agricultural lands (Schmidt et al. 1982). The soil loss rate of 11.2 t ha⁻¹ y⁻¹ is considered to be the maximum sustainable erosion rate at which productivity can be maintained (Wischmeierer and Smith 1978, Schmidt et al. 1982, Wight and Siddoway 1982). Weltz et al. (1998) suggested, however, that since there had been no research linking changes in plant productivity and sustainability to erosion on rangelands, the current concept of T-values for rangelands may not be valid.

Accelerated erosion rates adversely affect many soil properties that promote plant growth. Erosion removes mineral particles, organic matter, and nutrients from the soil, reducing surface horizon thickness and water-holding capacity (Singer and Munns 1991). Loss of soil nutrients and organic matter through erosional processes has been shown to reduce the productivity of croplands (Ives and Shykewich 1987, Larney et al. 1995, Ithori et al. 1995, Pradhan et al. 1997, Tengberg et al. 1997). However, it has not been established how these losses affect primary productivity of western rangelands. It is assumed that as erosion rates increase, rangeland plant cover and productivity decline (SRM-Task Group 1995, Rasmussen et al. 1998). Although there is little quantitative evidence for this assumption, management decisions on western rangelands are made based on this relationship (SRM-Task Group 1995, Rasmussen et al. 1998).

A decline in primary productivity coupled with a loss of soil organic matter and nitrogen through erosion may greatly influence the efflux of CO₂ from the soil (Singh and Gupta 1978). Soil respiration is a combination of the respiration of plant roots and soil organisms as they decompose litter and soil organic matter. The net production of biomass in terrestrial ecosystems contributes directly to the soil organic carbon (C) pool (Schlesinger 1997). Soil chronosequence studies show that soil organic matter accumulates at rates ranging between 1-12 g C m⁻² y⁻¹ during soil development (Schlesinger 1990, Chadwick et al. 1994, Schlesinger 1997). The production of organic C compounds must equal their removal through erosion for soils to exhibit a steady state in soil C content (Schlesinger 1997). How accelerated rates of soil loss affect this balance in arid and semi-arid rangelands, where rates of C accumulation without

disturbance are relatively slow ($0.8 - 2.2 \text{ g C m}^{-2} \text{ yr}^{-1}$; Schlesinger 1990), is not well understood.

Raich and Schlesinger (1992) noted that measurements of CO_2 efflux from the soil provide an estimate of total soil respiration and an alternative approach to estimate the turnover of the soil C pool. The coupling of soil respiration and photosynthetic rates provides insight into the cycling of C through an ecosystem. Rangeland ecosystems have been considered important C sinks on a global scale (Svejcar et al. 1997). Therefore, understanding how soil loss affects net assimilation and respiration rates of CO_2 on western rangelands may provide both new information regarding the importance of rangelands to the global C cycle and incentives for improved management.

Objective and Hypotheses The effects of soil loss on the net photosynthetic rates of the dominant species of the shortgrass prairie and sagebrush steppe have been reported in Chapters II and III. The specific objective of this research was to determine the effects of 3 levels of soil loss (0, 11.2, and 22.4 t ha^{-1}) on total, bare soil, and plant respiration rates within the shortgrass prairie and sagebrush steppe ecosystems. The soil loss levels chosen for comparison represent no soil loss (0 t ha^{-1}), a soil loss level that is widely accepted to be the maximum allowable T-value (11.2 t ha^{-1} , Schmidt et al. 1982), and twice the maximum allowable T-value (22.4 t ha^{-1}). It was hypothesized that: a) Bare soil respiration rates in both ecosystems would decline with increasing soil loss; b) Plant respiration rates in both ecosystems would increase with increasing soil loss; and c) Total soil respiration rates in both ecosystems would remain constant with increasing soil loss.

Materials and Methods

Study Sites The shortgrass prairie site was located at the USDA-Agricultural Research Service, Central Plains Experimental Range (CPER, 40°50' N latitude, 104°43' W longitude), a 6,280 ha research area in northeastern Colorado. The shortgrass prairie has a long history of grazing (Milchunas et al. 1992). Currently, CPER is moderately grazed by cattle during the growing season. The study site however, was fenced in the spring of 1998 to protect it from livestock grazing.

Long-term (1939-1990) annual temperature at CPER averaged about 9 °C with an average annual precipitation of 321 mm (Lauenroth and Sala 1992). Soils at the shortgrass prairie research area were formed from calcareous sandy alluvial and eolian material and are classified as a Vona Sandy Loam, which are coarse-loamy, mixed, mesic Ustollic Haplargids (USDA 1982). The vegetation at the study site was representative of the shortgrass prairie ecosystem (Milchunas et al. 1989) and was dominated by blue grama [*Bouteloua gracilis* (Kunth) Lag. ex Steud.] and buffalograss [*Buchloë dactyloides* (Nutt.) Englem.]. Western wheatgrass [*Pascopyrium smithii* (Rydb.) A. Love] is also an important component of the shortgrass ecosystem (Brown and Trlica 1977, Kemp and Williams 1980, Monson et al. 1982, 1986) and was present at our study site.

The sagebrush steppe site was located within the 10,000 ha Arapaho National Wildlife Refuge (ANWR) approximately 15 km south of Walden, Colorado (40°38' N latitude, 106°17' W longitude). The refuge is managed by the U.S. Fish and Wildlife Service as a bird sanctuary and has been protected from livestock grazing since 1967. However, between 200 and 500 head of elk (*Cervus elaphus nelsoni* Nelson) graze

ANWR ranges annually in the winter (Lanier 1999). The sagebrush research site was fenced to exclude livestock and wildlife grazing during the project.

The study site at ANWR was located on a dry exposure range site representative of a sagebrush steppe. Soils at this research site were formed in gravelly alluvium and were classified as a cabin sandy loam, which are fine-loamy over sandy or sandy-skeletal, mixed, Argic Cryoborolls (USDA 1981). Wyoming big sagebrush [*Artemisia tridentata* var. *wyominenses* (Beetle and Young) Welsh] was the dominant shrub component, with numerous C₃ grass species, including western wheatgrass, bluebunch wheatgrass [*Pseudoroegneria spicata* (Prush) A. Love], and sheep fescue (*Festuca ovina* L.) in the understory and interspaces. Average annual temperature at Walden is 3 °C with a mean annual precipitation of 275 mm received mostly as snow in the winter (Western Regional Climate Center 2001).

Experimental Design The experimental design was a split-plot, randomized block, with a factorial arrangement of treatments. For the shortgrass site, the factor levels consisted of 2 range condition classes (NRCS 1997), good and fair, and 3 levels of soil removal (0, 11.2 and 22.4 t ha⁻¹), with 3 replications of each level (18 plots). Only a range condition class of good was present at the sagebrush site, so treatments there were reduced to 3 levels of soil removal (0, 11.2, and 22.4 t ha⁻¹) with 3 replications of each (9 plots).

Treatment and Data Collection At the shortgrass site, nine (3 soil removal levels x 3 replications) permanent, 0.6 x 2 m steel frame plots were randomly placed within both the good and fair condition class sites (18 total plots) in the spring of 1998. Nine similar

plots were installed at the sagebrush site in the spring of 1999. Top soil from all treatment plots at both study sites was removed to the desired level using a vacuum and a collection bag. At the shortgrass site, treatments were imposed during the summer of 1998, while at the sagebrush site treatments were conducted in the early summer of 1999. The removed soil was transported to Colorado State University for analysis of carbon (C) and nitrogen (N) content by plot using a LECO CHN-1000 Analyzer.

Within each plot at both sites, four 5 x 10 cm diameter poly-vinyl-chloride (pvc) rings were inserted 2.5 cm deep into the soil leaving 2.5 cm of head space between the soil surface and the top of the ring. The rings were inserted into the plots at the shortgrass site in May 1999, and in September at the sagebrush site. At both study sites, 2 of the 4 rings were placed in natural gaps in the vegetative cover for measuring bare soil respiration. The remaining 2 rings were placed within the vegetative cover for measuring total soil respiration rates. Plant respiration rates were then estimated by subtracting bare soil respiration from total respiration. Respiration measurements were made on all 4 rings within each plot with a Li-Cor 6400-09 Soil CO₂ Flux Chamber at weekly intervals throughout the growing season. At each sampling period, 3 consecutive measurements of respiration were taken on each ring. Measurements were collected for both the 1999 and 2000 growing seasons on the shortgrass site, while measurements at the sagebrush site were made only during the 2000 growing season.

Because soil CO₂ efflux rate is influenced by soil and air temperature, soil water content, and relative humidity (Crain et al. 1999, Raich and Schlesinger 1992, Schlesinger 1997, Singh and Gupta 1978, Wiant 1967, Witkamp 1966, 1969), each of

these variables were measured as covariates with respiration during each sampling period. Soil temperature measurements were made by inserting a soil probe 10 cm deep into the soil in the vicinity of each ring at the time of sampling and data were recorded by the Li-Cor 6400. The soil probe was inserted into either bare or vegetated soil to correspond with the ring type being sampled. Air temperature and relative humidity were recorded by the Li-Cor 6400 in conjunction with each respiration measurement made. Gravimetric water content of study site soils was estimated from soil cores removed from the vicinity of each plot at depths of 0-5 and 5-10 cm on weekly intervals.

Statistical Analyses Total, bare soil, and plant respiration rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for the shortgrass site were analyzed using a repeated measures analysis of covariance (ANCOVA) procedure (Vonesh and Chinchilli 1997). Only air temperature met all assumptions concerning the use of covariates and also proved to be significant for all 3 response variables (Vonesh and Chinchilli 1997). Thus, all other covariates were dropped from the analyses. For the sagebrush site, air temperature was not significant as a covariate and was also dropped from the analysis for this site. Consequently, total, bare soil, and plant respiration rates for the sagebrush site were analyzed using a repeated measures analysis of variance (ANOVA) procedure (Vonesh and Chinchilli 1997). Repeated measures ANOVA was also used to test for differences in total, bare soil and plant respiration rates between the shortgrass and sagebrush sites for the 2000 growing season. In all analyses, differences were considered significant a $P \leq 0.10$. Fisher's Least Significant Difference (LSD) was used to separate group means when appropriate. Pearson's Correlation Analysis was conducted to determine the type of relationship for

total and bare soil respiration with soil and air temperature, soil water content (at 0-5 and 5-10 cm depths), and relative humidity as independent variables. Correlation coefficients (r) between variables were considered significant at $P \leq 0.01$. Data, statistical outputs, and supporting material for this chapter are located in Appendix C.

Results

Total soil respiration rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for both years at the shortgrass site were significantly positively correlated with ambient air temperature ($r = 0.49$) and gravimetric soil water content at 5-10 cm ($r = 0.47$, Figure 4-1). Relative humidity ($r = 0.26$), soil temperature ($r = 0.23$), and soil water content at 0-5 cm ($r = 0.28$) were also correlated ($P < 0.01$) with total respiration at the shortgrass site. Bare soil respiration rates at the shortgrass site were significantly positively correlated with ambient air temperature ($r = 0.44$), relative humidity ($r = 0.25$), soil water content at 0-5 and 5-10 cm ($r = 0.22$ and 0.45 , respectively), and soil temperature ($r = 0.29$).

Total soil respiration rates at the sagebrush site were positively correlated ($P < 0.01$) with soil water content at the 0-5 cm depth ($r = 0.47$, Figures 4-2) and relative humidity ($r = 0.43$). The correlation between total respiration and soil water content at the 5-10 cm depth ($r = 0.17$, $P < 0.01$) was low. Total soil respiration rate at the sagebrush site was negatively correlated ($r = -0.17$, $P < 0.01$) with soil temperature, but was not correlated with ambient air temperature ($P > 0.01$). Significant ($P < 0.01$) correlations existed between bare soil respiration at the sagebrush site and soil water content at 0-5 and 5-10 cm depths ($r = 0.56$ and 0.27 , respectively), relative humidity ($r = 0.18$), and soil

temperature ($r = -0.30$). Ambient air temperature at the sagebrush site was not correlated ($P > 0.01$) with bare soil respiration.

Gravimetric soil water content (%) at the shortgrass research site varied ($P < 0.10$) by depth across sampling periods and years (Figure 4-1). Generally, the 5-10 cm soil depth had a higher soil water content than the 0-5 cm depth (Figure 4-1). The differences in soil water content observed among periods between 1999 and 2000 at the shortgrass site was explained by the differences in the timing of precipitation events as well as total amount received. Peak soil water content in both years followed precipitation events, but occurred at different times of the year (Figure 4-1).

Total precipitation received at the shortgrass site in 1999 (419 mm) was approximately 29% greater than the long term average total annual precipitation of 321 mm (Lauenroth and Sala 1992). Conversely, in 2000 total precipitation (240 mm) was about 26% below the long term average. This difference in total precipitation between years at the shortgrass site was reflected in the differences in average soil water content, which was approximately 28% lower in 2000 ($6.1 \pm 0.2\%$ SE, $n = 324$) than in 1999 ($8.5 \pm 0.2\%$ SE, $n = 324$).

In 2000, the Arapaho National Wildlife Refuge (ANWR) received approximately 290 mm of precipitation, approximately 5% more than the long-term annual average of 275 mm (Western Regional Climate Center 2001). Of the 290 mm of precipitation received at the sagebrush site, 44% occurred between June and September of 2000. However, June and July precipitation accounted for only 29 mm of the 128 mm received between June and September of 2000. Most of the precipitation events that occurred

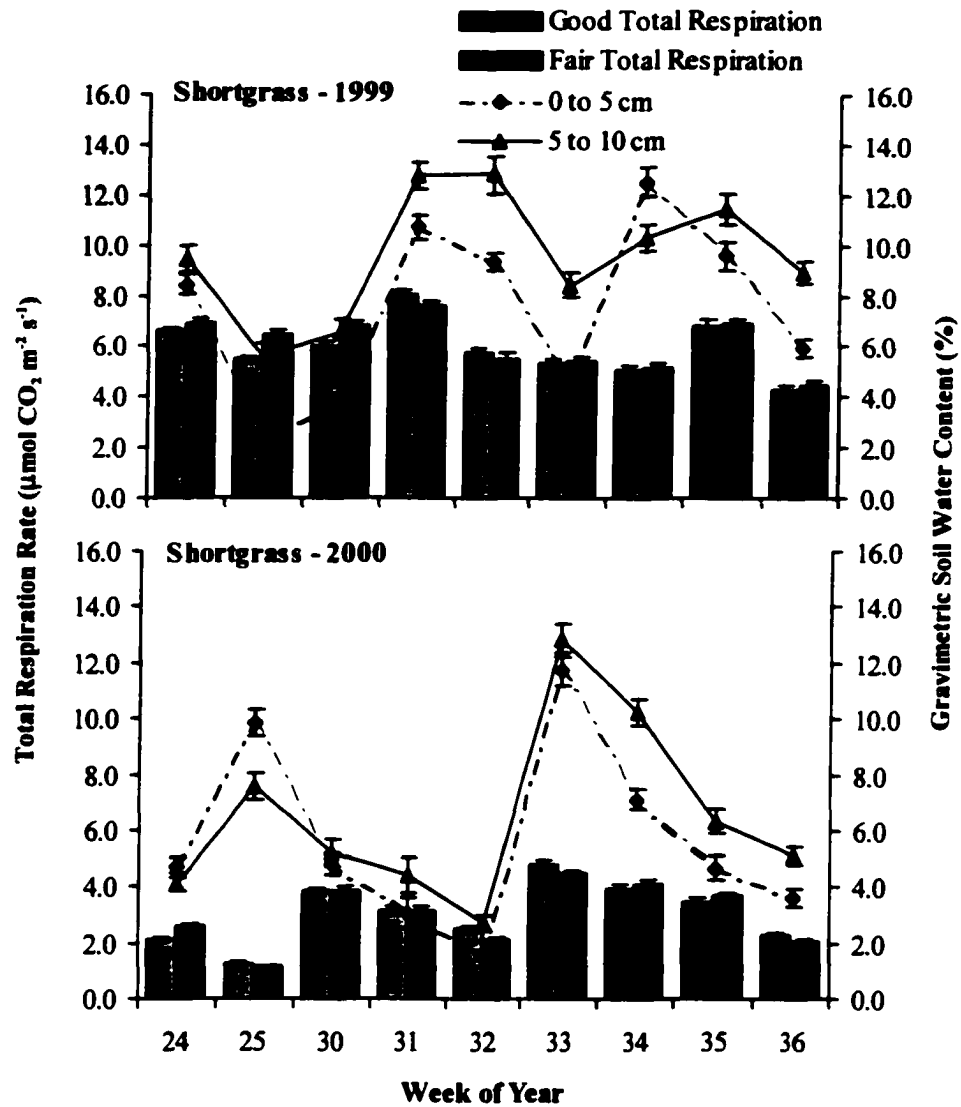


Figure 4-1. Weekly average (\pm SE) total soil respiration rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $n = 54$) for the good and fair condition classes and gravimetric soil water content (%; $n = 18$) at the 0-5 and 5-10 cm depths for the Central Plains Experimental Range research area during the 1999 and 2000 growing seasons.

during the 4 months of observation at the sagebrush site were short duration, low intensity storms that produced less than 2.5 mm of precipitation and consequently were not large enough to recharge the soil profile. This lack of adequate precipitation between June and September of 2000 at the sagebrush research site resulted in droughty soils low in water content. In fact, the gravimetric soil water content only varied by 1 or 2 % for both depths and never exceeded 5% of the total soil mass (Figure 4-2). Nevertheless, gravimetric soil water content at the sagebrush site varied significantly ($P < 0.10$) between depths and across sampling periods. Soil water content in the 5-10 cm depth was generally greater than in the 0-5 cm depth and also less variable between weeks (Figure 4-2). Weekly variation of soil water in the 0-5 cm depth likely resulted from higher evaporative losses in the upper 5 cm of the soil than in the 5-10 cm depth (Figure 4-2). For example, significant losses in soil water content in the 0-5 cm depth were observed from week 26 through week 29, but in the 5-10 cm depth soil moisture did not decrease significantly until week 32.

Between Site Differences Total, bare soil, and plant respiration rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) during the 2000 growing season were significantly different between the shortgrass and sagebrush sites, but these differences varied across sampling periods ($P < 0.10$). In general, total respiration rates were greater at the shortgrass site than at the drier sagebrush site (Figures 4-1 and 4-2). Likewise, bare soil and plant respiration rates were greater ($P < 0.10$) at the shortgrass site than at the sagebrush site. Soil removal level (0, 11.2, and 22.4 t ha^{-1}) had little effect ($P > 0.10$) on total, bare soil, or plant respiration rates at the sagebrush site.

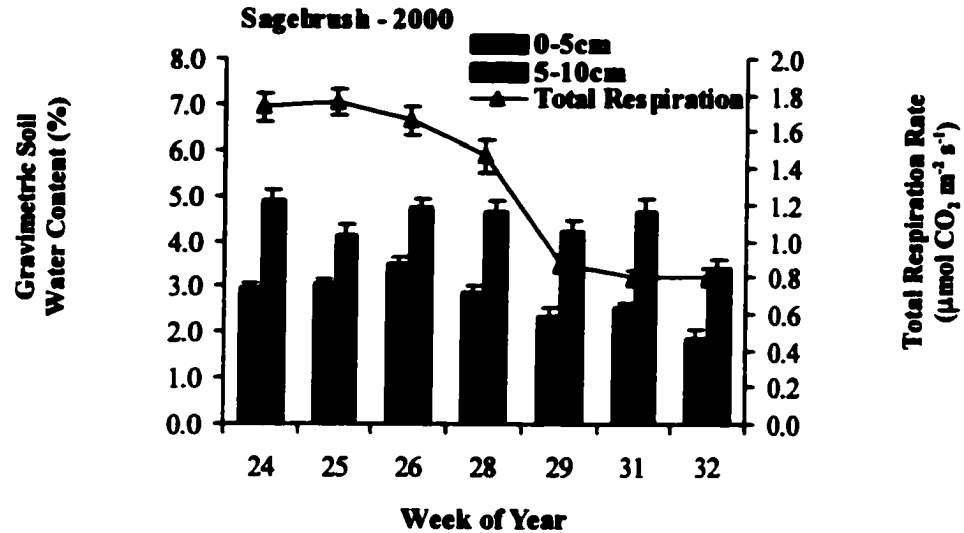


Figure 4-2. Weekly average (\pm SE) total respiration rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $n = 54$) and gravimetric soil water content (%; $n = 9$) at the 0-5 and 5-10 cm depths for the Arapaho National Wildlife Refuge research area during the 2000 growing season.

Respiration Rates at the Sagebrush Site Total respiration averaged (\pm SE, $n = 54$)

1.73 ± 0.075 , 1.76 ± 0.071 , and $1.66 \pm 0.075 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at the sagebrush site during weeks 24, 25, and 26, respectively (Figure 4-2). During this same period, plant respiration accounted for 45, 44, and 46% (weeks 24, 25, and 26, respectively) of the total CO_2 efflux at the sagebrush site. Significant decreases in the average total respiration rates from those observed in weeks 24, 25, and 26 occurred during weeks 28 ($1.47 \pm 0.085 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), 29 ($0.871 \pm 0.049 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), 31 ($0.798 \pm 0.039 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and 32 ($0.804 \pm 0.047 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Over this same period, the

contribution of plant respiration to total CO₂ efflux also declined to 42, 40, 34, and 35% for weeks 28, 29, 31, and 32, respectively.

Respiration Rates at the Shortgrass Prairie Site When adjusted for ambient air temperature, total respiration at the shortgrass prairie site increased ($P < 0.10$) with increasing soil removal (Figure 4-3). This effect of soil removal level (0, 11.2, and 22.4 t ha⁻¹) on total respiration did not vary ($P > 0.10$) between condition class, year, or sample periods, nor was it affected ($P > 0.10$) by 3 or 4-way interactions involving these variables. However, differences in total respiration rates between condition classes (good and fair) did vary ($P < 0.10$) among years (1999 and 2000) and sample periods, but showed no consistent trend.

Bare soil respiration at the shortgrass site varied little between condition class ($P > 0.10$) or soil removal level ($P > 0.10$), nor was there a condition class x soil removal level interaction ($P > 0.10$). Average (\pm SE, $n = 972$) bare soil respiration rate in 1999 ($3.8 \pm 0.033 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was greater ($P < 0.10$) than in the drier 2000 ($1.93 \pm 0.027 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) growing season. Efflux of CO₂ from bare soil accounted for more than 65% of the total respiration rate in the 0 and 11.2 t ha⁻¹ soil removal levels, but declined to 59% in the 22.4 t ha⁻¹ level. However, since bare soil respiration rates at the shortgrass site were relatively constant among soil removal treatments for both the good and fair condition classes, and between years (averaging $2.87 \pm 0.03 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ SE, $n = 1940$, with $< 0.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ between any 2 soil removal levels), it did not contribute to the increases observed in total respiration as soil removal level increased.

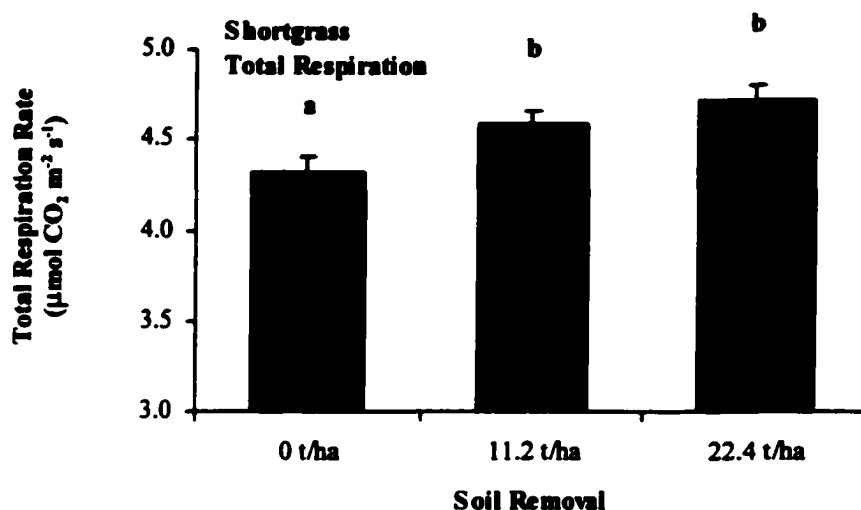


Figure 4-3. Average (\pm SE; covariate = ambient air temperature) total respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at the Central Plains Experimental Range research area for 0 ($n = 644$), 11.2 ($n = 648$), and 22.4 ($n = 648$) t ha^{-1} soil removal levels. Similar letters above bars are not significantly different (Fisher's LSD = 0.256 (adjusted), $t = 1.782$, MSE = 6.724).

Differences in plant respiration rates between the good and fair condition classes varied across sample periods ($P < 0.10$), but not between years ($P > 0.10$). The response of plant respiration rates to soil removal level did not vary between condition classes ($P > 0.10$), but did vary between sample periods and years ($P > 0.10$; Figure 4-4). Plant respiration at the shortgrass site was 35 and 36% of the total CO_2 efflux in the 0 and 11.2 t ha^{-1} soil removal levels, respectively, but increased to 42% in the 22.4 t ha^{-1} level.

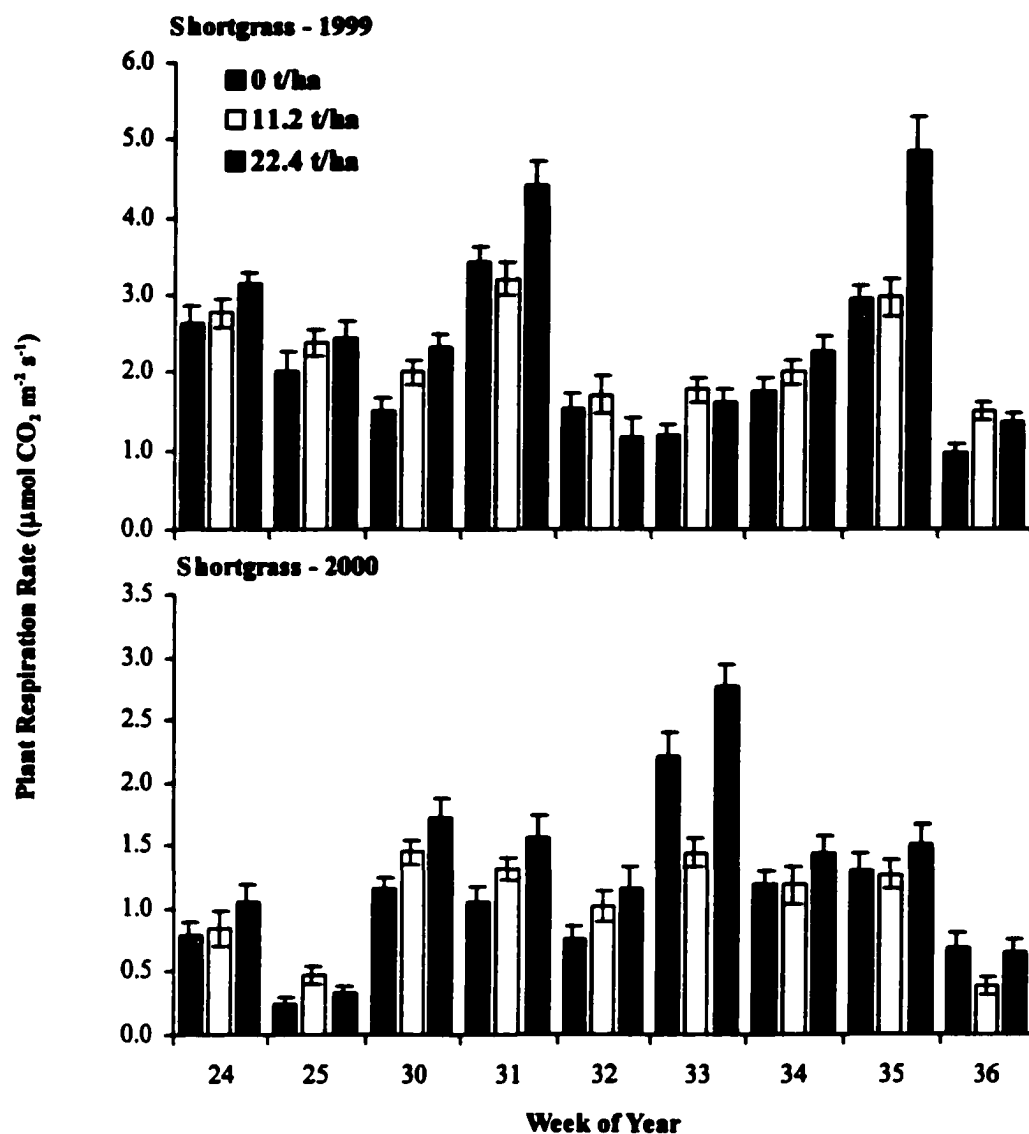


Figure 4-4. Weekly average (\pm SE, $n = 36$) plant respiration rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for the 0, 11.2, and 22.4 t ha^{-1} soil removal treatments at the Central Plains Experimental Range research area during the 1999 and 2000 growing seasons.

Discussion

The efflux of CO₂ from the soil results in part, from plant root respiration, microbial respiration as they decompose soil organic matter, faunal respiration, and the nonbiological, chemical oxidation of carbonate compounds (Witkamp 1966, Witkamp 1969, Singh and Gupta 1977). Soil respiration can thus be divided into 2 basic sources, that which is inherent to primary productivity (i.e. root respiration) and that which results from soil processes (i.e. microbial decomposition, faunal respiration, and chemical oxidation). However, these 2 sources of soil respiration are inescapably confounded. For example, primary production (above- and belowground) is the major contributor to soil organic matter (Charley and West 1975, Klemmedson 1989, Raich and Schlesinger 1992), which in turn is the energy source for microbial growth. Total respiration was separated into its plant and soil components in the present study to determine whether or not soil loss affected their respective contributions to the total CO₂ efflux.

Direct comparison between the rates of total and bare soil respiration observed for the shortgrass and sagebrush sites with other studies is difficult because of the variety of methods and definitions used and conditions under which soil respiration were measured (Clark and Coleman 1972, Raich and Schlesinger 1992, Bowden et al. 1993, Crain et al. 1999, Chen and Stark 2000). Generally, rates of total and bare soil respiration at the shortgrass and sagebrush research sites were within the range of values reported in the literature for other studies using similar methods and in similar environments (Clark and Coleman 1972, Crain et al. 1999). For example, in a study in the shortgrass prairie, Clark and Coleman (1972) reported rates of total respiration ranging from 0.3 to 4.4

$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ depending on the season and soil environment. In a Minnesota grassland study, Crain et al. (1999) reported rates of total respiration as high as $9.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$.

Total, bare soil, and plant respiration rates at the shortgrass site were considerably greater than at the sagebrush site during the 2000 growing season. These differences between the 2 sites can be explained, in part, by the greater productivity and higher soil C content at the shortgrass site than at the sagebrush site (Chapter II and III). Ecosystems with larger net primary production typically have larger soil C pools and consequently, higher rates of total CO_2 efflux (Charley and West 1975, Klemmedson 1989, Raich and Schlesinger 1992). The higher rate of total soil CO_2 efflux in ecosystems with greater productivity results from not only increased root respiration, but also increased microbial activity because of greater soil C availability. For example, Klein (1977) found that microbial activity was positively correlated with the soil organic matter of shortgrass soils. Thus, the larger soil C pool at the shortgrass site likely supported a larger and more active microbial population than at the sagebrush site and undoubtedly accounted for a portion of the higher total and bare soil respiration rates observed at the shortgrass site than at the sagebrush site.

Plant and bare soil respiration rates declined sharply at both sites as soil water content decreased, indicating increased plant and microbial stress. Wiant (1967), Witkamp (1969), and Klein (1977) noted that along with primary production, CO_2 efflux was suppressed during periods when soil water content was low, and air and soil temperatures were high. Plant and microbial stress occurs when environmental

conditions, such as air and soil temperatures, and soil water content are not optimal for growth and consequently results in reduced soil respiration rates (Witkamp 1969, Clark and Coleman 1972, Klein 1977). Thus, as the soil dried at the shortgrass and sagebrush research areas, the contribution of plant and microbial respiration to the total efflux of CO₂ decreased. This resulted in the lower total respiration rates observed at both sites during weeks when soil water content was low (Figures 4-1 and 4-2).

The characteristic seasonal trend in total respiration for both sites followed the fluctuations in soil water content and can be attributed to differences in the timing, amount, and frequency of precipitation received at both sites (Figures 4-1 and 4-2). Similar results were found by Clark and Coleman (1972) in a study of shortgrass prairie soils. For example, they found that the soil CO₂ efflux rate increased from 0.6 μmol CO₂ m⁻² s⁻¹ in June when soil water content (0-10 cm depth) was 2% to 4.4 μmol CO₂ m⁻² s⁻¹ in July when soil water content was 10 % (Clark and Coleman 1972). The study by Clark and Coleman (1972) also showed that 85% of the daily CO₂ efflux from shortgrass prairie soils occurred in the top 10 cm. This would help explain the strong correlation observed in this study for total and bare soil respiration rates with soil water content at the 5-10 cm depth at the shortgrass site. At the sagebrush site however, respiration rates were more strongly correlated with soil water content at the 0-5 cm depth. This, coupled with the likely shallow distribution of soil organic matter at the sagebrush site, would suggest that soil within the 0-5 cm depth contributed most of the CO₂ respired at the sagebrush site.

The lack of adequate precipitation to support herbaceous production at the sagebrush site resulted in a relatively short growing season in 2000 compared to that

experienced at the shortgrass site. While plant growth began at both sites during week 24 (June 11-17), herbaceous production ended at the sagebrush site during week 29 (July 16-22), but continued at the shortgrass site through week 36 (September 3-9, Figures 4-1 and 4-2). Over this same period, total respiration at the sagebrush site was highest ($> 1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) early in the growing season when soil water content in the 0-5 cm depth was greatest (3 - 3.5%), but total respiration declined ($< 1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) as the soil dried (2 - 2.5%). This trend in total respiration at the sagebrush site was coincident with the loss of herbaceous production beginning in week 29, and was reflected in the decline in the contribution of plant respiration to the total CO_2 efflux rate. For example, plant respiration decreased from a high of 46% of total respiration in week 26 to a low of 34% in week 31. Plant respiration therefore, contributed significantly to the total CO_2 efflux at the sagebrush site when conditions supported herbaceous growth (i.e. weeks 24-28).

Total respiration rate at the shortgrass site showed a different seasonal trend in 2000 than at the sagebrush site, reflecting a different pattern in precipitation received. Nevertheless, total respiration rates at the shortgrass site also declined as soil water content decreased (Figure 4-1). However, a major difference between the shortgrass and sagebrush sites was the response of their respective total, bare soil, and plant respiration rates to the soil removal treatments.

Differences in plant respiration rates among the soil removal treatments across periods and between years can be explained by fluctuations in soil water content at the shortgrass site (Figure 4-4). Higher plant respiration rates were observed for all soil removal levels when soil water content was greatest. Generally, during sample periods

with adequate soil water content to support plant growth, plant respiration increased with increasing soil removal. This relationship did not hold however, when respiration rates were low, such as when plant growth was limited by low soil water content, air temperature or some other environmental factor. For example, conditions were cold (mean temperature = 19.4°C) and cloudy [mean photosynthetically active radiation (PAR) = 491.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$] the day samples were taken during week 25 in 2000 at the shortgrass site (Figures 4-1 and 4-4). Consequently, because plant growth was limited, respiration rates at that time were low ($< 0.5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), despite nearly 8% soil water content. Additionally, early in the growing seasons (weeks 24-32) of both years, proportionally less soil water was required to support plant respiration than during the late season periods (weeks 33-34). During these late season periods, the increased response of plant respiration to soil removal that had been observed during the early season was not as well defined (Figure 4-4) and total respiration rates declined in all 3 soil removal treatments. This suggests that as the growing season progressed, plant growth rate slowed, thus plant respiration rates were reduced, and this resulted in lower total CO_2 efflux.

At the shortgrass site, plant respiration accounted for 35, 36, and 41% of the total respiration rate for the 0, 11.2, and 22.4 t ha^{-1} soil removal levels, respectively, when averaged across both years. This is consistent with the observed increase in total respiration with increasing soil removal level. Moreover, plant photosynthetic rates observed at the shortgrass site during the same times showed similar increases with increasing soil removal (Chapter II). It appears therefore, that the response of total

respiration to the soil removal treatments at the shortgrass site was driven by a plant physiological response to increasing levels of soil removal. Indeed, plant respiration rates typically become elevated in response to increased need of metabolic energy for growth, ion uptake and transport, or stress (Chapin et al. 1987, Coyne et al. 1995, Larcher 1995).

Roots account for a significant portion (50-80%) of the annual dry matter production of most plants, and only through continual growth can the roots explore enough soil volume to meet the nutritional needs of the plant (Chapin et al. 1987). It is possible that the removal of soil in the 11.2 and 22.4 t ha⁻¹ treatments altered 1 or more soil properties that generally supports plant growth (i.e. soil nutrient and organic matter content, water-holding capacity, etc. Singer and Munns 1991). If alteration of these soil properties was not severe, but sufficient enough to create a deficiency with the rooting zone, then more C might be allocated for root growth to maintain plant function (Ares 1976, Bloom et al. 1985, Chapin et al. 1987). Thus, the general trend for plant respiration rates to be higher in the 11.2 and 22.4 t ha⁻¹ soil removal treatments than in the control at the shortgrass site may have been a result of increased root growth.

Since the response of total respiration to the soil removal treatments at the shortgrass site was probably a function of primary production, it stands to reason that the culmination of low production, low soil water content, and a short growing season at the sagebrush site resulted in no detectable responses in total, bare soil, and plant respiration to soil removal. For all 3 responses at the sagebrush site, differences among soil removal levels were generally less than 0.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, and at no time did total respiration exceed 2 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. When total respiration rates at the shortgrass site were less

than $2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, plant respiration rates varied little among soil removal levels. Thus, primary production at the sagebrush site was likely not great enough to contribute a significant quantity of respired CO_2 to the total efflux. Consequently, unlike at the shortgrass site where respiration rates often exceeded $2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, differences in total respiration among soil removal levels at the sagebrush site could not be detected.

Summary and Conclusions

The objective of this study was to determine if 3 levels of soil loss (0, 11.2, and 22.4 t ha^{-1}) would affect total, bare soil, and plant respiration rates within the shortgrass prairie and sagebrush steppe ecosystems. Total and bare soil respiration rates were measured directly using a soil respiration chamber. Plant respiration rates were estimated by subtracting bare soil respiration from the total CO_2 efflux. It was hypothesized that as soil loss increased in both ecosystems: a) bare soil respiration rates would decline, plant respiration rates would increase, and total respiration rates would remain constant.

For the shortgrass site, total respiration rates increased with increasing soil removal level. This was not observed for the sagebrush site; the lack of response for this site can be explained by the culmination of low soil moisture levels, low primary productivity, and a short growing season. Consequently, results for total respiration rates at the sagebrush site were inconclusive and therefore, neither supported nor disproved the assumption regarding the response of total respiration to soil removal. Thus, the hypothesis that total respiration would remain constant as soil removal rate increased was rejected on the basis of observations from the shortgrass prairie site.

Bare soil respiration rates for both the shortgrass and sagebrush sites were unaffected by soil removal level. Therefore, the hypothesis that bare soil respiration rates would decrease with increasing soil removal level was rejected. Since bare soil respiration rates remained unchanged among soil removal levels, plant respiration rates likely accounted for most of the differences observed in total respiration rates at the shortgrass site as soil removal level increased.

Plant respiration rates on the shortgrass site generally increased with increasing soil removal level. This was dependent on environmental conditions that favored plant activity such as adequate soil water content, light, and temperature. When conditions were not favorable for plant growth, plant respiration rates were low and few differences in CO₂ flux among soil removal levels were found. Since favorable growing conditions at the sagebrush site were relatively brief and likely did not adequately support plant growth, a plant respiration response to increasing soil removal similar to that found at the shortgrass site was not observed. Therefore, the hypothesis that plant respiration rates would increase with increasing soil loss was not rejected on the basis of the observations at the shortgrass site. However, this response was dependent on seasonal variations in growing conditions and thus, would likely change with seasonal fluctuations in primary productivity.

Total respiration rates on the shortgrass prairie can be expected to increase with increasing soil loss. This increase in total respiration however, will be driven by a plant physiological response to conditions imposed by the loss of soil. Bare soil respiration rates on the other hand, contributed little to the total respiration response, and in fact

seem to be relatively stable when compared with plant respiration rates. It is possible that because of this stability, more severe soil removal levels than those imposed in this study, and that are repeated through time, may be needed to cause a response in bare soil respiration rates. This poses 2 important questions for future study; 1) would more severe levels of soil loss than those imposed in this study result in different responses in total, bare soil, and plant respiration rates than what was observed in the present study? and, 2) what would the response of total, bare soil, and plant respiration rates be to annual soil removal treatments? Answers to these questions would further our understanding of the effects of soil losses on rangeland productivity and carbon budgets.

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CHAPTER V

SUMMARY

Improved management of rangeland resources is dependent on the continual discovery of mechanisms and processes that define their responses to the numerous disturbances that occur in these ecosystems. Soil erosion is an important and common disturbance factor on most rangelands in the western United States. Concern about the extent of accelerated erosion rates on western rangelands have been expressed by investigators since the 1920's (Sampson and Weyl 1918, Chapline 1929, Weaver and Noll 1935). Much of the research on erosion has focused on the link between the amount of vegetative cover and rates of soil loss (Sampson and Weyl 1918, Chapline 1929, Weaver and Noll 1935, Bennett and Lowdermilk 1938, Blackburn 1980, Branson et al. 1981, Schmidt et al. 1982, Wight and Siddoway 1982, Pierson et al. 1994, Weltz et al. 1998). Thus, it has been thoroughly documented that as vegetative cover decreases, soil erosion increases. However, it is not understood how erosion affects the plant community or individual plants. In other words, while vegetation cover has been shown to be an important factor for the control of erosion, it is not clear whether erosion causes a loss in cover or productivity on rangelands. Therefore, research that increases our understanding of how soil loss affects the productivity of rangeland ecosystems is needed. Such

research will increase the ability of rangeland managers to establish effective goals and objectives that conserve and protect our rangeland resources.

Summary of Study Results

Productivity of rangelands can be measured through direct and indirect methods. Direct methods usually rely on measures of the CO₂ exchange rate of plant species and soils within the ecosystem in question. The purpose of the study reported in this dissertation was to determine the effects of 3 different levels of soil loss (0, 11.2, and 22.4 t ha⁻¹) on CO₂ exchange rates of 2 important rangeland ecosystems, a shortgrass prairie and a sagebrush steppe. The results of this investigation are reported in Chapters II, III, and IV. The responses of net photosynthesis of western wheatgrass and blue grama to the soil removal treatments at the Central Plains Experimental Range (CPER) research area was discussed in Chapter II. Western wheatgrass and blue grama are 2 important grasses within the shortgrass prairie ecosystem that have different physiologies (C₃ and C₄, respectively) and thus, tend to exploit their environments differently. In Chapter III, the photosynthetic response of bluebunch wheatgrass and Wyoming big sagebrush to these same soil removal treatments at the Arapaho National Wildlife Refuge (ANWR) research area was reported. Bluebunch wheatgrass, a C₃ grass, and Wyoming big sagebrush, a C₃ shrub, are 2 species common in the sagebrush steppe. Because of their different morphologies, bluebunch wheatgrass and big sagebrush also exploit their environments differently. Finally, in Chapter IV the response of total, bare soil, and plant respiration rates to increasing soil removal at both research areas was reported.

At the shortgrass site, the net photosynthetic rates of western wheatgrass and blue grama plants in the 11.2 and 22.4 t ha⁻¹ soil removal treatments was greater than in the control (0 t ha⁻¹). This response was coupled to a similar increase in nitrogen use efficiency (NUE) and a decrease in intercellular CO₂ concentration (C_i). The consistency and similarity of the responses of net photosynthesis, NUE, and C_i exhibited by western wheatgrass and blue grama was remarkable considering their different physiologies. Indeed, the consistency and similarity of their responses suggested that it was driven by a common physiological process, most likely the Calvin cycle. Carbon turnover in the Calvin cycle is controlled by the activity of ribulose 1,5-bisphosphate carboxylase (Rubisco) (Coyne et al. 1995, Bowyer and Leegood.1997). A higher quantity of Rubisco, or more active Rubisco, would result in a faster turnover of carbon in the Calvin cycle and an increase in the apparent photosynthetic rate. It appears therefore, that western wheatgrass and blue grama plants within the 11.2 and 22.4 t ha⁻¹ soil removal treatments allocated more nitrogen into the production of Rubisco or increasing this enzymes level of activity than did plants within the control.

The greater rates of photosynthesis in western wheatgrass and blue grama plants in the 11.2 and 22.4 t ha⁻¹ soil removal treatments than in control plants could be coupled to the response in total, bare soil, and plant respiration rates observed at the shortgrass research site. While total soil respiration at the shortgrass site increased as soil removal level increased, bare soil respiration rates did not vary among the 3 soil removal treatments. Therefore, it appears that an increase in plant respiration rates as the level of soil removal increased likely accounted for the increase in total soil respiration observed

at the shortgrass site. This apparent increase in plant respiration rates with increasing level of soil removal at the shortgrass site corresponds to the increase in the photosynthetic rates observed at this site in western wheatgrass and blue grama. Plant respiration rates typically become elevated in response to increased need for metabolic energy for growth, ion uptake and transport, or stress (Chapin et al. 1987, Coyne et al. 1995, Larcher 1995). The additional carbon required when plant respiration rates become elevated is supplied either through mobilization of stored carbohydrate reserves or by increasing the rate of photosynthesis (Coyne et al. 1995, Larcher 1995). Therefore, it appears that at the shortgrass site western wheatgrass and blue grama plants in the 11.2 and 22.4 t ha⁻¹ soil removal treatments increased their respective photosynthetic rates over those in the control plots to meet additional metabolic demands possibly imposed on those plants by the loss of soil properties that support plant growth.

The photosynthetic and respiratory responses observed for western wheatgrass and blue grama at the shortgrass site were not observed for bluebunch wheatgrass and big sagebrush at the sagebrush steppe research area. The photosynthetic rates of big sagebrush were unaffected by the soil removal treatments. The large volume of soil exploited by big sagebrush roots likely buffered these plants from any changes in soil properties caused by the soil removal treatments, since most of those changes occurred at the soil surface.

Overall, the net photosynthetic rate of bluebunch wheatgrass varied little between the 0 and 11.2 t ha⁻¹ soil removal levels, but decreased sharply at the 22.4 t ha⁻¹ soil removal level. This abrupt decrease in bluebunch wheatgrass net photosynthetic rates

between the 11.2 and 22.4 t ha⁻¹ soil removal treatments may be evidence of a soil loss tolerance threshold for this species of grass. However, it is important to note that the seasonal response of bluebunch wheatgrass net photosynthesis to the soil removal treatments could be separated into 2 distinct periods. In the first period, early in the growing season, the response of bluebunch wheatgrass photosynthesis was similar to that observed for western wheatgrass and blue grama at the shortgrass prairie research area. This response though, was limited by developing water stress, and by mid season the photosynthetic rate of bluebunch wheatgrass had decreased to very low levels. The second period in the photosynthetic response of bluebunch wheatgrass plants was defined by a differential rate of recovery to pre-drought net photosynthetic rates among the soil removal treatments following several short duration precipitation events. As soil removal level increased, the ability of bluebunch wheatgrass to recover pre-drought net photosynthetic rates decreased.

The lack of similarity in the photosynthetic and respiratory responses observed at the shortgrass and sagebrush research sites likely resulted from several interrelated factors. First, high temperatures and inadequate precipitation at the sagebrush site shortened the growing season and significantly reduced the productivity of bluebunch wheatgrass at the sagebrush site. Consequently this may have precluded a similar coupling between the photosynthetic and respiratory response in bluebunch wheatgrass plants to that observed for western wheatgrass and blue grama at the shortgrass site. In addition, because of the droughty growing conditions at the sagebrush site, there was considerable variability in the photosynthetic and respiratory rates of plants among the

soil removal treatments. Thus, while the sample size at the shortgrass research site was adequate to detect differences among the soil removal treatments, the sample size at the sagebrush site may have not been adequate. Moreover, unlike at the shortgrass site where data were collected for 2 growing seasons, data were collected at the sagebrush site for only 1 growing season. Consequently, this further reduced the sample size and limited the power of the repeated measures analysis of variance design at the sagebrush site.

Results from this study suggested that the effect of soil loss on plant photosynthetic rates is: 1) the same regardless of the physiology of the plant (i.e. C_3 and C_4), indicating that the response occurs within a common physiological process; 2) affects grasses such as western wheatgrass, blue grama and bluebunch wheatgrass, more than Wyoming big sagebrush, indicating that where soil loss is severe, the C_3 shrub, Wyoming big sagebrush may have a competitive advantage over grasses; and 3) may complicate post-drought recovery of photosynthesis to pre-drought levels in bluebunch wheatgrass. In addition, it appears from this research that soil loss at the levels used in this study at the shortgrass site resulted in some level of plant stress, or otherwise increased the metabolic requirements of the plants within the 11.2 and 22.4 t ha⁻¹ soil removal levels relative to the control. Thus, along with an increase in the net photosynthetic rate in western wheatgrass and blue grama as the level of soil removal increased, there was a general increase in plant respiration rates. While this coupling of photosynthetic and respiratory rates was not observed at the sagebrush research site for bluebunch wheatgrass, the harsh growing conditions may have precluded detection of differences in these responses among the soil removal treatments at this site.

Future Research Needs and Recommendations

Additional research is needed to investigate several issues that were not included in this study. Erosion is a process that occurs continually and at different intensities. Moreover, different rangeland ecosystems may respond differently to the loss of soil than what was observed for the shortgrass prairie and sagebrush steppe ecosystems used in this study. Soil removal treatments of greater intensity and that are repeated through time may result in different photosynthetic and respiratory responses than what was found in this study. In addition, more intense and repeated soil removal treatments may provide an indication as to the limits of sustainable soil loss levels on different rangeland ecosystems. Therefore, to improve our understanding of the effects of soil loss on rangeland productivity it is important that new studies are designed that include different intensities of repeated soil removal treatments, not only on the shortgrass prairie and sagebrush steppe, but on other rangeland ecosystems as well.

The results of this study suggest that the photosynthetic response to the soil removal levels occurred within a common physiological process, most likely the Calvin cycle. Additional research is needed to detect and isolate the enzymes involved in the photosynthetic response observed in this study. I hypothesize that the increases in net photosynthesis with increasing level of soil removed occurred because of an increase in the activity or quantity of Rubisco. Quantifying the amount or activity of Rubisco within plant species following a soil loss event may provide an answer to the mechanism through which they respond to environmental stress (for example of methods see Collatz et al. 1979, Lorimer et al. 1976, 1977). Understanding the mechanisms underlying plant

responses to soil loss will allow managers to make better decisions regarding rangeland sustainability. It may also clarify some lingering questions about the dynamics of rangeland plant communities where soil loss is an important disturbance factor.

No effort was made in this study to quantify possible changes in the soil microbial communities that may have occurred as a result of the soil removal treatments. Since there was no response in the bare soil respiration rate to the soil removal treatments, there remains a question of whether or not the treatments impacted the soil biota. Research should be done that identifies and quantifies changes in the soil microbial community as soil loss occurs. In addition, an effort should be made to link any changes in microbial biomass resulting from soil removal to observed plant responses. New research should also include quantifying the changes in various soil properties that support plant growth (i.e. soil nutrients, water, etc.) as soil removal level increases. A better understanding of the changes in soil properties under different soil loss levels may provide an answer as to why western wheatgrass and blue grama responded as they did in this study.

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Appendix A

Chapter II Data and Statistical Outputs

Table A-1. Mean ($n = 5$) net photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$), total conductance to CO_2 ($\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), intercellular CO_2 concentration ($\mu\text{mol CO}_2 \text{ mol air}^{-1}$), transpiration rate ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), ambient air temperature ($^{\circ}\text{C}$), and leaf chamber and ambient photosynthetically active radiation ($\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$) by plot for western wheatgrass (Pasm) and blue grama (Bogr) during the 1999 and 2000 growing season at the Central Plains Experimental Range research area.

Year	Week of Year	Soil Removal Level (t/ha)	Cond. Class	Plant Species	Photo-synthesis	Conduct-ance	Intercellular CO_2 Concentration	Trans-piration	Air Temperature	Photosynthetically Active Radiation	
										Chamber	Ambient
1999	24	22.4	Good	Pasm	13.4	0.219	237.8	6.9	31.4	1500	1683
1999	24	22.4	Good	Bogr	16.6	0.145	158.2	5.1	31.9	1501	1619
1999	24	0.0	Good	Pasm	16.2	0.371	265.8	9.3	30.3	1500	1285
1999	24	0.0	Good	Bogr	10.5	0.109	185.4	3.2	29.4	1501	1154
1999	24	11.2	Good	Pasm	12.3	0.269	266.2	6.4	28.0	1500	1017
1999	24	11.2	Good	Bogr	11.4	0.138	204.8	3.9	28.3	1500	1798
1999	24	22.4	Good	Pasm	18.2	0.384	258.2	10.9	31.2	1501	1062
1999	24	22.4	Good	Bogr	18.7	0.224	201.6	6.5	30.1	1500	369
1999	24	11.2	Fair	Bogr	36.6	0.318	147.8	9.0	29.1	1500	624
1999	24	0.0	Fair	Bogr	26.8	0.204	129.0	5.7	28.7	1500	339
1999	24	0.0	Fair	Bogr	28.7	0.349	203.4	8.3	27.0	1500	280
1999	24	22.4	Fair	Bogr	34.0	0.300	156.7	8.6	28.1	1500	1656
1999	24	22.4	Fair	Bogr	30.2	0.235	126.1	6.8	29.0	1500	903
1999	24	22.4	Fair	Bogr	32.2	0.314	169.4	9.5	29.7	1500	1157
1999	24	0.0	Fair	Bogr	28.3	0.210	116.2	7.0	31.0	1500	1649
1999	24	11.2	Fair	Bogr	21.0	0.160	127.4	6.1	32.4	1500	1565
1999	24	11.2	Fair	Bogr	22.6	0.153	100.9	5.5	32.0	1500	905
1999	24	11.2	Good	Pasm	17.7	0.254	220.8	7.4	30.2	1499	1997
1999	24	11.2	Good	Bogr	25.3	0.181	97.4	5.6	30.5	1500	1014
1999	24	11.2	Good	Pasm	18.5	0.213	197.4	6.3	30.3	1500	1932
1999	24	11.2	Good	Bogr	27.6	0.176	76.3	5.9	31.3	1500	2050
1999	24	22.4	Good	Pasm	18.9	0.238	205.0	7.3	31.7	1500	1364
1999	24	22.4	Good	Bogr	33.5	0.254	118.8	7.8	31.0	1500	394
1999	24	0.0	Good	Pasm	17.4	0.214	203.2	6.3	30.2	1500	612
1999	24	0.0	Good	Bogr	31.4	0.199	74.4	7.1	31.1	1500	955
1999	24	0.0	Good	Pasm	13.2	0.152	192.2	4.8	29.7	1501	297
1999	24	0.0	Good	Bogr	17.4	0.156	155.6	4.5	28.2	1500	302
1999	25	22.4	Good	Pasm	14.2	0.210	233.6	6.1	32.3	1500	1536
1999	25	22.4	Good	Bogr	13.9	0.085	84.1	2.9	32.8	1500	1619
1999	25	0.0	Good	Pasm	14.3	0.243	226.0	7.2	33.3	1500	1593
1999	25	0.0	Good	Bogr	15.8	0.087	44.5	3.6	34.8	1501	1670
1999	25	11.2	Good	Pasm	18.4	0.373	257.0	11.5	34.4	1500	1678
1999	25	11.2	Good	Bogr	17.1	0.095	37.1	3.8	34.5	1500	1641
1999	25	22.4	Good	Pasm	16.5	0.255	228.2	7.9	34.2	1500	1716
1999	25	22.4	Good	Bogr	11.6	0.070	80.8	2.8	34.6	1500	1756
1999	25	11.2	Fair	Bogr	11.5	0.066	56.9	2.6	34.6	1501	1746
1999	25	0.0	Fair	Bogr	12.7	0.088	108.5	3.5	34.9	1500	1787
1999	25	0.0	Fair	Bogr	13.4	0.081	78.1	3.4	35.4	1501	1789
1999	25	22.4	Fair	Bogr	13.7	0.080	61.0	3.5	35.9	1500	171
1999	25	22.4	Fair	Bogr	15.4	0.067	-88.0	3.1	36.4	1501	1811
1999	25	22.4	Fair	Bogr	13.9	0.072	21.7	3.6	37.0	1500	1800
1999	25	0.0	Fair	Bogr	13.4	0.096	116.9	4.5	35.5	1500	1728

Table A-1. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Cond. Class	Plant Species	Photo-synthesis	Conduct-ance	Intercellular CO ₂ Concentration	Trans-piration	Air Temperature	Photosynthetically Active Radiation	
										Chamber	Ambient
1999	25	11.2	Fair	Bogr	12.3	0.090	124.1	4.3	35.5	1500	1725
1999	25	11.2	Fair	Bogr	4.5	0.037	163.4	1.8	35.5	1501	1766
1999	25	11.2	Good	Pasm	11.1	0.184	237.4	8.2	35.7	1501	1721
1999	25	11.2	Good	Bogr	6.5	0.043	96.4	2.3	35.7	1501	1704
1999	25	11.2	Good	Pasm	8.2	0.131	238.2	6.1	35.6	1500	1636
1999	25	11.2	Good	Bogr	6.0	0.059	184.2	3.0	35.5	1500	1721
1999	25	22.4	Good	Pasm	11.0	0.164	226.0	7.8	35.6	1500	1701
1999	25	22.4	Good	Bogr	8.7	0.072	146.9	3.9	35.7	1500	1752
1999	25	0.0	Good	Pasm	8.3	0.140	239.4	7.1	35.8	1500	1318
1999	25	0.0	Good	Bogr	3.5	0.043	192.0	2.1	34.8	1501	235
1999	25	0.0	Good	Pasm	4.9	0.055	196.0	2.7	34.2	1500	189
1999	25	0.0	Good	Bogr	2.0	0.020	203.0	0.8	29.8	1500	70
1999	30	22.4	Good	Pasm	7.3	0.065	158.2	2.7	34.1	1499	1529
1999	30	22.4	Good	Bogr	16.5	0.092	45.6	3.8	34.5	1501	1585
1999	30	0.0	Good	Pasm	9.1	0.122	209.8	4.7	34.4	1500	1508
1999	30	0.0	Good	Bogr	13.6	0.071	26.8	3.1	34.9	1500	1585
1999	30	11.2	Good	Pasm	10.6	0.148	219.4	6.0	35.2	1500	991
1999	30	11.2	Good	Bogr	15.8	0.086	39.7	3.8	35.6	1501	1554
1999	30	22.4	Good	Pasm	11.5	0.129	186.6	5.8	35.5	1500	1612
1999	30	22.4	Good	Bogr	18.8	0.131	100.7	6.3	35.8	1501	1654
1999	30	11.2	Fair	Bogr	14.1	0.115	138.0	5.7	35.4	1499	1688
1999	30	0.0	Fair	Bogr	10.3	0.087	147.0	4.5	35.7	1500	1726
1999	30	0.0	Fair	Bogr	10.3	0.089	159.2	4.8	35.9	1500	1727
1999	30	22.4	Fair	Bogr	11.9	0.125	189.6	6.8	35.8	1500	1753
1999	30	22.4	Fair	Bogr	13.4	0.121	156.6	6.6	35.9	1501	1771
1999	30	22.4	Fair	Bogr	20.9	0.103	1.2	6.0	36.4	1500	1403
1999	30	0.0	Fair	Bogr	11.7	0.075	90.4	4.5	36.7	1500	1686
1999	30	11.2	Fair	Bogr	7.1	0.072	181.6	4.3	36.8	1500	1669
1999	30	11.2	Fair	Bogr	10.1	0.075	120.3	4.5	36.3	1500	1683
1999	30	11.2	Good	Pasm	13.2	0.237	234.8	13.6	37.6	1500	1563
1999	30	11.2	Good	Bogr	10.4	0.080	121.7	5.6	38.6	1500	1551
1999	30	11.2	Good	Pasm	8.1	0.186	255.2	10.7	37.8	1501	1630
1999	30	11.2	Good	Bogr	7.0	0.086	211.8	5.3	37.1	1500	1321
1999	30	22.4	Good	Pasm	8.2	0.158	240.0	8.8	37.0	1499	1570
1999	30	22.4	Good	Bogr	9.5	0.077	131.4	4.9	37.2	1501	1583
1999	30	0.0	Good	Pasm	7.0	0.149	250.2	8.6	37.5	1499	1494
1999	30	0.0	Good	Bogr	5.8	0.059	172.6	3.8	37.1	1501	1457
1999	30	0.0	Good	Pasm	6.3	0.083	204.2	5.6	37.9	1500	1497
1999	30	0.0	Good	Bogr	7.5	0.056	116.5	4.0	38.4	1500	1433
1999	31	22.4	Good	Pasm	17.2	0.348	257.6	8.2	27.8	1501	586
1999	31	22.4	Good	Bogr	19.9	0.170	152.8	4.7	28.3	1500	917
1999	31	0.0	Good	Pasm	23.2	0.468	254.4	10.5	28.8	1500	879
1999	31	0.0	Good	Bogr	21.5	0.159	122.8	4.5	29.0	1500	873
1999	31	11.2	Good	Pasm	15.7	0.257	235.6	6.5	30.0	1499	1439
1999	31	11.2	Good	Bogr	15.5	0.129	139.6	4.2	31.2	1500	1870
1999	31	22.4	Good	Pasm	20.8	0.378	246.6	9.1	30.1	1500	1299
1999	31	22.4	Good	Bogr	21.8	0.175	135.6	5.8	31.4	1500	2199

Table A-1. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Cond. Class	Plant Species	Photo- synthesis	Conduct- ance	Intercellular CO ₂ Concentration	Trans- piration	Air Temperature	Photosynthetically Active Radiation	
										Chamber	Ambient
1999	31	11.2	Fair	Bogr	19.9	0.151	122.0	5.1	32.3	1500	1959
1999	31	0.0	Fair	Bogr	21.8	0.144	85.0	5.2	32.8	1499	2191
1999	31	0.0	Fair	Bogr	15.0	0.110	114.3	4.1	33.5	1500	1732
1999	31	22.4	Fair	Bogr	19.2	0.148	127.0	5.2	32.6	1500	1556
1999	31	22.4	Fair	Bogr	12.0	0.140	201.6	4.5	30.7	1500	986
1999	31	22.4	Fair	Bogr	11.3	0.138	205.8	4.3	30.1	1500	618
1999	31	0.0	Fair	Bogr	16.7	0.152	164.6	4.6	29.6	1500	401
1999	31	11.2	Fair	Bogr	15.0	0.163	192.0	5.0	29.4	1500	610
1999	31	11.2	Fair	Bogr	11.6	0.110	173.2	3.6	30.3	1500	619
1999	31	11.2	Good	Pasm	17.1	0.349	258.2	9.8	30.0	1500	386
1999	31	11.2	Good	Bogr	11.0	0.107	177.0	3.4	29.9	1500	263
1999	31	11.2	Good	Pasm	12.4	0.223	248.0	6.6	29.7	1500	275
1999	31	11.2	Good	Bogr	10.7	0.127	205.8	4.1	29.8	1500	286
1999	31	22.4	Good	Pasm	12.2	0.231	253.4	6.8	29.4	1500	272
1999	31	22.4	Good	Bogr	10.2	0.118	206.2	3.8	29.3	1500	221
1999	31	0.0	Good	Pasm	9.7	0.269	281.4	7.6	28.7	1500	132
1999	31	0.0	Good	Bogr	5.7	0.125	268.0	3.8	28.5	1500	135
1999	31	0.0	Good	Pasm	5.9	0.135	274.2	4.0	28.1	1500	140
1999	31	0.0	Good	Bogr	7.7	0.095	211.4	2.9	28.4	1500	144
1999	32	22.4	Good	Pasm	23.2	0.370	239.6	5.3	20.9	1500	646
1999	32	22.4	Good	Bogr	29.7	0.374	213.0	5.7	21.7	1499	678
1999	32	0.0	Good	Pasm	28.9	0.580	258.6	7.8	22.2	1500	806
1999	32	0.0	Good	Bogr	27.8	0.316	198.8	5.1	22.9	1500	1367
1999	32	11.2	Good	Pasm	31.6	0.686	264.2	10.7	24.3	1500	1323
1999	32	11.2	Good	Bogr	31.0	0.246	135.2	4.9	25.2	1500	1486
1999	32	22.4	Good	Pasm	28.4	0.529	246.8	9.9	27.5	1500	1659
1999	32	22.4	Good	Bogr	37.6	0.245	84.2	6.2	28.8	1500	1661
1999	32	11.2	Fair	Bogr	44.6	0.336	117.2	8.0	29.0	1500	1706
1999	32	0.0	Fair	Bogr	49.9	0.310	53.2	7.8	29.1	1500	1731
1999	32	0.0	Fair	Bogr	43.4	0.275	76.7	7.1	29.5	1500	1759
1999	32	22.4	Fair	Bogr	42.0	0.240	54.6	6.3	29.5	1500	1757
1999	32	22.4	Fair	Bogr	41.3	0.285	102.0	6.8	28.9	1499	1684
1999	32	22.4	Fair	Bogr	31.8	0.206	85.2	4.4	27.9	1501	1648
1999	32	0.0	Fair	Bogr	28.9	0.164	58.5	3.3	27.5	1499	1331
1999	32	11.2	Fair	Bogr	28.6	0.192	92.8	3.9	27.9	1500	1680
1999	32	11.2	Fair	Bogr	29.6	0.185	62.5	4.2	28.7	1500	1759
1999	32	11.2	Good	Pasm	34.9	0.473	203.8	11.2	30.4	1499	1746
1999	32	11.2	Good	Bogr	45.1	0.262	54.1	6.9	30.3	1501	1725
1999	32	11.2	Good	Pasm	32.6	0.447	204.0	9.8	30.1	1500	693
1999	32	11.2	Good	Bogr	34.6	0.191	43.7	4.8	29.8	1500	111
1999	32	22.4	Good	Pasm	30.9	0.383	203.6	8.5	29.9	1500	744
1999	32	22.4	Good	Bogr	33.8	0.179	23.9	4.3	29.4	1500	1500
1999	32	0.0	Good	Pasm	22.2	0.402	246.8	8.0	29.1	1499	1653
1999	32	0.0	Good	Bogr	22.7	0.219	171.4	4.9	28.9	1499	1584
1999	32	0.0	Good	Pasm	23.0	0.422	246.8	9.3	29.6	1499	1386
1999	32	0.0	Good	Bogr	21.1	0.217	175.3	5.6	30.1	1500	1647
1999	33	22.4	Good	Pasm	22.3	0.399	242.0	13.1	33.7	1500	1542

Table A-1. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Cond. Class	Plant Species	Photo-synthesis	Conduct-ance	Intercellular		Air Temperature	Photosynthetically Active Radiation	
							CO ₂ Concentration	Trans-piration		Chamber	Ambient
1999	33	22.4	Good	Bogr	21.4	0.198	165.2	7.4	34.2	1500	1369
1999	33	0.0	Good	Pasm	21.8	0.426	247.6	13.3	33.5	1500	1323
1999	33	0.0	Good	Bogr	17.2	0.230	218.8	8.4	33.5	1500	997
1999	33	11.2	Good	Pasm	13.9	0.365	276.2	11.1	32.4	1499	699
1999	33	11.2	Good	Bogr	8.5	0.158	251.2	5.7	32.4	1499	1218
1999	33	22.4	Good	Pasm	17.6	0.370	256.6	12.2	33.5	1500	1429
1999	33	22.4	Good	Bogr	8.3	0.166	256.4	6.8	34.0	1501	1210
1999	33	11.2	Fair	Bogr	14.0	0.183	213.8	7.5	34.2	1500	1496
1999	33	0.0	Fair	Bogr	6.8	0.107	237.6	4.5	34.0	1499	1358
1999	33	0.0	Fair	Bogr	11.3	0.139	207.2	5.6	33.9	1500	1544
1999	33	22.4	Fair	Bogr	11.5	0.147	210.8	6.4	34.8	1500	1553
1999	33	22.4	Fair	Bogr	16.0	0.157	169.4	7.2	35.7	1500	1545
1999	33	22.4	Fair	Bogr	17.3	0.155	150.4	7.0	35.9	1500	1493
1999	33	0.0	Fair	Bogr	16.6	0.181	183.8	7.6	35.3	1500	301
1999	33	11.2	Fair	Bogr	5.2	0.153	284.6	6.2	33.3	1500	1017
1999	33	11.2	Fair	Bogr	10.1	0.133	215.6	6.1	34.4	1499	1211
1999	33	11.2	Good	Pasm	22.1	0.441	248.8	18.5	35.6	1500	1550
1999	33	11.2	Good	Bogr	17.5	0.145	133.8	7.3	36.4	1500	1577
1999	33	11.2	Good	Pasm	21.8	0.344	222.6	16.2	36.9	1500	1449
1999	33	11.2	Good	Bogr	18.3	0.185	172.8	9.5	37.2	1501	1178
1999	33	22.4	Good	Pasm	16.8	0.322	243.2	13.7	36.0	1500	1431
1999	33	22.4	Good	Bogr	14.9	0.157	177.6	8.0	36.5	1500	438
1999	33	0.0	Good	Pasm	10.2	0.267	270.8	11.1	34.6	1500	263
1999	33	0.0	Good	Bogr	5.0	0.158	288.8	6.7	33.5	1500	228
1999	33	0.0	Good	Pasm	5.3	0.201	292.8	8.4	33.0	1500	346
1999	33	0.0	Good	Bogr	3.5	0.139	284.4	5.3	31.0	1501	319
1999	34	22.4	Good	Pasm	27.1	0.543	254.6	11.4	28.4	1500	1077
1999	34	22.4	Good	Bogr	21.7	0.171	131.5	4.2	28.6	1500	603
1999	34	0.0	Good	Pasm	24.6	0.538	264.8	10.9	28.3	1500	749
1999	34	0.0	Good	Bogr	16.4	0.171	179.6	4.2	28.8	1500	831
1999	34	11.2	Good	Pasm	22.1	0.487	261.2	9.8	29.0	1500	672
1999	34	11.2	Good	Bogr	16.5	0.137	147.4	3.3	28.8	1500	629
1999	34	22.4	Good	Pasm	23.2	0.448	253.4	8.4	28.7	1500	627
1999	34	22.4	Good	Bogr	14.0	0.150	193.8	3.4	28.5	1500	568
1999	34	11.2	Fair	Bogr	22.4	0.218	177.0	5.3	29.0	1499	1304
1999	34	0.0	Fair	Bogr	23.1	0.149	89.0	4.0	30.1	1500	1233
1999	34	0.0	Fair	Bogr	20.9	0.148	112.3	3.7	30.0	1500	934
1999	34	22.4	Fair	Bogr	17.7	0.163	168.0	3.8	29.3	1499	873
1999	34	22.4	Fair	Bogr	21.1	0.182	151.8	4.5	29.6	1499	1324
1999	34	22.4	Fair	Bogr	15.3	0.135	142.9	2.4	26.2	1500	383
1999	34	0.0	Fair	Bogr	16.9	0.164	176.6	3.2	26.4	1500	500
1999	34	11.2	Fair	Bogr	14.0	0.142	184.2	3.1	27.5	1500	611
1999	34	11.2	Fair	Bogr	17.6	0.132	128.1	3.2	29.2	1500	659
1999	34	11.2	Good	Pasm	31.4	0.565	244.8	11.2	29.1	1499	594
1999	34	11.2	Good	Bogr	20.0	0.140	114.7	3.6	29.6	1499	704
1999	34	11.2	Good	Pasm	30.1	0.510	239.2	10.5	29.5	1500	453
1999	34	11.2	Good	Bogr	19.8	0.137	106.4	3.1	28.8	1500	382

Table A-1. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Cond. Class	Plant Species	Photo-synthesis	Conduct-ance	Intercellular CO ₂ Concentration	Trans-piration	Air Temperature	Photosynthetically Active Radiation	
										Chamber	Ambient
1999	34	22.4	Good	Pasm	24.3	0.466	253.4	8.8	28.1	1500	322
1999	34	22.4	Good	Bogr	14.5	0.109	134.6	2.5	28.1	1500	299
1999	34	0.0	Good	Pasm	17.3	0.333	257.0	6.3	27.3	1500	233
1999	34	0.0	Good	Bogr	5.6	0.062	204.6	1.3	26.6	1500	166
1999	34	0.0	Good	Pasm	8.8	0.147	250.4	2.8	25.7	1500	139
1999	34	0.0	Good	Bogr	8.0	0.098	226.2	1.9	25.4	1500	212
1999	35	22.4	Good	Pasm	19.6	0.193	163.4	5.4	29.9	1500	1277
1999	35	22.4	Good	Bogr	21.2	0.118	50.8	3.5	30.2	1500	1235
1999	35	0.0	Good	Pasm	23.3	0.282	203.6	8.2	30.4	1500	1370
1999	35	0.0	Good	Bogr	24.4	0.163	94.6	5.4	30.8	1499	1422
1999	35	11.2	Good	Pasm	18.3	0.193	188.2	6.5	31.2	1500	1188
1999	35	11.2	Good	Bogr	15.3	0.097	84.0	3.3	30.8	1500	1413
1999	35	22.4	Good	Pasm	24.5	0.340	216.2	9.9	30.7	1500	1456
1999	35	22.4	Good	Bogr	21.2	0.176	117.7	6.0	31.0	1501	1473
1999	35	11.2	Fair	Bogr	25.2	0.207	141.4	7.2	31.3	1500	1421
1999	35	0.0	Fair	Bogr	19.9	0.159	127.0	5.7	31.0	1500	1517
1999	35	0.0	Fair	Bogr	18.7	0.150	136.0	5.5	31.1	1499	1652
1999	35	22.4	Fair	Bogr	26.5	0.271	170.8	9.8	30.8	1500	1692
1999	35	22.4	Fair	Bogr	25.1	0.197	128.0	7.8	31.5	1499	1633
1999	35	22.4	Fair	Bogr	27.7	0.233	134.0	9.8	32.5	1500	1549
1999	35	0.0	Fair	Bogr	25.4	0.203	127.6	8.5	32.3	1500	1553
1999	35	11.2	Fair	Bogr	27.0	0.235	141.2	9.6	32.3	1500	1674
1999	35	11.2	Fair	Bogr	20.0	0.178	152.4	7.6	32.2	1500	1688
1999	35	11.2	Good	Pasm	32.2	0.419	203.4	16.6	32.9	1500	1689
1999	35	11.2	Good	Bogr	31.8	0.169	29.1	8.3	34.1	1500	1677
1999	35	11.2	Good	Pasm	26.3	0.286	177.6	12.7	34.3	1500	1619
1999	35	11.2	Good	Bogr	22.2	0.165	116.2	7.6	33.4	1500	1728
1999	35	22.4	Good	Pasm	26.2	0.295	184.6	13.5	33.9	1499	1634
1999	35	22.4	Good	Bogr	27.8	0.129	-9.0	6.6	34.5	1501	1598
1999	35	0.0	Good	Pasm	27.6	0.291	173.2	13.3	34.5	1499	1401
1999	35	0.0	Good	Bogr	17.8	0.123	98.9	6.1	33.8	1499	1536
1999	35	0.0	Good	Pasm	17.8	0.216	195.6	9.7	33.4	1500	1566
1999	35	0.0	Good	Bogr	22.8	0.138	67.9	6.6	33.3	1500	1410
1999	36	22.4	Good	Pasm	27.9	0.266	167.0	3.7	21.5	1499	708
1999	36	22.4	Good	Bogr	19.8	0.151	132.0	2.4	21.8	1501	849
1999	36	0.0	Good	Pasm	27.0	0.508	253.4	6.5	20.6	1500	848
1999	36	0.0	Good	Bogr	15.1	0.183	215.0	3.0	21.0	1500	623
1999	36	11.2	Good	Pasm	26.0	0.521	260.4	7.8	21.3	1500	1474
1999	36	11.2	Good	Bogr	18.2	0.150	143.6	2.6	21.6	1500	498
1999	36	22.4	Good	Pasm	21.3	0.413	259.8	5.3	19.3	1500	460
1999	36	22.4	Good	Bogr	13.0	0.208	234.2	3.1	19.6	1500	1414
1999	36	11.2	Fair	Bogr	10.4	0.142	225.4	2.4	21.0	1500	1752
1999	36	0.0	Fair	Bogr	16.6	0.169	176.0	3.3	22.6	1500	1711
1999	36	0.0	Fair	Bogr	17.5	0.144	149.6	3.0	23.9	1501	1705
1999	36	22.4	Fair	Bogr	18.8	0.179	173.0	3.4	23.0	1500	1705
1999	36	22.4	Fair	Bogr	12.0	0.128	196.7	2.5	23.3	1500	1542
1999	36	22.4	Fair	Bogr	10.7	0.121	171.7	2.3	23.1	1501	1433

Table A-1. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Cond. Class	Plant Species	Photo-synthesis	Conduct-ance	Intercellular CO ₂ Concentration	Trans-piration	Air Temperature	Photosynthetically Active Radiation	
										Chamber	Ambient
1999	36	0.0	Fair	Bogr	7.7	0.111	55.0	1.8	21.5	1500	1504
1999	36	11.2	Fair	Bogr	15.4	0.161	194.8	2.8	21.7	1499	1498
1999	36	11.2	Fair	Bogr	20.3	0.147	119.5	3.0	23.1	1500	1650
1999	36	11.2	Good	Pasm	35.5	0.631	245.8	11.5	23.7	1500	1651
1999	36	11.2	Good	Bogr	21.4	0.155	123.0	3.5	24.6	1500	1666
1999	36	11.2	Good	Pasm	33.4	0.423	205.4	9.3	26.0	1499	1619
1999	36	11.2	Good	Bogr	24.4	0.158	97.0	3.7	25.4	1500	1600
1999	36	22.4	Good	Pasm	28.1	0.373	217.4	7.9	25.0	1500	1339
1999	36	22.4	Good	Bogr	23.2	0.139	68.3	3.3	25.0	1499	1564
1999	36	0.0	Good	Pasm	28.0	0.312	168.0	7.7	26.5	1499	1560
1999	36	0.0	Good	Bogr	29.3	0.147	20.8	3.9	26.9	1500	1483
1999	36	0.0	Good	Pasm	27.6	0.262	164.2	6.7	27.1	1499	1450
1999	36	0.0	Good	Bogr	25.8	0.120	-12.2	3.3	27.3	1499	1462
2000	24	22.4	Good	Pasm	9.2	0.108	206.2	5.0	29.1	1500	764
2000	24	22.4	Good	Bogr	10.2	0.118	201.4	5.4	28.4	1500	788
2000	24	0.0	Good	Pasm	17.6	0.185	184.8	8.0	28.0	1500	843
2000	24	0.0	Good	Bogr	14.2	0.114	135.5	5.1	27.9	1499	929
2000	24	11.2	Good	Pasm	18.3	0.201	191.0	8.4	27.7	1500	870
2000	24	11.2	Good	Bogr	14.0	0.128	173.6	5.7	27.8	1500	783
2000	24	22.4	Good	Pasm	11.5	0.110	170.6	5.1	28.6	1499	1406
2000	24	22.4	Good	Bogr	5.2	0.063	161.8	3.3	30.3	1500	1461
2000	24	11.2	Fair	Bogr	9.8	0.092	164.0	4.9	31.0	1500	1055
2000	24	0.0	Fair	Bogr	11.0	0.110	180.6	5.5	29.7	1500	1005
2000	24	0.0	Fair	Bogr	11.4	0.098	153.2	5.1	30.1	1500	1199
2000	24	22.4	Fair	Bogr	16.3	0.129	126.9	6.7	30.6	1500	962
2000	24	22.4	Fair	Bogr	9.9	0.091	166.2	5.0	31.0	1500	1807
2000	24	22.4	Fair	Bogr	15.5	0.108	104.9	6.3	32.2	1500	1333
2000	24	0.0	Fair	Bogr	16.2	0.116	114.5	6.4	31.7	1500	752
2000	24	11.2	Fair	Bogr	17.8	0.132	129.1	6.6	30.0	1500	579
2000	24	11.2	Fair	Bogr	19.6	0.162	143.0	8.0	29.7	1500	823
2000	24	11.2	Good	Pasm	17.3	0.190	182.6	9.4	30.4	1500	1108
2000	24	11.2	Good	Bogr	15.1	0.127	152.6	6.1	29.4	1501	406
2000	24	11.2	Good	Pasm	7.8	0.098	221.4	3.4	23.9	1500	327
2000	24	11.2	Good	Bogr	19.3	0.224	206.8	7.3	23.0	1500	378
2000	24	22.4	Good	Pasm	22.3	0.193	152.0	6.0	22.5	1499	336
2000	24	22.4	Good	Bogr	23.5	0.166	115.4	5.5	22.9	1499	342
2000	24	0.0	Good	Pasm	16.9	0.138	144.0	4.5	22.7	1499	149
2000	24	0.0	Good	Bogr	17.4	0.115	96.0	3.9	23.0	1500	93
2000	24	0.0	Good	Pasm	3.2	0.061	264.0	2.1	22.7	1500	183
2000	24	0.0	Good	Bogr	4.8	0.129	281.4	4.4	23.2	1500	224
2000	25	22.4	Good	Pasm	16.4	0.258	241.0	4.2	22.0	1500	1152
2000	25	22.4	Good	Bogr	4.2	0.106	292.0	2.1	23.1	1500	1138
2000	25	0.0	Good	Pasm	17.2	0.373	267.8	6.6	24.0	1499	1587
2000	25	0.0	Good	Bogr	5.5	0.125	286.8	2.6	24.8	1505	1239
2000	25	11.2	Good	Pasm	21.5	0.335	236.6	6.7	25.9	1500	1811
2000	25	11.2	Good	Bogr	6.5	0.059	164.3	1.4	26.2	1509	1348
2000	25	22.4	Good	Pasm	16.8	0.213	214.8	4.3	25.9	1505	1138

Table A-1. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Cond. Class	Plant Species	Photo-synthesis	Conduct-ance	Intercellular CO ₂ Concentration	Trans-piration	Air Temperature	Photosynthetically Active Radiation	
										Chamber	Ambient
2000	25	22.4	Good	Bogr	6.7	0.067	179.2	1.5	25.9	1500	739
2000	25	11.2	Fair	Bogr	9.8	0.073	118.1	1.7	26.4	1500	1893
2000	25	0.0	Fair	Bogr	10.2	0.071	115.2	1.9	28.4	1501	1922
2000	25	0.0	Fair	Bogr	10.3	0.039	-87.3	1.1	29.2	1510	1748
2000	25	22.4	Fair	Bogr	10.0	0.057	53.3	1.3	28.0	1506	833
2000	25	22.4	Fair	Bogr	12.7	0.061	8.4	1.6	28.1	1501	2069
2000	25	22.4	Fair	Bogr	10.7	0.062	22.5	2.1	31.8	1501	2134
2000	25	0.0	Fair	Bogr	10.2	0.063	84.5	1.7	29.2	1507	1344
2000	25	11.2	Fair	Bogr	9.6	0.107	184.2	3.1	29.1	1505	2156
2000	25	11.2	Fair	Bogr	12.3	0.068	6.2	2.3	31.3	1504	1979
2000	25	11.2	Good	Pasm	15.7	0.197	210.2	5.4	29.8	1488	1372
2000	25	11.2	Good	Bogr	9.2	0.063	123.1	1.8	28.9	1504	1793
2000	25	11.2	Good	Pasm	16.8	0.181	189.2	5.1	28.8	1502	1708
2000	25	11.2	Good	Bogr	12.1	0.085	108.5	2.8	30.0	1501	1790
2000	25	22.4	Good	Pasm	15.8	0.179	189.4	5.2	29.8	1501	859
2000	25	22.4	Good	Bogr	6.5	0.059	150.1	1.8	29.5	1501	659
2000	25	0.0	Good	Pasm	11.3	0.130	203.0	3.4	27.9	1501	538
2000	25	0.0	Good	Bogr	9.3	0.080	143.9	2.2	27.4	1490	763
2000	25	0.0	Good	Pasm	10.9	0.142	210.4	3.8	27.3	1504	603
2000	25	0.0	Good	Bogr	7.0	0.057	147.7	1.5	26.7	1500	370
2000	30	22.4	Good	Pasm	13.5	0.217	225.4	10.4	31.3	1500	1031
2000	30	22.4	Good	Bogr	19.9	0.070	-114.6	2.2	31.7	1500	686
2000	30	0.0	Good	Pasm	16.9	0.201	201.8	6.2	32.7	1500	1076
2000	30	0.0	Good	Bogr	19.1	0.062	-356.7	2.3	33.6	1501	1331
2000	30	11.2	Good	Pasm	18.3	0.188	180.8	6.7	33.8	1500	1037
2000	30	11.2	Good	Bogr	19.2	0.086	-15.2	3.2	33.5	1500	1128
2000	30	22.4	Good	Pasm	25.6	0.306	200.0	11.5	35.3	1500	1476
2000	30	22.4	Good	Bogr	34.5	0.166	8.7	7.3	35.7	1500	1490
2000	30	11.2	Fair	Bogr	18.3	0.125	106.8	5.9	36.0	1500	1500
2000	30	0.0	Fair	Bogr	20.8	0.108	38.0	5.3	36.5	1500	1488
2000	30	0.0	Fair	Bogr	20.0	0.165	151.2	8.2	37.1	1500	1463
2000	30	22.4	Fair	Bogr	16.8	0.217	209.2	10.4	36.4	1500	1492
2000	30	22.4	Fair	Bogr	26.1	0.219	140.1	11.2	37.1	1500	1469
2000	30	22.4	Fair	Bogr	25.6	0.276	183.8	15.3	38.6	1500	1547
2000	30	0.0	Fair	Bogr	23.6	0.181	127.1	10.5	38.7	1500	1592
2000	30	11.2	Fair	Bogr	29.0	0.179	71.3	10.8	39.3	1500	1367
2000	30	11.2	Fair	Bogr	22.7	0.182	130.7	10.2	38.4	1500	1170
2000	30	11.2	Good	Pasm	16.2	0.359	263.6	18.2	37.6	1500	1288
2000	30	11.2	Good	Bogr	19.9	0.193	170.6	11.2	38.0	1501	1132
2000	30	11.2	Good	Pasm	18.6	0.370	252.6	20.0	38.1	1499	1606
2000	30	11.2	Good	Bogr	22.6	0.198	154.4	12.0	38.4	1500	1132
2000	30	22.4	Good	Pasm	19.2	0.305	229.0	16.5	38.4	1499	1511
2000	30	22.4	Good	Bogr	25.3	0.150	61.5	10.1	39.5	1499	1324
2000	30	0.0	Good	Pasm	18.0	0.286	229.6	16.8	39.6	1500	1212
2000	30	0.0	Good	Bogr	19.9	0.163	131.9	10.8	39.7	1501	1310
2000	30	0.0	Good	Pasm	11.3	0.246	261.8	14.0	38.3	1500	679
2000	30	0.0	Good	Bogr	13.8	0.196	224.4	10.8	36.7	1500	457

Table A-1. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Cond. Class	Plant Species	Photo-synthesis	Conduct-ance	Intercellular CO ₂ Concentration	Trans-piration	Air Temperature	Photosynthetically Active Radiation	
										Chamber	Ambient
2000	31	22.4	Good	Pasm	8.3	0.113	234.2	4.5	35.0	1500	973
2000	31	22.4	Good	Bogr	4.9	0.038	243.6	1.7	35.2	1500	1183
2000	31	0.0	Good	Pasm	9.0	0.106	219.8	4.8	35.7	1499	1291
2000	31	0.0	Good	Bogr	4.7	0.060	261.2	2.9	36.1	1500	1410
2000	31	11.2	Good	Pasm	14.2	0.134	168.3	6.7	36.6	1499	1424
2000	31	11.2	Good	Bogr	10.1	0.049	30.2	2.7	37.3	1499	1401
2000	31	22.4	Good	Pasm	15.3	0.160	178.8	8.2	37.5	1499	1170
2000	31	22.4	Good	Bogr	13.1	0.104	146.2	5.9	37.6	1500	1029
2000	31	11.2	Fair	Bogr	10.4	0.073	148.5	4.5	37.8	1500	1526
2000	31	0.0	Fair	Bogr	16.8	0.059	-109.8	4.2	40.0	1500	1554
2000	31	0.0	Fair	Bogr	9.5	0.057	39.2	3.8	39.6	1500	1420
2000	31	22.4	Fair	Bogr	13.5	0.055	-89.6	4.0	39.9	1500	1581
2000	31	22.4	Fair	Bogr	8.5	0.095	201.6	6.8	39.8	1500	1621
2000	31	22.4	Fair	Bogr	5.4	0.093	253.2	5.9	38.4	1500	696
2000	31	0.0	Fair	Bogr	8.0	0.132	252.4	8.1	37.5	1489	447
2000	31	11.2	Fair	Bogr	24.0	0.083	-259.3	5.9	38.9	1499	1865
2000	31	11.2	Fair	Bogr	11.8	0.069	69.1	5.5	41.2	1500	1142
2000	31	11.2	Good	Pasm	14.1	0.202	219.8	14.1	40.2	1499	1436
2000	31	11.2	Good	Bogr	11.4	0.108	162.6	7.9	40.0	1501	923
2000	31	11.2	Good	Pasm	23.3	0.278	187.4	18.3	39.1	1500	1317
2000	31	11.2	Good	Bogr	23.2	0.091	-101.5	6.8	40.4	1500	576
2000	31	22.4	Good	Pasm	9.2	0.191	259.4	11.9	38.6	1500	228
2000	31	22.4	Good	Bogr	13.4	0.087	103.5	5.4	36.9	1501	128
2000	31	0.0	Good	Pasm	17.0	0.241	229.0	11.0	32.4	1499	1019
2000	31	0.0	Good	Bogr	23.7	0.214	158.8	10.0	32.7	1499	1210
2000	31	0.0	Good	Pasm	19.8	0.255	205.0	12.2	34.4	1500	773
2000	31	0.0	Good	Bogr	12.6	0.112	164.4	5.1	32.7	1500	493
2000	32	22.4	Good	Pasm	16.1	0.119	66.1	3.4	31.3	1499	1108
2000	32	22.4	Good	Bogr	4.8	0.021	-133.5	0.6	31.9	1500	1277
2000	32	0.0	Good	Pasm	13.0	0.192	229.8	5.2	31.4	1500	1351
2000	32	0.0	Good	Bogr	5.7	0.037	101.5	1.0	30.3	1500	1380
2000	32	11.2	Good	Pasm	11.2	0.115	187.6	3.2	30.4	1500	1399
2000	32	11.2	Good	Bogr	8.1	0.045	78.7	1.3	30.7	1500	1416
2000	32	22.4	Good	Pasm	18.8	0.218	201.6	6.8	31.6	1500	1490
2000	32	22.4	Good	Bogr	12.7	0.080	91.2	2.9	32.4	1501	1539
2000	32	11.2	Fair	Bogr	2.2	0.038	270.4	1.6	34.0	1500	1591
2000	32	0.0	Fair	Bogr	6.4	0.054	178.0	2.5	34.8	1501	1626
2000	32	0.0	Fair	Bogr	3.9	0.062	257.6	2.9	35.3	1500	1665
2000	32	22.4	Fair	Bogr	6.3	0.048	165.0	2.1	34.4	1500	1363
2000	32	22.4	Fair	Bogr	7.6	0.059	85.9	2.4	33.6	1500	1681
2000	32	22.4	Fair	Bogr	15.2	0.061	-126.6	2.7	34.1	1499	1341
2000	32	0.0	Fair	Bogr	4.4	0.047	219.6	2.2	34.7	1500	1284
2000	32	11.2	Fair	Bogr	6.5	0.056	170.6	2.7	35.1	1500	1695
2000	32	11.2	Fair	Bogr	11.4	0.098	159.2	4.6	34.9	1500	1610
2000	32	11.2	Good	Pasm	20.7	0.303	226.8	13.6	34.9	1500	1690
2000	32	11.2	Good	Bogr	18.9	0.092	11.2	4.7	35.8	1500	1702
2000	32	11.2	Good	Pasm	19.9	0.212	158.1	10.6	36.6	1500	1687

Table A-1. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Cond. Class	Plant Species	Photo-synthesis	Conduct-ance	Intercellular CO ₂ Concentration	Trans-piration	Air Temperature	Photosynthetically Active Radiation	
										Chamber	Ambient
2000	32	11.2	Good	Bogr	17.6	0.117	92.2	6.1	36.3	1500	1699
2000	32	22.4	Good	Pasm	7.7	0.111	229.2	6.1	37.0	1500	1611
2000	32	22.4	Good	Bogr	9.6	0.076	150.7	4.0	36.1	1500	1171
2000	32	0.0	Good	Pasm	12.4	0.176	223.2	8.5	35.6	1500	1430
2000	32	0.0	Good	Bogr	13.7	0.115	138.0	6.0	35.8	1500	1634
2000	32	0.0	Good	Pasm	8.9	0.109	208.6	5.5	35.6	1500	1634
2000	32	0.0	Good	Bogr	6.0	0.088	221.4	4.6	35.6	1500	1604
2000	33	22.4	Good	Pasm	23.1	0.321	237.4	5.2	21.4	1500	373
2000	33	22.4	Good	Bogr	16.1	0.101	95.0	1.9	22.5	1500	372
2000	33	0.0	Good	Pasm	16.2	0.371	282.8	6.3	22.7	1500	389
2000	33	0.0	Good	Bogr	6.3	0.051	136.8	1.0	23.0	1501	437
2000	33	11.2	Good	Pasm	16.5	0.255	246.4	4.9	23.6	1501	560
2000	33	11.2	Good	Bogr	14.4	0.077	50.8	1.7	24.4	1500	612
2000	33	22.4	Good	Pasm	19.4	0.311	251.0	6.1	25.2	1500	614
2000	33	22.4	Good	Bogr	13.9	0.123	166.9	2.6	25.4	1500	519
2000	33	11.2	Fair	Bogr	9.7	0.093	185.0	2.0	25.4	1500	475
2000	33	0.0	Fair	Bogr	10.5	0.081	159.8	1.8	25.4	1500	537
2000	33	0.0	Fair	Bogr	11.5	0.100	173.0	2.2	25.5	1500	552
2000	33	22.4	Fair	Bogr	14.9	0.123	163.0	2.6	25.2	1500	471
2000	33	22.4	Fair	Bogr	19.7	0.172	167.6	3.8	25.6	1500	924
2000	33	22.4	Fair	Bogr	21.2	0.131	76.3	3.3	27.2	1500	940
2000	33	0.0	Fair	Bogr	16.8	0.078	6.9	1.9	27.5	1500	564
2000	33	11.2	Fair	Bogr	14.7	0.133	165.0	3.2	27.4	1500	559
2000	33	11.2	Fair	Bogr	9.9	0.149	247.4	3.4	26.5	1500	580
2000	33	11.2	Good	Pasm	24.2	0.410	252.8	8.6	26.1	1499	681
2000	33	11.2	Good	Bogr	15.4	0.170	205.0	4.0	26.2	1501	661
2000	33	11.2	Good	Pasm	24.4	0.436	256.4	9.9	26.9	1500	945
2000	33	11.2	Good	Bogr	21.4	0.152	119.1	3.9	27.1	1500	990
2000	33	22.4	Good	Pasm	21.6	0.304	232.4	7.7	27.8	1500	1058
2000	33	22.4	Good	Bogr	17.1	0.125	115.9	3.5	27.9	1500	1298
2000	33	0.0	Good	Pasm	22.3	0.342	239.0	8.3	27.8	1500	753
2000	33	0.0	Good	Bogr	17.7	0.162	171.4	4.4	27.8	1500	994
2000	33	0.0	Good	Pasm	20.4	0.292	232.2	8.4	29.6	1500	1399
2000	33	0.0	Good	Bogr	25.0	0.187	131.7	5.8	30.2	1500	1027
2000	34	22.4	Good	Pasm	18.6	0.323	258.4	10.3	31.6	1499	899
2000	34	22.4	Good	Bogr	17.0	0.152	176.1	5.3	31.7	1499	1124
2000	34	0.0	Good	Pasm	23.4	0.466	267.2	13.1	31.1	1500	697
2000	34	0.0	Good	Bogr	17.1	0.165	186.4	5.2	30.8	1500	934
2000	34	11.2	Good	Pasm	23.4	0.416	258.8	12.8	31.1	1500	978
2000	34	11.2	Good	Bogr	20.1	0.156	138.3	5.5	31.3	1500	978
2000	34	22.4	Good	Pasm	22.3	0.392	256.0	12.2	31.6	1499	1320
2000	34	22.4	Good	Bogr	26.3	0.175	108.3	6.9	32.6	1501	1367
2000	34	11.2	Fair	Bogr	25.7	0.206	145.6	8.4	33.0	1500	1446
2000	34	0.0	Fair	Bogr	23.0	0.168	131.8	7.0	33.5	1500	1475
2000	34	0.0	Fair	Bogr	18.6	0.161	163.0	6.6	33.2	1500	700
2000	34	22.4	Fair	Bogr	33.5	0.262	139.6	10.2	33.2	1500	1567
2000	34	22.4	Fair	Bogr	26.1	0.268	190.2	11.6	34.1	1500	1549

Table A-1. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Cond. Class	Plant Species	Photo-synthesis	Conduct-ance	Intercellular CO ₂ Concentration	Trans-piration	Air Temperature	Photosynthetically Active Radiation	
										Chamber	Ambient
2000	34	22.4	Fair	Bogr	25.6	0.195	139.5	8.7	34.2	1499	1516
2000	34	0.0	Fair	Bogr	25.0	0.170	110.8	7.5	34.1	1500	1541
2000	34	11.2	Fair	Bogr	28.2	0.196	112.8	8.9	34.5	1500	1577
2000	34	11.2	Fair	Bogr	18.5	0.172	176.6	8.4	35.1	1500	1598
2000	34	11.2	Good	Pasm	19.3	0.332	247.8	15.0	35.0	1500	1640
2000	34	11.2	Good	Bogr	14.7	0.129	165.2	6.4	35.1	1500	1675
2000	34	11.2	Good	Pasm	20.6	0.394	255.0	17.4	35.2	1501	1636
2000	34	11.2	Good	Bogr	22.3	0.216	174.4	10.6	35.0	1500	1613
2000	34	22.4	Good	Pasm	25.8	0.361	221.2	17.3	35.9	1501	1631
2000	34	22.4	Good	Bogr	24.2	0.140	64.9	7.6	36.2	1501	1651
2000	34	0.0	Good	Pasm	16.1	0.304	255.4	14.6	36.4	1500	1611
2000	34	0.0	Good	Bogr	18.7	0.192	185.0	10.3	36.3	1500	1605
2000	34	0.0	Good	Pasm	18.5	0.353	247.0	17.0	36.0	1500	1544
2000	34	0.0	Good	Bogr	19.5	0.134	107.0	7.3	36.3	1500	1543
2000	35	22.4	Good	Pasm	17.4	0.436	280.4	8.3	23.9	1500	375
2000	35	22.4	Good	Bogr	13.9	0.210	244.8	4.6	23.9	1500	347
2000	35	0.0	Good	Pasm	20.3	0.479	277.6	9.1	23.6	1500	511
2000	35	0.0	Good	Bogr	17.2	0.272	242.4	5.7	23.6	1500	535
2000	35	11.2	Good	Pasm	23.8	0.556	274.8	10.4	24.2	1500	574
2000	35	11.2	Good	Bogr	13.9	0.125	174.4	2.8	24.6	1500	743
2000	35	22.4	Good	Pasm	18.7	0.440	276.6	7.9	24.4	1500	1101
2000	35	22.4	Good	Bogr	17.6	0.227	217.4	4.9	24.8	1500	1345
2000	35	11.2	Fair	Bogr	15.4	0.169	195.4	3.8	25.6	1500	1273
2000	35	0.0	Fair	Bogr	22.5	0.162	121.7	4.0	26.9	1500	1406
2000	35	0.0	Fair	Bogr	20.6	0.243	207.4	6.4	27.8	1501	1425
2000	35	22.4	Fair	Bogr	28.2	0.233	149.4	5.8	27.2	1500	1518
2000	35	22.4	Fair	Bogr	25.8	0.257	180.8	6.9	28.0	1500	1535
2000	35	22.4	Fair	Bogr	23.5	0.244	185.8	6.3	27.7	1500	1466
2000	35	0.0	Fair	Bogr	18.9	0.172	168.8	4.4	27.3	1500	1469
2000	35	11.2	Fair	Bogr	24.9	0.209	152.2	5.4	27.4	1500	1472
2000	35	11.2	Fair	Bogr	20.4	0.178	149.8	4.7	27.9	1500	1582
2000	35	11.2	Good	Pasm	26.5	0.466	250.4	11.1	28.2	1500	1642
2000	35	11.2	Good	Bogr	24.1	0.196	151.6	5.5	28.4	1500	1630
2000	35	11.2	Good	Pasm	30.5	0.527	242.4	13.0	28.9	1500	1628
2000	35	11.2	Good	Bogr	27.2	0.209	122.4	6.3	29.4	1500	1644
2000	35	22.4	Good	Pasm	24.7	0.328	218.4	9.4	29.8	1500	1640
2000	35	22.4	Good	Bogr	34.5	0.241	100.9	7.6	30.3	1500	1649
2000	35	0.0	Good	Pasm	23.8	0.349	224.6	9.5	29.5	1500	1433
2000	35	0.0	Good	Bogr	24.6	0.215	149.0	5.7	28.0	1500	1558
2000	35	0.0	Good	Pasm	18.8	0.240	217.0	6.5	28.2	1500	1571
2000	35	0.0	Good	Bogr	22.1	0.160	110.4	4.7	28.5	1500	1550
2000	36	22.4	Good	Pasm	19.7	0.385	271.0	6.5	20.2	1500	98
2000	36	22.4	Good	Bogr	11.9	0.186	252.8	3.5	20.3	1500	777
2000	36	0.0	Good	Pasm	20.4	0.375	259.0	6.6	20.8	1499	1298
2000	36	0.0	Good	Bogr	17.2	0.190	209.0	3.9	21.7	1500	1331
2000	36	11.2	Good	Pasm	25.5	0.417	249.2	8.1	22.9	1500	1254
2000	36	11.2	Good	Bogr	16.0	0.121	135.4	2.8	23.0	1500	1255

Table A-1. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Cond. Class	Plant Species	Photo- synthesis	Conduct- ance	Intercellular CO ₂ Concentration	Trans- piration	Air Temperature	Photosynthetically Active Radiation	
										Chamber	Ambient
2000	36	22.4	Good	Pasm	21.6	0.363	251.8	7.1	22.7	1500	1444
2000	36	22.4	Good	Bogr	16.5	0.129	135.0	3.0	23.0	1500	1476
2000	36	11.2	Fair	Bogr	18.1	0.152	153.2	3.7	23.5	1499	1389
2000	36	0.0	Fair	Bogr	23.8	0.161	106.3	4.2	24.4	1500	1446
2000	36	0.0	Fair	Bogr	17.5	0.175	191.8	4.4	24.0	1501	1514
2000	36	22.4	Fair	Bogr	18.6	0.179	181.2	4.5	24.1	1500	1541
2000	36	22.4	Fair	Bogr	19.7	0.205	195.6	5.2	24.3	1500	1526
2000	36	22.4	Fair	Bogr	27.7	0.256	170.0	6.2	24.3	1500	1494
2000	36	0.0	Fair	Bogr	27.3	0.213	130.9	5.2	24.0	1500	1528
2000	36	11.2	Fair	Bogr	16.4	0.166	184.0	4.4	24.8	1500	1300
2000	36	11.2	Fair	Bogr	13.4	0.120	160.4	3.2	25.1	1500	1628
2000	36	11.2	Good	Pasm	25.9	0.445	248.2	11.6	26.0	1499	1604
2000	36	11.2	Good	Bogr	21.9	0.133	86.9	3.7	25.6	1500	1525
2000	36	11.2	Good	Pasm	26.7	0.379	228.4	9.6	25.8	1499	1493
2000	36	11.2	Good	Bogr	15.8	0.112	115.0	3.2	25.7	1500	1548
2000	36	22.4	Good	Pasm	24.5	0.382	239.6	10.1	26.6	1500	1572
2000	36	22.4	Good	Bogr	26.0	0.155	75.7	4.8	27.2	1500	1680
2000	36	0.0	Good	Pasm	16.9	0.244	230.6	6.8	26.7	1500	1152
2000	36	0.0	Good	Bogr	20.4	0.137	103.2	4.1	26.7	1500	1575
2000	36	0.0	Good	Pasm	17.4	0.212	210.6	6.6	27.8	1500	1515
2000	36	0.0	Good	Bogr	24.4	0.149	70.8	4.9	28.3	1500	1565

Table A-2. Mean ($n = 5$) water use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), nitrogen use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$), percent leaf carbon and nitrogen, and leaf water potential (MPa, $n = 3$) by plot for western wheatgrass (Pasm) and blue grama (Bogr) during the 1999 and 2000 growing seasons at the Central Plains Experimental Range research area.

Year	Week of Year	Soil Removal Level (t/ha)	Condition Class	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
1999	24	22.4	Good	Pasm	1.96	0.035	45.7	1.8	-2.5
1999	24	22.4	Good	Bogr	3.17	0.109	43.0	1.4	-2.0
1999	24	0.0	Good	Pasm	1.73	0.044	45.1	1.8	-2.3
1999	24	0.0	Good	Bogr	3.32	0.064	44.1	1.4	-2.2
1999	24	11.2	Good	Pasm	1.93	0.038	45.3	1.5	-2.4
1999	24	11.2	Good	Bogr	2.98	0.068	44.8	1.5	-1.9
1999	24	22.4	Good	Pasm	1.67	0.049	45.6	1.8	-2.4
1999	24	22.4	Good	Bogr	2.91	0.089	45.9	2.0	-2.2
1999	24	11.2	Fair	Bogr	4.11	0.202	43.8	1.7	-2.1
1999	24	0.0	Fair	Bogr	4.64	0.146	44.3	1.7	-2.3
1999	24	0.0	Fair	Bogr	3.50	0.216	43.2	1.3	-2.0
1999	24	22.4	Fair	Bogr	3.92	0.193	42.4	1.7	-2.0
1999	24	22.4	Fair	Bogr	4.49	0.206	42.8	1.4	-1.7
1999	24	22.4	Fair	Bogr	3.42	0.192	42.8	1.6	-1.4
1999	24	0.0	Fair	Bogr	4.08	0.153	42.6	1.7	-1.9
1999	24	11.2	Fair	Bogr	3.43	0.191	43.7	1.0	-2.0
1999	24	11.2	Fair	Bogr	4.17	0.157	43.7	1.3	-2.0
1999	24	11.2	Good	Pasm	2.41	0.060	45.1	1.4	-2.3
1999	24	11.2	Good	Bogr	4.74	0.153	44.6	1.5	-2.1
1999	24	11.2	Good	Pasm	2.95	0.045	45.5	2.0	-2.3
1999	24	11.2	Good	Bogr	4.76	0.172	45.5	1.5	-2.2
1999	24	22.4	Good	Pasm	2.59	0.051	44.7	1.8	-2.3
1999	24	22.4	Good	Bogr	4.34	0.172	43.2	1.8	-2.7
1999	24	0.0	Good	Pasm	2.78	0.043	45.1	1.9	-2.5
1999	24	0.0	Good	Bogr	4.49	0.218	43.8	1.3	-2.6
1999	24	0.0	Good	Pasm	2.84	0.038	44.2	1.7	-2.4
1999	24	0.0	Good	Bogr	3.92	0.097	44.6	1.6	-2.4
1999	25	22.4	Good	Pasm	2.31	0.040	45.5	1.7	-3.0
1999	25	22.4	Good	Bogr	4.77	0.086	43.6	1.4	-3.4
1999	25	0.0	Good	Pasm	2.20	0.044	44.6	1.6	-3.1
1999	25	0.0	Good	Bogr	4.59	0.103	43.2	1.4	-3.6
1999	25	11.2	Good	Pasm	1.62	0.050	45.4	1.8	-3.3
1999	25	11.2	Good	Bogr	4.80	0.106	44.1	1.5	-3.4
1999	25	22.4	Good	Pasm	2.12	0.044	45.5	1.8	-3.6
1999	25	22.4	Good	Bogr	4.10	0.064	42.5	1.6	-3.3
1999	25	11.2	Fair	Bogr	4.47	0.072	44.7	1.4	-3.7
1999	25	0.0	Fair	Bogr	3.72	0.071	44.4	1.6	-3.6
1999	25	0.0	Fair	Bogr	3.95	0.091	43.7	1.3	-3.6
1999	25	22.4	Fair	Bogr	3.94	0.107	43.3	1.1	-3.8
1999	25	22.4	Fair	Bogr	5.79	0.117	42.9	1.1	-2.9
1999	25	22.4	Fair	Bogr	3.94	0.099	42.8	1.2	-3.2
1999	25	0.0	Fair	Bogr	2.96	0.081	43.0	1.4	-2.9
1999	25	11.2	Fair	Bogr	2.81	0.085	42.8	1.3	-2.6
1999	25	11.2	Fair	Bogr	2.29	0.034	43.3	1.1	-2.7
1999	25	11.2	Good	Pasm	1.35	0.030	44.7	1.8	-3.2

Table A-2. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Condition Class	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
1999	25	11.2	Good	Bogr	2.89	0.042	43.9	1.3	-3.6
1999	25	11.2	Good	Pasm	1.30	0.026	44.8	1.6	-2.5
1999	25	11.2	Good	Bogr	1.89	0.044	42.6	1.2	-2.8
1999	25	22.4	Good	Pasm	1.40	0.034	44.0	1.6	-2.6
1999	25	22.4	Good	Bogr	2.22	0.065	43.3	1.2	-2.9
1999	25	0.0	Good	Pasm	1.16	0.026	44.7	1.5	-2.7
1999	25	0.0	Good	Bogr	1.91	0.025	43.3	1.2	-2.5
1999	25	0.0	Good	Pasm	1.79	0.015	45.4	1.6	-2.7
1999	25	0.0	Good	Bogr	2.23	0.010	43.7	1.7	-3.3
1999	30	22.4	Good	Pasm	2.74	0.024	45.6	1.4	-3.1
1999	30	22.4	Good	Bogr	4.37	0.107	44.6	1.4	-3.3
1999	30	0.0	Good	Pasm	2.00	0.036	45.4	1.2	-3.2
1999	30	0.0	Good	Bogr	4.54	0.098	44.5	1.3	-3.3
1999	30	11.2	Good	Pasm	1.77	0.034	45.4	1.5	-3.4
1999	30	11.2	Good	Bogr	4.17	0.098	43.1	1.5	-2.7
1999	30	22.4	Good	Pasm	2.02	0.031	45.0	1.8	-3.8
1999	30	22.4	Good	Bogr	3.02	0.105	43.9	1.6	-3.3
1999	30	11.2	Fair	Bogr	2.47	0.099	41.4	1.3	-3.9
1999	30	0.0	Fair	Bogr	2.22	0.057	44.3	1.6	-4.3
1999	30	0.0	Fair	Bogr	2.01	0.077	42.7	1.2	-3.4
1999	30	22.4	Fair	Bogr	1.62	0.076	42.6	1.4	-3.9
1999	30	22.4	Fair	Bogr	1.98	0.107	38.7	1.1	-3.8
1999	30	22.4	Fair	Bogr	3.54	0.159	42.0	1.2	-3.2
1999	30	0.0	Fair	Bogr	2.51	0.082	42.3	1.3	-4.1
1999	30	11.2	Fair	Bogr	1.52	0.044	42.5	1.4	-3.1
1999	30	11.2	Fair	Bogr	2.21	0.079	42.8	1.1	-4.2
1999	30	11.2	Good	Pasm	0.97	0.037	42.9	1.7	-3.1
1999	30	11.2	Good	Bogr	1.83	0.073	42.6	1.2	-3.1
1999	30	11.2	Good	Pasm	0.76	0.032	43.8	1.2	-3.6
1999	30	11.2	Good	Bogr	1.17	0.045	42.3	1.4	-3.2
1999	30	22.4	Good	Pasm	0.95	0.031	42.5	1.3	-3.5
1999	30	22.4	Good	Bogr	1.93	0.056	42.7	1.5	-3.2
1999	30	0.0	Good	Pasm	0.80	0.021	44.8	1.7	-3.5
1999	30	0.0	Good	Bogr	1.52	0.043	43.6	1.2	-3.9
1999	30	0.0	Good	Pasm	1.12	0.022	45.7	1.4	-3.7
1999	30	0.0	Good	Bogr	1.86	0.048	42.7	1.3	-4.8
1999	31	22.4	Good	Pasm	2.12	0.050	46.4	1.6	-3.0
1999	31	22.4	Good	Bogr	4.25	0.084	45.6	2.1	-2.2
1999	31	0.0	Good	Pasm	2.23	0.069	45.4	1.6	-2.7
1999	31	0.0	Good	Bogr	4.83	0.118	44.9	1.6	-2.2
1999	31	11.2	Good	Pasm	2.44	0.051	45.4	1.5	-3.0
1999	31	11.2	Good	Bogr	3.84	0.095	43.8	1.5	-2.3
1999	31	22.4	Good	Pasm	2.29	0.055	45.7	1.8	-3.1
1999	31	22.4	Good	Bogr	3.84	0.102	14.5	1.9	-3.0
1999	31	11.2	Fair	Bogr	3.99	0.111	43.3	1.6	-2.4
1999	31	0.0	Fair	Bogr	4.34	0.109	43.0	1.8	-2.6
1999	31	0.0	Fair	Bogr	3.68	0.104	42.7	1.3	-2.7
1999	31	22.4	Fair	Bogr	3.71	0.111	41.5	1.5	-2.3

Table A-2. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Condition Class	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
1999	31	22.4	Fair	Bogr	2.67	0.087	40.8	1.2	-2.6
1999	31	22.4	Fair	Bogr	2.66	0.068	42.3	1.5	-2.4
1999	31	0.0	Fair	Bogr	3.57	0.111	41.4	1.3	-2.5
1999	31	11.2	Fair	Bogr	3.01	0.085	42.5	1.6	-2.6
1999	31	11.2	Fair	Bogr	3.16	0.075	42.8	1.4	-2.1
1999	31	11.2	Good	Pasm	1.75	0.050	42.8	1.6	-2.5
1999	31	11.2	Good	Bogr	3.22	0.073	42.2	1.3	-1.9
1999	31	11.2	Good	Pasm	1.90	0.032	43.7	1.9	-2.3
1999	31	11.2	Good	Bogr	2.59	0.062	42.1	1.5	-1.8
1999	31	22.4	Good	Pasm	1.82	0.043	43.2	1.4	-2.5
1999	31	22.4	Good	Bogr	2.64	0.058	44.0	1.5	-1.9
1999	31	0.0	Good	Pasm	1.29	0.033	43.1	1.4	-2.6
1999	31	0.0	Good	Bogr	1.53	0.033	42.5	1.5	-1.1
1999	31	0.0	Good	Pasm	1.42	0.018	45.8	1.6	-1.9
1999	31	0.0	Good	Bogr	2.64	0.040	43.5	1.7	-1.2
1999	32	22.4	Good	Pasm	4.48	0.056	45.8	1.9	-2.0
1999	32	22.4	Good	Bogr	5.30	0.149	43.9	1.9	-2.0
1999	32	0.0	Good	Pasm	3.72	0.070	46.2	1.9	-2.7
1999	32	0.0	Good	Bogr	5.46	0.156	44.1	1.7	-1.9
1999	32	11.2	Good	Pasm	2.97	0.082	45.9	1.7	-2.6
1999	32	11.2	Good	Bogr	6.45	0.200	45.3	1.5	-2.1
1999	32	22.4	Good	Pasm	2.90	0.056	46.1	2.4	-2.8
1999	32	22.4	Good	Bogr	6.16	0.195	43.7	1.8	-1.9
1999	32	11.2	Fair	Bogr	5.62	0.250	42.9	1.7	-2.5
1999	32	0.0	Fair	Bogr	6.80	0.245	43.4	2.0	-2.3
1999	32	0.0	Fair	Bogr	6.23	0.253	43.3	1.7	-1.9
1999	32	22.4	Fair	Bogr	6.75	0.242	42.3	1.7	-2.1
1999	32	22.4	Fair	Bogr	6.14	0.229	42.0	1.8	-2.1
1999	32	22.4	Fair	Bogr	7.40	0.177	43.1	1.7	-2.4
1999	32	0.0	Fair	Bogr	8.76	0.174	41.6	1.6	-2.5
1999	32	11.2	Fair	Bogr	7.68	0.168	43.0	1.6	-2.1
1999	32	11.2	Fair	Bogr	7.63	0.196	42.1	1.4	-2.4
1999	32	11.2	Good	Pasm	3.31	0.080	44.0	1.9	-2.6
1999	32	11.2	Good	Bogr	6.61	0.248	42.9	1.7	-2.5
1999	32	11.2	Good	Pasm	3.53	0.067	45.2	2.2	-2.2
1999	32	11.2	Good	Bogr	7.34	0.178	41.6	1.8	-2.4
1999	32	22.4	Good	Pasm	3.64	0.083	44.6	1.7	-2.5
1999	32	22.4	Good	Bogr	8.20	0.221	40.9	1.4	-2.7
1999	32	0.0	Good	Pasm	2.80	0.056	45.0	1.8	-2.9
1999	32	0.0	Good	Bogr	4.69	0.137	42.8	1.5	-2.1
1999	32	0.0	Good	Pasm	2.52	0.054	45.8	2.0	-2.6
1999	32	0.0	Good	Bogr	3.94	0.107	43.8	1.8	-2.3
1999	33	22.4	Good	Pasm	1.73	0.053	45.5	1.9	-3.2
1999	33	22.4	Good	Bogr	2.83	0.110	44.4	1.8	-2.6
1999	33	0.0	Good	Pasm	1.66	0.047	45.9	2.1	-3.3
1999	33	0.0	Good	Bogr	1.98	0.097	43.3	1.6	-3.0
1999	33	11.2	Good	Pasm	1.26	0.030	45.4	2.1	-3.3
1999	33	11.2	Good	Bogr	1.48	0.051	43.4	1.5	-2.4

Table A-2. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Condition Class	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
1999	33	22.4	Good	Pasm	1.44	0.038	45.5	2.2	-3.3
1999	33	22.4	Good	Bogr	1.19	0.043	40.8	1.8	-2.4
1999	33	11.2	Fair	Bogr	1.85	0.083	41.7	1.5	-2.5
1999	33	0.0	Fair	Bogr	1.50	0.036	42.6	1.7	-3.0
1999	33	0.0	Fair	Bogr	2.00	0.063	42.0	1.6	-2.5
1999	33	22.4	Fair	Bogr	1.79	0.077	38.9	1.3	-2.7
1999	33	22.4	Fair	Bogr	2.22	0.118	39.5	1.2	-2.9
1999	33	22.4	Fair	Bogr	2.50	0.100	41.2	1.6	-3.2
1999	33	0.0	Fair	Bogr	2.22	0.099	41.5	1.5	-3.0
1999	33	11.2	Fair	Bogr	0.80	0.033	41.9	1.4	-2.6
1999	33	11.2	Fair	Bogr	1.61	0.072	41.3	1.3	-2.7
1999	33	11.2	Good	Pasm	1.19	0.042	43.7	2.3	-2.8
1999	33	11.2	Good	Bogr	2.48	0.108	41.2	1.4	-3.2
1999	33	11.2	Good	Pasm	1.37	0.051	43.8	1.9	-2.8
1999	33	11.2	Good	Bogr	1.90	0.105	40.1	1.6	-2.9
1999	33	22.4	Good	Pasm	1.24	0.048	43.1	1.6	-3.1
1999	33	22.4	Good	Bogr	1.89	0.097	41.9	1.4	-3.1
1999	33	0.0	Good	Pasm	0.93	0.027	44.5	1.7	-3.8
1999	33	0.0	Good	Bogr	0.70	0.033	41.7	1.4	-2.7
1999	33	0.0	Good	Pasm	0.62	0.011	44.9	2.2	-3.3
1999	33	0.0	Good	Bogr	0.88	0.019	41.4	1.6	-3.2
1999	34	22.4	Good	Pasm	2.37	0.057	45.2	2.2	-2.4
1999	34	22.4	Good	Bogr	5.33	0.101	42.7	2.0	-2.4
1999	34	0.0	Good	Pasm	2.26	0.055	44.6	2.1	-2.9
1999	34	0.0	Good	Bogr	4.15	0.088	43.6	1.7	-2.0
1999	34	11.2	Good	Pasm	2.27	0.052	45.2	2.0	-2.8
1999	34	11.2	Good	Bogr	5.10	0.101	41.1	1.5	-2.4
1999	34	22.4	Good	Pasm	2.80	0.047	44.6	2.4	-2.6
1999	34	22.4	Good	Bogr	4.17	0.063	42.1	2.0	-2.2
1999	34	11.2	Fair	Bogr	4.25	0.116	41.9	1.8	-2.1
1999	34	0.0	Fair	Bogr	5.93	0.103	42.2	2.0	-2.2
1999	34	0.0	Fair	Bogr	5.78	0.152	40.4	1.3	-2.5
1999	34	22.4	Fair	Bogr	4.68	0.130	42.1	1.3	-2.5
1999	34	22.4	Fair	Bogr	4.78	0.125	40.6	1.5	-2.6
1999	34	22.4	Fair	Bogr	7.00	0.101	41.4	1.4	-2.1
1999	34	0.0	Fair	Bogr	5.34	0.099	41.8	1.6	-1.9
1999	34	11.2	Fair	Bogr	4.55	0.097	40.8	1.3	-2.0
1999	34	11.2	Fair	Bogr	5.45	0.130	39.6	1.2	-2.4
1999	34	11.2	Good	Pasm	2.81	0.068	43.6	2.1	-2.7
1999	34	11.2	Good	Bogr	5.52	0.135	40.4	1.3	-2.4
1999	34	11.2	Good	Pasm	2.89	0.059	43.5	2.3	-2.7
1999	34	11.2	Good	Bogr	6.42	0.120	40.1	1.5	-2.7
1999	34	22.4	Good	Pasm	2.77	0.061	43.2	1.8	-2.8
1999	34	22.4	Good	Bogr	5.72	0.089	41.8	1.5	-2.1
1999	34	0.0	Good	Pasm	2.75	0.043	43.8	1.8	-2.5
1999	34	0.0	Good	Bogr	4.34	0.037	40.9	1.4	-2.1
1999	34	0.0	Good	Pasm	3.12	0.019	44.1	2.2	-2.4
1999	34	0.0	Good	Bogr	3.87	0.044	41.3	1.6	-2.1

Table A-2. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Condition Class	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
1999	35	22.4	Good	Pasm	3.89	0.040	46.6	2.1	-3.9
1999	35	22.4	Good	Bogr	6.04	0.102	43.5	1.9	-3.0
1999	35	0.0	Good	Pasm	2.84	0.048	46.3	2.2	-3.9
1999	35	0.0	Good	Bogr	4.62	0.132	44.0	1.7	-3.0
1999	35	11.2	Good	Pasm	2.76	0.038	46.2	2.1	-3.5
1999	35	11.2	Good	Bogr	4.69	0.123	42.3	1.1	-3.3
1999	35	22.4	Good	Pasm	2.49	0.044	46.1	2.6	-3.8
1999	35	22.4	Good	Bogr	4.04	0.128	41.7	1.6	-3.6
1999	35	11.2	Fair	Bogr	3.51	0.172	41.9	1.4	-3.1
1999	35	0.0	Fair	Bogr	3.68	0.116	42.7	1.6	-3.1
1999	35	0.0	Fair	Bogr	3.41	0.121	41.3	1.5	-3.4
1999	35	22.4	Fair	Bogr	2.80	0.171	41.5	1.5	-2.6
1999	35	22.4	Fair	Bogr	3.26	0.151	40.9	1.6	-2.7
1999	35	22.4	Fair	Bogr	2.96	0.195	41.8	1.3	-3.4
1999	35	0.0	Fair	Bogr	3.08	0.218	41.5	1.2	-3.3
1999	35	11.2	Fair	Bogr	2.89	0.195	40.4	1.3	-2.6
1999	35	11.2	Fair	Bogr	2.65	0.177	41.9	1.1	-2.9
1999	35	11.2	Good	Pasm	1.95	0.060	45.0	2.3	-2.8
1999	35	11.2	Good	Bogr	3.86	0.180	42.2	1.6	-2.6
1999	35	11.2	Good	Pasm	2.09	0.052	45.6	2.3	-2.5
1999	35	11.2	Good	Bogr	2.93	0.136	40.5	1.5	-3.0
1999	35	22.4	Good	Pasm	1.94	0.061	44.3	1.9	-3.2
1999	35	22.4	Good	Bogr	4.20	0.220	41.5	1.1	-3.4
1999	35	0.0	Good	Pasm	2.08	0.058	45.5	2.1	-3.6
1999	35	0.0	Good	Bogr	2.95	0.130	42.0	1.2	-3.0
1999	35	0.0	Good	Pasm	1.84	0.040	45.8	2.1	-3.4
1999	35	0.0	Good	Bogr	3.45	0.108	42.2	1.9	-2.7
1999	36	22.4	Good	Pasm	7.70	0.059	45.5	2.1	-3.8
1999	36	22.4	Good	Bogr	8.52	0.116	43.0	1.6	-3.2
1999	36	0.0	Good	Pasm	4.19	0.053	46.2	2.3	-4.1
1999	36	0.0	Good	Bogr	5.03	0.084	44.1	1.7	-2.7
1999	36	11.2	Good	Pasm	3.34	0.056	46.2	2.1	-3.9
1999	36	11.2	Good	Bogr	7.43	0.128	43.2	1.4	-3.6
1999	36	22.4	Good	Pasm	4.09	0.043	46.6	2.3	-3.7
1999	36	22.4	Good	Bogr	4.66	0.067	42.4	1.8	-3.4
1999	36	11.2	Fair	Bogr	4.47	0.070	42.5	1.4	-3.0
1999	36	0.0	Fair	Bogr	5.51	0.085	43.0	1.8	-3.7
1999	36	0.0	Fair	Bogr	5.92	0.117	42.3	1.4	-2.6
1999	36	22.4	Fair	Bogr	5.71	0.116	40.5	1.5	-2.8
1999	36	22.4	Fair	Bogr	4.75	0.079	41.6	1.5	-2.5
1999	36	22.4	Fair	Bogr	5.75	0.074	41.4	1.4	N/A
1999	36	0.0	Fair	Bogr	10.80	0.059	42.2	1.2	N/A
1999	36	11.2	Fair	Bogr	5.46	0.092	41.1	1.6	-2.5
1999	36	11.2	Fair	Bogr	6.96	0.157	42.2	1.2	-3.0
1999	36	11.2	Good	Pasm	3.09	0.067	44.9	2.2	-3.6
1999	36	11.2	Good	Bogr	6.11	0.143	41.0	1.4	-3.1
1999	36	11.2	Good	Pasm	3.64	0.078	44.1	1.9	-3.2
1999	36	11.2	Good	Bogr	6.59	0.160	42.1	1.4	-3.6

Table A-2. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Condition Class	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
1999	36	22.4	Good	Pasm	3.58	0.066	43.8	1.9	-4.2
1999	36	22.4	Good	Bogr	7.14	0.185	41.0	1.2	-3.7
1999	36	0.0	Good	Pasm	4.12	0.073	44.7	1.7	-3.8
1999	36	0.0	Good	Bogr	7.44	0.199	42.3	1.4	-4.1
1999	36	0.0	Good	Pasm	4.16	0.059	46.1	2.2	-3.7
1999	36	0.0	Good	Bogr	7.90	0.151	42.1	1.5	-3.1
2000	24	22.4	Good	Pasm	1.76	0.025	46.6	1.7	-4.3
2000	24	22.4	Good	Bogr	1.88	0.077	42.9	1.2	-2.6
2000	24	0.0	Good	Pasm	2.20	0.053	45.8	1.5	-3.5
2000	24	0.0	Good	Bogr	2.85	0.098	45.4	1.3	-3.5
2000	24	11.2	Good	Pasm	2.16	0.053	45.4	1.6	-3.4
2000	24	11.2	Good	Bogr	2.35	0.107	45.0	1.2	-2.6
2000	24	22.4	Good	Pasm	2.26	0.031	46.5	1.8	-3.6
2000	24	22.4	Good	Bogr	2.23	0.033	45.1	1.4	-3.1
2000	24	11.2	Fair	Bogr	2.04	0.068	44.4	1.3	-3.6
2000	24	0.0	Fair	Bogr	1.97	0.077	42.6	1.3	-3.5
2000	24	0.0	Fair	Bogr	2.24	0.114	44.5	0.9	-3.4
2000	24	22.4	Fair	Bogr	2.50	0.113	44.4	1.3	-2.8
2000	24	22.4	Fair	Bogr	1.95	0.093	44.4	1.0	-2.7
2000	24	22.4	Fair	Bogr	2.47	0.136	44.6	1.1	-3.5
2000	24	0.0	Fair	Bogr	2.51	0.118	44.8	1.3	-3.4
2000	24	11.2	Fair	Bogr	2.62	0.150	44.3	1.1	-2.9
2000	24	11.2	Fair	Bogr	2.45	0.183	43.1	1.0	-2.9
2000	24	11.2	Good	Pasm	1.88	0.050	45.7	1.6	-3.3
2000	24	11.2	Good	Bogr	2.40	0.124	43.2	1.1	-2.6
2000	24	11.2	Good	Pasm	2.20	0.023	46.1	1.6	-2.4
2000	24	11.2	Good	Bogr	2.62	0.173	45.1	1.1	-2.1
2000	24	22.4	Good	Pasm	3.73	0.055	46.1	1.9	-2.4
2000	24	22.4	Good	Bogr	4.27	0.164	43.9	1.3	-2.7
2000	24	0.0	Good	Pasm	3.80	0.057	45.9	1.4	-3.5
2000	24	0.0	Good	Bogr	4.57	0.124	44.6	1.3	-2.7
2000	24	0.0	Good	Pasm	1.53	0.009	47.1	1.6	-2.7
2000	24	0.0	Good	Bogr	1.15	0.031	45.5	1.4	-2.5
2000	25	22.4	Good	Pasm	3.91	0.048	46.8	1.6	-2.8
2000	25	22.4	Good	Bogr	1.81	0.028	44.9	1.3	-3.0
2000	25	0.0	Good	Pasm	2.61	0.053	46.0	1.5	-2.9
2000	25	0.0	Good	Bogr	1.77	0.038	45.1	1.3	-2.1
2000	25	11.2	Good	Pasm	3.17	0.071	45.3	1.4	-3.7
2000	25	11.2	Good	Bogr	4.93	0.049	44.4	1.2	-2.6
2000	25	22.4	Good	Pasm	3.92	0.046	47.3	1.7	-3.5
2000	25	22.4	Good	Bogr	4.87	0.042	45.4	1.4	-2.2
2000	25	11.2	Fair	Bogr	6.19	0.065	45.4	1.3	-2.0
2000	25	0.0	Fair	Bogr	5.38	0.058	44.5	1.6	-3.0
2000	25	0.0	Fair	Bogr	9.92	0.097	44.7	1.0	-2.5
2000	25	22.4	Fair	Bogr	7.58	0.087	43.5	1.0	-2.1
2000	25	22.4	Fair	Bogr	7.86	0.101	44.2	1.1	-2.6
2000	25	22.4	Fair	Bogr	5.86	0.098	39.4	1.0	-2.8
2000	25	0.0	Fair	Bogr	6.11	0.079	49.1	1.2	-2.1

Table A-2. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Condition Class	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
2000	25	11.2	Fair	Bogr	3.40	0.079	42.9	1.1	-2.4
2000	25	11.2	Fair	Bogr	6.13	0.118	43.8	0.9	-2.2
2000	25	11.2	Good	Pasm	2.84	0.046	45.0	1.6	-2.6
2000	25	11.2	Good	Bogr	4.80	0.076	43.1	1.1	-2.5
2000	25	11.2	Good	Pasm	3.32	0.053	45.2	1.5	-3.1
2000	25	11.2	Good	Bogr	4.49	0.090	43.0	1.2	-2.5
2000	25	22.4	Good	Pasm	3.13	0.049	45.8	1.5	-3.5
2000	25	22.4	Good	Bogr	3.93	0.059	43.7	1.0	-3.1
2000	25	0.0	Good	Pasm	3.27	0.045	45.3	1.2	-3.4
2000	25	0.0	Good	Bogr	4.52	0.076	43.7	1.1	-2.5
2000	25	0.0	Good	Pasm	3.04	0.040	46.3	1.3	-3.2
2000	25	0.0	Good	Bogr	4.80	0.058	44.1	1.1	-1.9
2000	30	22.4	Good	Pasm	1.80	0.036	42.9	1.8	-3.5
2000	30	22.4	Good	Bogr	9.22	0.102	42.8	1.8	-3.4
2000	30	0.0	Good	Pasm	2.84	0.051	44.4	1.6	-3.9
2000	30	0.0	Good	Bogr	11.78	0.120	42.1	1.4	-3.2
2000	30	11.2	Good	Pasm	2.84	0.055	44.3	1.5	-3.7
2000	30	11.2	Good	Bogr	6.11	0.136	40.8	1.3	-3.3
2000	30	22.4	Good	Pasm	2.27	0.054	44.8	2.2	-3.8
2000	30	22.4	Good	Bogr	4.74	0.143	42.4	2.2	-3.0
2000	30	11.2	Fair	Bogr	3.13	0.105	41.7	1.6	-3.4
2000	30	0.0	Fair	Bogr	3.88	0.088	42.9	2.2	-3.8
2000	30	0.0	Fair	Bogr	2.37	0.152	41.2	1.2	-3.1
2000	30	22.4	Fair	Bogr	1.70	0.119	41.4	1.4	-3.1
2000	30	22.4	Fair	Bogr	2.40	0.169	43.1	1.5	-3.6
2000	30	22.4	Fair	Bogr	1.68	0.159	41.6	1.5	-3.5
2000	30	0.0	Fair	Bogr	2.26	0.170	42.0	1.3	-2.6
2000	30	11.2	Fair	Bogr	2.73	0.189	42.8	1.4	-3.5
2000	30	11.2	Fair	Bogr	2.28	0.158	41.4	1.3	-3.3
2000	30	11.2	Good	Pasm	0.89	0.046	43.9	1.5	-3.9
2000	30	11.2	Good	Bogr	1.77	0.123	42.0	1.5	-3.5
2000	30	11.2	Good	Pasm	0.93	0.048	44.0	1.7	-3.8
2000	30	11.2	Good	Bogr	1.87	0.145	43.1	1.5	-3.6
2000	30	22.4	Good	Pasm	1.18	0.048	45.4	1.9	-3.8
2000	30	22.4	Good	Bogr	2.52	0.167	43.4	1.4	-2.5
2000	30	0.0	Good	Pasm	1.07	0.058	45.2	1.4	-3.9
2000	30	0.0	Good	Bogr	1.89	0.125	42.8	1.5	-2.6
2000	30	0.0	Good	Pasm	0.80	0.030	46.2	1.8	-2.1
2000	30	0.0	Good	Bogr	1.30	0.063	43.9	2.0	-2.5
2000	31	22.4	Good	Pasm	1.80	0.020	47.0	1.8	-3.8
2000	31	22.4	Good	Bogr	1.52	0.025	43.6	1.7	-4.3
2000	31	0.0	Good	Pasm	1.78	0.025	46.7	1.7	-4.1
2000	31	0.0	Good	Bogr	1.12	0.028	44.2	1.6	-4.8
2000	31	11.2	Good	Pasm	2.21	0.036	46.5	1.8	-3.9
2000	31	11.2	Good	Bogr	3.71	0.070	43.5	1.3	-4.2
2000	31	22.4	Good	Pasm	1.95	0.032	46.8	2.2	-3.8
2000	31	22.4	Good	Bogr	2.20	0.056	43.6	2.1	-4.5
2000	31	11.2	Fair	Bogr	2.00	0.063	43.1	1.5	-5.3

Table A-2. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Condition Class	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
2000	31	0.0	Fair	Bogr	4.03	0.090	43.2	1.7	-5.7
2000	31	0.0	Fair	Bogr	2.80	0.063	42.9	1.4	-4.2
2000	31	22.4	Fair	Bogr	3.74	0.085	43.8	1.5	-4.3
2000	31	22.4	Fair	Bogr	1.18	0.051	43.7	1.6	-3.8
2000	31	22.4	Fair	Bogr	0.84	0.029	43.3	1.7	-4.4
2000	31	0.0	Fair	Bogr	0.90	0.049	41.9	1.5	-3.2
2000	31	11.2	Fair	Bogr	5.24	0.146	43.1	1.5	-4.0
2000	31	11.2	Fair	Bogr	2.12	0.078	41.0	1.4	-4.2
2000	31	11.2	Good	Pasm	1.02	0.033	45.6	1.9	-3.9
2000	31	11.2	Good	Bogr	1.45	0.064	43.5	1.6	-2.4
2000	31	11.2	Good	Pasm	1.34	0.049	45.8	2.1	-3.1
2000	31	11.2	Good	Bogr	3.65	0.132	43.2	1.6	-3.4
2000	31	22.4	Good	Pasm	0.77	0.024	47.0	1.8	-3.6
2000	31	22.4	Good	Bogr	2.43	0.069	44.5	1.8	-3.1
2000	31	0.0	Good	Pasm	1.57	0.047	46.7	1.6	-2.0
2000	31	0.0	Good	Bogr	2.45	0.134	44.4	1.6	-2.8
2000	31	0.0	Good	Pasm	1.76	0.042	46.7	2.2	-3.6
2000	31	0.0	Good	Bogr	2.53	0.060	44.1	1.9	-2.7
2000	32	22.4	Good	Pasm	5.88	0.044	45.2	1.7	-4.2
2000	32	22.4	Good	Bogr	9.86	0.028	43.6	1.6	-4.7
2000	32	0.0	Good	Pasm	2.61	0.038	45.7	1.5	-4.2
2000	32	0.0	Good	Bogr	5.74	0.038	43.0	1.4	-5.4
2000	32	11.2	Good	Pasm	3.60	0.033	46.2	1.5	-4.4
2000	32	11.2	Good	Bogr	5.75	0.057	42.7	1.3	-5.4
2000	32	22.4	Good	Pasm	2.79	0.042	45.6	2.1	-4.6
2000	32	22.4	Good	Bogr	4.34	0.059	42.6	2.0	-5.3
2000	32	11.2	Fair	Bogr	1.04	0.017	41.2	1.3	-4.8
2000	32	0.0	Fair	Bogr	2.25	0.042	42.2	1.4	-5.2
2000	32	0.0	Fair	Bogr	1.10	0.031	41.2	1.2	-4.7
2000	32	22.4	Fair	Bogr	2.50	0.049	42.0	1.3	-4.2
2000	32	22.4	Fair	Bogr	3.83	0.059	42.6	1.2	-5.6
2000	32	22.4	Fair	Bogr	6.61	0.107	40.2	1.3	-6.1
2000	32	0.0	Fair	Bogr	1.66	0.031	42.4	1.3	-5.7
2000	32	11.2	Fair	Bogr	2.23	0.038	43.4	1.6	-6.1
2000	32	11.2	Fair	Bogr	2.43	0.080	41.5	1.4	-5.7
2000	32	11.2	Good	Pasm	1.50	0.059	41.3	1.5	-4.1
2000	32	11.2	Good	Bogr	4.01	0.103	44.4	1.7	-5.4
2000	32	11.2	Good	Pasm	2.12	0.054	45.4	1.6	-3.6
2000	32	11.2	Good	Bogr	2.92	0.114	41.0	1.5	-5.3
2000	32	22.4	Good	Pasm	1.21	0.019	46.5	1.8	-3.8
2000	32	22.4	Good	Bogr	2.24	0.064	43.0	1.4	-5.2
2000	32	0.0	Good	Pasm	1.44	0.031	45.4	1.8	-4.2
2000	32	0.0	Good	Bogr	2.37	0.102	41.6	1.3	-4.6
2000	32	0.0	Good	Pasm	1.57	0.020	46.6	2.0	-3.9
2000	32	0.0	Good	Bogr	1.38	0.032	43.7	1.7	-4.6
2000	33	22.4	Good	Pasm	4.43	0.056	46.9	1.8	-2.9
2000	33	22.4	Good	Bogr	8.58	0.102	44.3	1.5	-2.1
2000	33	0.0	Good	Pasm	2.58	0.045	46.4	1.6	-3.2

Table A-2. Continued.

Year	Week of	Soil Removal Level (t/ha)	Condition Class	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
2000	33	0.0	Good	Bogr	6.97	0.043	44.5	1.3	-1.5
2000	33	11.2	Good	Pasm	3.47	0.050	46.8	1.5	-3.5
2000	33	11.2	Good	Bogr	8.78	0.101	43.8	1.3	-2.1
2000	33	22.4	Good	Pasm	3.19	0.039	46.0	2.3	-3.8
2000	33	22.4	Good	Bogr	5.42	0.070	42.9	1.8	-2.3
2000	33	11.2	Fair	Bogr	4.86	0.052	44.2	1.7	-1.9
2000	33	0.0	Fair	Bogr	5.60	0.049	43.6	1.9	-2.5
2000	33	0.0	Fair	Bogr	5.19	0.097	43.1	1.1	-2.1
2000	33	22.4	Fair	Bogr	5.54	0.091	43.3	1.5	-2.7
2000	33	22.4	Fair	Bogr	5.18	0.133	43.1	1.5	-2.6
2000	33	22.4	Fair	Bogr	6.86	0.148	42.4	1.3	-2.8
2000	33	0.0	Fair	Bogr	8.86	0.117	43.3	1.4	-2.5
2000	33	11.2	Fair	Bogr	4.84	0.095	44.2	1.4	-2.3
2000	33	11.2	Fair	Bogr	2.89	0.075	42.2	1.3	-2.4
2000	33	11.2	Good	Pasm	2.81	0.063	44.5	1.7	-3.9
2000	33	11.2	Good	Bogr	3.88	0.100	40.9	1.4	-2.8
2000	33	11.2	Good	Pasm	2.48	0.074	44.4	1.5	-3.4
2000	33	11.2	Good	Bogr	5.68	0.143	42.2	1.4	-3.0
2000	33	22.4	Good	Pasm	2.81	0.056	45.6	1.7	-3.7
2000	33	22.4	Good	Bogr	5.30	0.122	43.3	1.3	-3.3
2000	33	0.0	Good	Pasm	2.73	0.054	45.9	1.8	-4.0
2000	33	0.0	Good	Bogr	4.08	0.116	43.6	1.4	-2.4
2000	33	0.0	Good	Pasm	2.44	0.045	47.1	2.1	-3.9
2000	33	0.0	Good	Bogr	4.35	0.119	43.9	1.9	-2.8
2000	34	22.4	Good	Pasm	1.78	0.042	45.1	2.1	-4.0
2000	34	22.4	Good	Bogr	3.21	0.076	44.4	2.0	-2.7
2000	34	0.0	Good	Pasm	1.80	0.047	46.4	2.2	-3.8
2000	34	0.0	Good	Bogr	3.35	0.086	43.4	1.8	-2.8
2000	34	11.2	Good	Pasm	1.82	0.057	46.7	1.8	-4.8
2000	34	11.2	Good	Bogr	3.83	0.126	44.3	1.5	-3.1
2000	34	22.4	Good	Pasm	1.83	0.042	46.8	2.5	-3.8
2000	34	22.4	Good	Bogr	3.83	0.137	44.0	1.8	-3.0
2000	34	11.2	Fair	Bogr	3.10	0.111	49.1	2.1	-3.2
2000	34	0.0	Fair	Bogr	3.28	0.078	44.7	2.7	-4.3
2000	34	0.0	Fair	Bogr	2.85	0.106	43.7	1.6	-3.4
2000	34	22.4	Fair	Bogr	3.30	0.130	43.9	2.4	-3.7
2000	34	22.4	Fair	Bogr	2.20	0.134	44.5	1.9	-3.3
2000	34	22.4	Fair	Bogr	2.88	0.158	40.9	1.6	-3.4
2000	34	0.0	Fair	Bogr	3.34	0.131	42.1	1.8	-4.0
2000	34	11.2	Fair	Bogr	3.17	0.160	43.4	1.6	-3.4
2000	34	11.2	Fair	Bogr	2.16	0.125	41.4	1.4	-4.1
2000	34	11.2	Good	Pasm	1.29	0.036	45.3	2.4	-4.5
2000	34	11.2	Good	Bogr	2.27	0.089	42.4	1.5	-3.5
2000	34	11.2	Good	Pasm	1.19	0.055	45.0	1.7	-4.2
2000	34	11.2	Good	Bogr	2.17	0.131	43.3	1.6	-4.5
2000	34	22.4	Good	Pasm	1.52	0.056	45.7	2.0	-3.7
2000	34	22.4	Good	Bogr	3.23	0.113	45.1	1.9	-3.4
2000	34	0.0	Good	Pasm	1.09	0.036	45.2	2.0	-5.5

Table A-2. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Condition Class	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
2000	34	0.0	Good	Bogr	1.82	0.108	42.5	1.6	-3.6
2000	34	0.0	Good	Pasm	1.19	0.030	45.0	2.8	-3.9
2000	34	0.0	Good	Bogr	2.71	0.087	44.3	2.0	-4.8
2000	35	22.4	Good	Pasm	2.12	0.037	45.9	2.1	-2.7
2000	35	22.4	Good	Bogr	2.97	0.062	44.4	2.1	-3.1
2000	35	0.0	Good	Pasm	2.22	0.039	46.4	2.4	-3.3
2000	35	0.0	Good	Bogr	3.14	0.066	44.4	2.4	-2.4
2000	35	11.2	Good	Pasm	2.31	0.044	47.0	2.4	-2.6
2000	35	11.2	Good	Bogr	4.84	0.082	44.8	1.6	-2.5
2000	35	22.4	Good	Pasm	2.38	0.030	46.7	2.9	-2.7
2000	35	22.4	Good	Bogr	3.71	0.063	44.2	2.5	-2.7
2000	35	11.2	Fair	Bogr	4.27	0.072	44.6	1.9	-2.5
2000	35	0.0	Fair	Bogr	5.58	0.066	44.5	3.1	-3.0
2000	35	0.0	Fair	Bogr	3.25	0.107	44.8	1.8	-2.8
2000	35	22.4	Fair	Bogr	4.89	0.115	43.9	2.3	-3.3
2000	35	22.4	Fair	Bogr	3.74	0.135	43.5	1.8	-2.7
2000	35	22.4	Fair	Bogr	3.77	0.110	42.0	2.0	-3.4
2000	35	0.0	Fair	Bogr	4.30	0.115	43.8	1.5	-3.3
2000	35	11.2	Fair	Bogr	4.67	0.138	43.2	1.7	-3.8
2000	35	11.2	Fair	Bogr	4.59	0.132	41.0	1.4	-3.3
2000	35	11.2	Good	Pasm	2.36	0.056	44.2	2.1	-4.1
2000	35	11.2	Good	Bogr	4.33	0.133	42.6	1.7	-3.9
2000	35	11.2	Good	Pasm	2.37	0.067	45.5	2.0	-3.5
2000	35	11.2	Good	Bogr	4.53	0.133	44.1	1.9	-3.5
2000	35	22.4	Good	Pasm	2.64	0.058	47.1	1.9	-3.2
2000	35	22.4	Good	Bogr	4.68	0.171	43.6	1.9	-4.2
2000	35	0.0	Good	Pasm	2.56	0.048	46.1	2.2	-3.7
2000	35	0.0	Good	Bogr	4.41	0.118	42.2	1.9	-4.2
2000	35	0.0	Good	Pasm	2.90	0.033	45.9	2.6	-3.6
2000	35	0.0	Good	Bogr	4.91	0.095	43.3	2.1	-3.4
2000	36	22.4	Good	Pasm	3.02	0.036	46.4	2.5	-3.3
2000	36	22.4	Good	Bogr	3.42	0.069	44.0	1.6	-2.0
2000	36	0.0	Good	Pasm	3.27	0.033	46.6	2.8	-3.7
2000	36	0.0	Good	Bogr	4.41	0.076	44.9	2.1	-2.6
2000	36	11.2	Good	Pasm	3.14	0.050	47.0	2.4	-3.2
2000	36	11.2	Good	Bogr	5.93	0.105	44.4	1.4	-2.3
2000	36	22.4	Good	Pasm	3.07	0.036	46.6	2.8	-3.3
2000	36	22.4	Good	Bogr	5.80	0.074	41.9	2.0	-2.6
2000	36	11.2	Fair	Bogr	5.05	0.081	44.3	2.0	-2.7
2000	36	0.0	Fair	Bogr	5.76	0.073	44.3	3.0	-3.4
2000	36	0.0	Fair	Bogr	3.97	0.101	44.1	1.6	-3.3
2000	36	22.4	Fair	Bogr	4.21	0.091	43.4	1.9	-1.9
2000	36	22.4	Fair	Bogr	3.82	0.099	43.7	1.9	-2.7
2000	36	22.4	Fair	Bogr	4.51	0.124	43.3	2.1	-4.0
2000	36	0.0	Fair	Bogr	5.51	0.137	43.9	1.9	-3.0
2000	36	11.2	Fair	Bogr	3.97	0.087	43.7	1.7	-3.0
2000	36	11.2	Fair	Bogr	4.38	0.092	42.7	1.4	-2.4
2000	36	11.2	Good	Pasm	2.32	0.049	46.1	2.3	-3.1

Table A-2. Continued.

Year	Week of Year	Soil Removal Level (t/ha)	Condition Class	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
2000	36	11.2	Good	Bogr	5.86	0.116	43.7	1.7	-2.5
2000	36	11.2	Good	Pasm	2.84	0.053	45.5	2.3	-3.1
2000	36	11.2	Good	Bogr	5.19	0.097	44.7	1.5	-3.1
2000	36	22.4	Good	Pasm	2.44	0.045	45.8	2.5	-3.0
2000	36	22.4	Good	Bogr	5.51	0.128	44.9	1.8	-2.7
2000	36	0.0	Good	Pasm	2.59	0.033	46.8	2.3	-3.6
2000	36	0.0	Good	Bogr	5.05	0.121	43.8	1.5	-2.5
2000	36	0.0	Good	Pasm	2.70	0.031	45.9	2.6	-2.8
2000	36	0.0	Good	Bogr	5.21	0.101	44.2	2.2	-3.0

Table A-3. Soil carbon and nitrogen content (%) at the end of the 1999 and 2000 growing seasons at the Central Plains Experimental Range research area.

Year	Plot	Soil Removal Level (t/ha)	Condition Class	Plot Section ¹	Sample	Carbon (%)	Nitrogen (%)
					Depth (cm)		
1999	1	22.4	Good	A	0-2.5	0.866	0.088
				A	2.5-5.0	0.551	0.069
				A	5.0-10.0	0.398	0.046
				B	0-2.5	0.670	0.083
				B	2.5-5.0	0.453	0.059
				B	5.0-10.0	0.513	0.075
	5	0.0	Good	A	0-2.5	0.746	0.084
				A	2.5-5.0	0.458	0.079
				A	5.0-10.0	0.616	0.090
				B	0-2.5	0.669	0.072
				B	2.5-5.0	0.441	0.062
				B	5.0-10.0	0.591	0.082
	6	11.2	Good	A	0-2.5	0.768	0.079
				A	2.5-5.0	0.662	0.081
				A	5.0-10.0	0.584	0.072
				B	0-2.5	0.775	0.069
				B	2.5-5.0	0.751	0.079
				B	5.0-10.0	0.714	0.088
	10	22.4	Good	A	0-2.5	1.207	0.107
				A	2.5-5.0	0.760	0.072
				A	5.0-10.0	0.524	0.050
				B	0-2.5	0.617	0.057
				B	2.0-5.0	0.444	0.052
				B	5.0-10.0	0.386	0.050
	12	11.2	Fair	A	0-2.5	0.938	0.097
				A	2.5-5.0	0.647	0.064
				A	5.0-10.0	0.765	0.095
				B	0-2.5	0.957	0.106
				B	2.5-5.0	0.676	0.066
				B	5.0-10.0	0.917	0.102
56	0.0	Fair	A	0-2.5	1.681	0.163	
			A	2.5-5.0	0.667	0.073	
			A	5.0-10.0	0.571	0.081	
			B	0-2.5	2.117	0.203	
			B	2.5-5.0	0.927	0.092	
			B	5.0-10.0	0.733	0.083	
15	0.0	Fair	A	0-2.5	0.706	0.071	
			A	2.5-5.0	0.589	0.078	
			A	5.0-10.0	0.879	0.098	

Table A-3. Continued.

Year	Plot	Soil Removal	Condition	Plot	Sample	Carbon (%)	Nitrogen (%)
		Level (t/ha)	Class	Section ¹	Depth (cm)		
1999	15	0.0	Fair	B	0-2.5	0.695	0.064
				B	2.5-5.0	0.609	0.055
				B	5.0-10.0	0.689	0.076
	20	22.4	Fair	A	0-2.5	0.827	0.080
				A	2.5-5.0	0.575	0.059
				A	5.0-10.0	0.727	0.068
				B	0-2.5	1.172	0.105
				B	2.5-5.0	0.585	0.067
				B	5.0-10.0	0.918	0.106
	23	22.4	Fair	A	0-2.5	0.713	0.078
				A	2.5-5.0	0.874	0.093
				A	5.0-10.0	0.739	0.097
				B	0-2.5	0.626	0.057
				B	2.5-5.0	0.609	0.065
				B	5.0-10.0	0.675	0.091
	24	22.4	Fair	A	0-2.5	0.865	0.090
				A	2.5-5.0	0.539	0.058
				A	5.0-10.0	0.619	0.084
				B	0-2.5	1.076	0.108
				B	2.5-5.0	0.705	0.084
				B	5.0-10.0	0.747	0.086
	25	0.0	Fair	A	0-2.5	0.894	0.080
				A	2.5-5.0	0.342	0.039
				A	5.0-10.0	0.510	0.072
				B	0-2.5	0.532	0.060
				B	2.5-5.0	0.555	0.063
				B	5.0-10.0	0.811	0.098
	30	11.2	Fair	A	0-2.5	0.803	0.080
				A	2.5-5.0	0.656	0.082
				A	5.0-10.0	0.660	0.086
				B	0-2.5	0.927	0.083
				B	2.5-5.0	0.788	0.076
				B	5.0-10.0	0.649	0.068
33	11.2	Fair	A	0-2.5	1.380	0.132	
			A	2.5-5.0	0.771	0.088	
			A	5.0-10.0	0.581	0.072	
			B	0-2.5	1.141	0.117	
			B	2.5-5.0	0.885	0.107	
			B	5.0-10.0	0.660	0.083	
54	11.2	Good	A	0-2.5	1.377	0.122	
			A	2.5-5.0	0.639	0.080	

Table A-3. Continued.

Year	Plot	Soil Removal	Condition	Plot	Sample	Carbon (%)	Nitrogen (%)
		Level (t/ha)	Class	Section ¹	Depth (cm)		
1999	54	11.2	Good	A	5.0-10.0	0.585	0.073
				B	0-2.5	0.939	0.102
				B	2.5-5.0	0.833	0.096
				B	5.0-10.0	0.687	0.085
	45	11.2	Good	A	0-2.5	0.807	0.083
				A	2.5-5.0	0.886	0.099
				A	5.0-10.0	0.738	0.085
				B	0-2.5	0.742	0.071
				B	2.5-5.0	0.443	0.048
				B	5.0-10.0	0.597	0.074
	43	22.4	Good	A	0-2.5	0.846	0.077
				A	2.5-5.0	0.399	0.057
				A	5.0-10.0	0.663	0.091
				B	0-2.5	0.983	0.092
				B	2.5-5.0	0.576	0.055
				B	5.0-10.0	0.627	0.084
				47	0.0	Good	A
	A	2.5-5.0	0.496				0.051
	A	5.0-10.0	0.388				0.056
	B	0-2.5	0.511				0.059
B	2.5-5.0	0.492	0.046				
B	5.0-10.0	0.540	0.070				
40	0.0	Good	A	0-2.5	0.779	0.084	
			A	2.5-5.0	0.541	0.065	
			A	5.0-10.0	0.504	0.054	
			B	0-2.5	1.432	0.112	
			B	2.5-5.0	0.577	0.050	
			B	5.0-10.0	0.340	0.041	
			2000	1	22.4	Good	A
A	2.5-5.0	0.481					0.022
A	5.0-10.0	0.955					0.071
B	0-2.5	0.879					0.106
B	2.5-5.0	0.651					0.086
B	5.0-10.0	0.468					0.056
5	0.0	Good		A	0-2.5	0.680	0.060
				A	2.5-5.0	0.867	0.058
				A	5.0-10.0	1.118	0.093
				B	0-2.5	1.510	0.134
				B	2.5-5.0	0.582	0.084
				B	5.0-10.0	0.757	0.111
				6	11.2	Good	A

Table A-3. Continued.

Year	Plot	Soil Removal	Condition	Plot	Sample	Carbon (%)	Nitrogen (%)
		Level (t/ha)	Class	Section ¹	Depth (cm)		
2000	6	11.2	Good	A	2.5-5.0	0.733	0.051
				A	5.0-10.0	0.601	0.054
				B	0-2.5	0.563	0.078
				B	2.5-5.0	0.648	0.091
				B	5.0-10.0	0.630	0.083
	10	22.4	Good	A	0-2.5	0.926	0.067
				A	2.5-5.0	0.678	0.044
				A	5.0-10.0	0.500	0.035
				B	0-2.5	0.843	0.079
				B	2.0-5.0	0.661	0.090
				B	5.0-10.0	0.350	0.039
				12	11.2	Fair	A
	A	2.5-5.0	0.862				0.071
	A	5.0-10.0	0.803				0.073
	B	0-2.5	0.831				0.114
	B	2.5-5.0	0.440				0.070
	B	5.0-10.0	0.625				0.077
	56	0.0	Fair				A
				A	2.5-5.0	0.684	0.078
				A	5.0-10.0	0.708	0.081
				B	0-2.5	1.859	0.205
				B	2.5-5.0	0.553	0.073
				B	5.0-10.0	0.688	0.069
				15	0.0	Fair	A
	A	2.5-5.0	0.711				0.065
	A	5.0-10.0	0.787				0.094
	B	0-2.5	0.703				0.095
	B	2.5-5.0	0.705				0.097
B	5.0-10.0	0.615	0.080				
20	22.4	Fair	A				0-2.5
			A	2.5-5.0	0.588	0.080	
			A	5.0-10.0	0.728	0.089	
			B	0-2.5	0.964	0.143	
			B	2.5-5.0	0.964	0.100	
			B	5.0-10.0	0.855	0.126	
			23	22.4	Fair	A	0-2.5
A	2.5-5.0	0.909				0.090	
A	5.0-10.0	0.856				0.081	
B	0-2.5	0.682				0.069	
B	2.5-5.0	0.706				0.109	
B	5.0-10.0	0.737				0.120	

Table A-3. Continued.

Year	Plot	Soil Removal	Condition	Plot	Sample	Carbon (%)	Nitrogen (%)
		Level (t/ha)	Class	Section ¹	Depth (cm)		
2000	24	22.4	Fair	A	0-2.5	0.856	0.084
				A	2.5-5.0	0.810	0.099
				A	5.0-10.0	0.870	0.096
				B	0-2.5	1.195	0.139
				B	2.5-5.0	1.140	0.143
				B	5.0-10.0	0.666	0.126
	25	0.0	Fair	A	0-2.5	0.798	0.072
				A	2.5-5.0	0.679	0.062
				A	5.0-10.0	0.829	0.082
				B	0-2.5	0.902	0.110
				B	2.5-5.0	0.545	0.087
				B	5.0-10.0	0.797	0.131
	30	11.2	Fair	A	0-2.5	0.876	0.090
				A	2.5-5.0	0.843	0.093
				A	5.0-10.0	0.852	0.079
				B	0-2.5	0.761	0.086
				B	2.5-5.0	0.726	0.087
				B	5.0-10.0	0.489	0.068
	33	11.2	Fair	A	0-2.5	1.344	0.125
				A	2.5-5.0	1.107	0.109
				A	5.0-10.0	0.906	0.091
				B	0-2.5	1.087	0.135
				B	2.5-5.0	0.856	0.123
				B	5.0-10.0	0.668	0.081
	54	11.2	Good	A	0-2.5	1.403	0.138
				A	2.5-5.0	1.021	0.107
				A	5.0-10.0	0.901	0.089
				B	0-2.5	1.182	0.134
				B	2.5-5.0	0.880	0.094
				B	5.0-10.0	0.743	0.106
45	11.2	Good	A	0-2.5	1.434	0.135	
			A	2.5-5.0	1.124	0.114	
			A	5.0-10.0	0.742	0.083	
			B	0-2.5	0.871	0.116	
			B	2.5-5.0	0.812	0.118	
			B	5.0-10.0	0.727	0.094	
43	22.4	Good	A	0-2.5	1.365	0.127	
			A	2.5-5.0	0.724	0.076	
			A	5.0-10.0	0.879	0.101	
			B	0-2.5	1.089	0.122	
			B	2.5-5.0	0.519	0.079	

Table A-3. Continued.

Year	Plot	Soil Removal	Condition	Plot	Sample	Carbon (%)	Nitrogen (%)			
		Level (t/ha)	Class	Section ¹	Depth (cm)					
2000	43	22.4	Good	B	5.0-10.0	0.693	0.108			
				A	0-2.5	0.859	0.081			
	47	0.0	Good	A	2.5-5.0	0.705	0.069			
				A	5.0-10.0	0.656	0.059			
				B	0-2.5	0.610	0.077			
				B	2.5-5.0	0.567	0.087			
				B	5.0-10.0	0.601	0.049			
				40	0.0	Good	A	0-2.5	0.791	0.080
							A	2.5-5.0	0.639	0.065
							A	5.0-10.0	0.515	0.060
							B	0-2.5	1.094	0.111
				40	0.0	Good	B	2.5-5.0	0.630	0.082
	B	5.0-10.0	0.563				0.114			

¹Plots were divided into upslope and downslope halves for sampling soil carbon and nitrogen; where A = upslope section and B = downslope section.

Table A-4. Weekly average (n = 18) soil water content (%) by sample depth (cm) for the 1999 and 2000 growing seasons at the Central Plains Experimental Range research area.

Year	Week of Year	Sample Depth	Soil Water Content
1999	24	0.0-5.0	8.43
	24	5.0-10.0	9.43
	25	0.0-5.0	2.45
	25	5.0-10.0	5.64
	30	0.0-5.0	3.66
	30	5.0-10.0	6.54
	31	0.0-5.0	10.71
	31	5.0-10.0	12.75
	32	0.0-5.0	9.39
	32	5.0-10.0	12.83
	33	0.0-5.0	4.65
	33	5.0-10.0	8.40
	34	0.0-5.0	12.54
	34	5.0-10.0	10.32
	35	0.0-5.0	9.59
	35	5.0-10.0	11.43
	36	0.0-5.0	5.93
	36	5.0-10.0	8.93
2000	24	0.0-5.0	4.74
	24	5.0-10.0	4.13
	25	0.0-5.0	9.84
	25	5.0-10.0	7.58
	30	0.0-5.0	4.81
	30	5.0-10.0	5.17
	31	0.0-5.0	3.09
	31	5.0-10.0	4.43
	32	0.0-5.0	1.56
	32	5.0-10.0	2.73
	33	0.0-5.0	11.78
	33	5.0-10.0	12.82
	34	0.0-5.0	7.13
	34	5.0-10.0	10.28
	35	0.0-5.0	4.67
	35	5.0-10.0	6.33
	36	0.0-5.0	3.63
	36	5.0-10.0	5.12

Table A-5. Repeated measures analysis of variance of weekly (period) net photosynthetic rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of western wheatgrass and blue grama (Species) leaves in the good condition class plots by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Species	1	1304.9	1304.9	3.83	0.074
Treatment	2	3530.3	1765.1	5.19	0.024
Species*Treatment	2	224.3	112.1	0.33	0.726
Plot(Species Treatment) ¹	12	4083.9	340.3	1.10	0.433
Year	1	866.8	866.8	3.01	0.109
Species*Year	1	40.5	40.5	0.14	0.714
Treatment*Year	2	406.9	203.5	0.71	0.513
Species*Treatment*Year	2	78.8	39.4	0.14	0.874
Year*Plot(Species Treatment)	12	3461.4	288.5	2.87	0.002
Period	8	24084.4	3010.6	24.52	0.001
Species*Period	8	3902.4	487.8	3.97	0.001
Treatment*Period	16	2244.3	140.3	1.14	0.329
Species*Treatment*Period	16	932.5	58.3	0.47	0.954
Period*Plot(Species Treatment)	96	11787.4	122.8	1.22	0.164
Year*Period	8	19399.3	2424.9	24.13	0.001
Species*Year*Period	8	1934.3	241.8	2.41	0.021
Treatment*Year*Period	16	1842.3	115.1	1.15	0.326
Species*Treatment*Year*Period	16	262.4	16.4	0.16	1.000
Year*Period*Plot(Species Treatment)	96	9645.7	100.5	4.54	0.001
Error	1296	28670.7	28670.7	22.12	
Total	1619	118703.4			

¹Plot within Species and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table A-6. Repeated measures analysis of variance of weekly (period) transpiration rates ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) of western wheatgrass and blue grama (Species) leaves in the good condition class plots by treatment (0, 11.2, and 22.4 t ha^{-1} soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Species	1	6844.0	6844.0	46.83	0.001
Treatment	2	546.5	273.2	1.87	0.196
Species*Treatment	2	310.1	155.0	1.06	0.377
Plot(Species Treatment) ¹	12	1753.8	146.2	3.04	0.033
Year	1	16.2	16.2	0.34	0.569
Species*Year	1	0.4	0.4	0.01	0.930
Treatment*Year	2	92.2	46.1	0.98	0.405
Species*Treatment*Year	2	3.5	1.8	0.04	0.963
Year*Plot(Species Treatment)	12	566.3	47.2	2.45	0.008
Period	8	2814.0	351.8	17.44	0.001
Species*Period	8	710.0	88.8	4.40	0.001
Treatment*Period	16	127.0	7.9	0.39	0.981
Species*Treatment*Period	16	73.2	4.6	0.23	0.999
Period*Plot(Species Treatment)	96	1936.5	20.2	1.05	0.413
Year*Period	8	3607.1	450.9	23.38	0.001
Species*Year*Period	8	194.7	24.3	1.26	0.272
Treatment*Year*Period	16	311.8	19.5	1.01	0.453
Species*Treatment*Year*Period	16	138.1	8.6	0.45	0.965
Year*Period*Plot(Species Treatment)	96	1851.1	19.3	5.58	0.001
Error	1296	4475.0	3.45		
Total	1619	26371.5			

¹Plot within Species and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table A-7. Repeated measures analysis of variance of weekly (period) intercellular CO₂ concentration ($\mu\text{mol CO}_2 \text{ mol air}^{-1}$) of western wheatgrass and blue grama (Species) leaves in the good condition class plots by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Species	1	3685504	3685504	356.95	0.001
Treatment	2	87572	43786	4.24	0.040
Species*Treatment	2	54600	27300	2.64	0.112
Plot(Species Treatment) ¹	12	123900	10325	1.04	0.493
Year	1	16000	16000	2.07	0.176
Species*Year	1	360	360	0.05	0.833
Treatment*Year	2	553	276	0.04	0.965
Species*Treatment*Year	2	1592	796	0.10	0.903
Year*Plot(Species Treatment)	12	92957	7746	0.45	0.940
Period	8	653228	81653	4.18	0.001
Species*Period	8	294045	36756	1.88	0.072
Treatment*Period	16	392194	24512	1.26	0.242
Species*Treatment*Period	16	119850	7491	0.38	0.984
Period*Plot(Species Treatment)	96	1874998	19531	1.13	0.281
Year*Period	8	638071	79759	4.60	0.001
Species*Year*Period	8	272846	34106	1.97	0.059
Treatment*Year*Period	16	180757	11297	0.65	0.834
Species*Treatment*Year*Period	16	105952	6622	0.38	0.984
Year*Period*Plot(Species Treatment)	96	1665571	17350	6.34	0.001
Error	1296	3545408	2736		
Total	1619	13805955			

¹Plot within Species and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table A-8. Repeated measures analysis of variance of weekly (period) nitrogen use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$) of western wheatgrass and blue grama (Species) leaves in the good condition class plots by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Species	1	1.168	1.168	79.45	0.001
Treatment	2	0.086	0.043	2.92	0.093
Species*Treatment	2	0.017	0.008	0.57	0.580
Plot(Species Treatment) ¹	12	0.176	0.015	2.09	0.092
Year	1	0.027	0.027	4.26	0.061
Species*Year	1	0.010	0.010	1.67	0.221
Treatment*Year	2	0.013	0.007	1.06	0.375
Species*Treatment*Year	2	0.004	0.002	0.28	0.758
Year*Plot(Species Treatment)	12	0.075	0.006	2.57	0.005
Period	8	0.239	0.030	9.25	0.001
Species*Period	8	0.144	0.018	5.57	0.001
Treatment*Period	16	0.035	0.002	0.68	0.811
Species*Treatment*Period	16	0.019	0.001	0.36	0.988
Period*Plot(Species Treatment)	96	0.311	0.003	1.33	0.080
Year*Period	8	0.338	0.042	17.43	0.001
Species*Year*Period	8	0.110	0.014	5.67	0.001
Treatment*Year*Period	16	0.027	0.002	0.69	0.801
Species*Treatment*Year*Period	16	0.017	0.001	0.44	0.966
Year*Period*Plot(Species Treatment)	96	0.233	0.002	4.30	0.001
Error	1296	0.732	0.001		
Total	1619	3.780			

¹Plot within Species and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table A-9. Repeated measures analysis of variance of weekly (period) water use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) of western wheatgrass and blue grama (Species) leaves in the good condition class plots by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Species	1	1144.80	1144.80	57.01	0.001
Treatment	2	60.18	30.09	1.50	0.262
Species*Treatment	2	14.94	7.47	0.37	0.697
Plot(Species Treatment) ¹	12	240.97	20.08	5.02	0.017
Year	1	0.70	0.70	0.20	0.665
Species*Year	1	0.18	0.18	0.05	0.824
Treatment*Year	2	0.75	0.38	0.11	0.900
Species*Treatment*Year	2	1.28	0.64	0.18	0.837
Year*Plot(Species Treatment)	12	42.65	3.55	0.51	0.902
Period	8	819.41	102.43	13.87	0.001
Species*Period	8	105.23	13.15	1.78	0.090
Treatment*Period	16	89.14	5.57	0.75	0.732
Species*Treatment*Period	16	38.24	2.39	0.32	0.993
Period*Plot(Species Treatment)	96	708.90	7.38	1.06	0.380
Year*Period	8	815.66	101.96	14.70	0.001
Species*Year*Period	8	147.68	18.46	2.66	0.011
Treatment*Year*Period	16	57.80	3.61	0.52	0.930
Species*Treatment*Year*Period	16	31.16	1.95	0.28	0.997
Year*Period*Plot(Species Treatment)	96	665.95	6.94	7.22	0.001
Error	1296	1245.73	0.96		
Total	1619	6231.34			

¹Plot within Species and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table A-10. Repeated measures analysis of variance of weekly (period) leaf water potential (MPa) of western wheatgrass and blue grama (Species) leaves in the good condition class plots by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Species	1	2.228	2.228	22.68	0.001
Treatment	2	0.025	0.013	0.13	0.881
Species*Treatment	2	0.116	0.058	0.59	0.570
Plot(Species Treatment) ¹	12	1.180	0.098	6.25	0.113
Year	1	6.870	6.870	419.19	0.001
Species*Year	1	0.020	0.020	1.24	0.288
Treatment*Year	2	0.197	0.099	6.02	0.015
Species*Treatment*Year	2	0.004	0.002	0.13	0.880
Year*Plot(Species Treatment)	12	0.197	0.016	0.26	0.993
Period	8	5.696	0.712	11.51	0.001
Species*Period	8	1.977	0.247	4.00	0.001
Treatment*Period	16	1.407	0.088	1.42	0.148
Species*Treatment*Period	16	0.528	0.033	0.53	0.923
Period*Plot(Species Treatment)	96	5.938	0.619	0.99	0.521
Year*Period	8	19.579	2.447	39.15	0.001
Species*Year*Period	8	3.081	0.385	6.16	0.001
Treatment*Year*Period	16	1.158	0.072	1.16	0.316
Species*Treatment*Year*Period	16	0.440	0.028	0.44	0.967
Year*Period*Plot(Species Treatment)	96	6.001	0.063	5.91	0.001
Error	648	6.860	0.011		
Total	971	63.502			

¹Plot within Species and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table A-11. Repeated measures analysis of variance of weekly (period) leaf carbon content (mg g^{-1} leaf) of western wheatgrass and blue grama (Species) leaves in the good condition class plots by treatment (0, 11.2, and 22.4 t ha^{-1} soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Species	1	4298.25	4298.25	47.96	0.001
Treatment	2	170.21	85.11	0.95	0.414
Species*Treatment	2	65.91	32.96	0.37	0.700
Plot(Species Treatment) ¹	12	1075.54	89.63	1.98	0.130
Year	1	798.84	798.84	18.53	0.001
Species*Year	1	11.03	11.03	0.26	0.622
Treatment*Year	2	95.61	47.81	1.11	0.361
Species*Treatment*Year	2	35.19	17.60	0.41	0.674
Year*Plot(Species Treatment)	12	517.33	43.11	1.31	0.225
Period	8	557.84	69.73	1.99	0.056
Species*Period	8	366.55	45.82	1.31	0.249
Treatment*Period	16	387.27	24.20	0.69	0.797
Species*Treatment*Period	16	493.34	30.83	0.88	0.594
Period*Plot(Species Treatment)	96	3364.66	35.05	1.07	0.377
Year*Period	8	674.01	84.25	2.56	0.014
Species*Year*Period	8	128.47	16.06	0.49	0.862
Treatment*Year*Period	16	367.78	22.99	0.70	0.788
Species*Treatment*Year*Period	16	373.21	23.33	0.71	0.778
Error ²	96	3156.35	32.88		
Total	323	16937.41			

¹Plot within Species and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

²Residual error term includes the Year*Period*Plot(Species Treatment) variance component because insufficient error degrees of freedom.

Table A-12. Repeated measures analysis of variance of weekly (period) leaf nitrogen content (mg g^{-1} leaf) of western wheatgrass and blue grama (Species) leaves in the good condition class plots by treatment (0, 11.2, and 22.4 t ha^{-1} soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Species	1	86.51	86.51	22.42	0.001
Treatment	2	15.70	7.85	2.03	0.173
Species*Treatment	2	2.49	1.25	0.32	0.730
Plot(Species Treatment) ¹	12	46.30	3.86	8.65	0.001
Year	1	1.95	1.95	4.77	0.050
Species*Year	1	0.25	0.025	0.06	0.809
Treatment*Year	2	4.16	2.08	5.08	0.025
Species*Treatment*Year	2	0.65	0.33	0.80	0.474
Year*Plot(Species Treatment)	12	4.91	0.41	1.68	0.083
Period	8	114.42	14.30	50.99	0.001
Species*Period	8	24.94	3.12	11.12	0.001
Treatment*Period	16	5.33	0.33	1.19	0.292
Species*Treatment*Period	16	4.42	0.28	0.99	0.479
Period*Plot(Species Treatment)	96	26.92	0.28	1.15	0.247
Year*Period	8	38.42	4.80	19.70	0.001
Species*Year*Period	8	6.11	0.76	3.13	0.003
Treatment*Year*Period	16	3.42	0.21	0.88	0.598
Species*Treatment*Year*Period	16	3.58	0.22	0.92	0.551
Error ²	96	23.40	0.24		
Total	323	413.67			

¹Plot within Species and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

²Residual error term includes the Year*Period*Plot(Species Treatment) variance component because insufficient error degrees of freedom.

Table A-13. Repeated measures analysis of variance of weekly (period) net photosynthetic rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of blue grama leaves in the good and fair condition class (Class) plots by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Class	1	576.8	576.8	2.96	0.111
Treatment	2	1284.3	642.2	3.30	0.072
Class*Treatment	2	824.7	412.3	2.12	0.163
Plot(Class Treatment) ¹	12	2338.5	194.9	0.48	0.895
Year	1	2425.4	2425.4	6.22	0.028
Class*Year	1	180.7	180.7	0.46	0.509
Treatment*Year	2	102.2	51.1	0.13	0.878
Class*Treatment*Year	2	458.6	229.3	0.59	0.571
Year*Plot(Class Treatment)	12	4679.5	390.0	3.70	0.001
Period	8	25244.5	3155.6	25.49	0.001
Class*Period	8	1932.7	241.6	1.95	0.061
Treatment*Period	16	1787.3	111.7	0.90	0.568
Class*Treatment*Period	16	1653.4	103.3	0.83	0.644
Period*Plot(Class Treatment)	96	11882.7	123.8	1.17	0.216
Year*Period	8	39932.6	4991.6	47.36	0.001
Class*Year*Period	8	2407.8	301.0	2.86	0.007
Treatment*Year*Period	16	1281.9	80.1	0.76	0.725
Class*Treatment*Year*Period	16	1198.6	74.9	0.71	0.777
Year*Period*Plot(Class Treatment)	96	10117.3	105.4	3.59	0.001
Error	1296	38061.0	29.4		
Total	1619	148370.4			

¹Plot within Class and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table A-14. Repeated measures analysis of variance of weekly (period) transpiration rates ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) of blue grama leaves in the good and fair condition class (Class) plots by treatment (0, 11.2, and 22.4 t ha^{-1} soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Class	1	103.06	103.06	2.26	0.158
Treatment	2	55.90	27.95	0.61	0.557
Class*Treatment	2	97.52	48.76	1.07	0.373
Plot(Class Treatment) ¹	12	546.55	45.56	1.43	0.283
Year	1	1.61	1.61	0.05	0.830
Class*Year	1	4.59	4.59	0.14	0.717
Treatment*Year	2	12.02	6.01	0.18	0.837
Class*Treatment*Year	2	65.87	32.94	0.99	0.400
Year*Plot(Class Treatment)	12	399.51	33.29	3.64	0.001
Period	8	2681.81	335.23	43.09	0.001
Class*Period	8	186.06	23.26	2.99	0.005
Treatment*Period	16	112.24	7.02	0.90	0.569
Class*Treatment*Period	16	106.82	6.68	0.86	0.618
Period*Plot(Class Treatment)	96	746.92	7.78	0.85	0.786
Year*Period	8	2885.51	360.69	39.40	0.001
Class*Year*Period	8	117.77	14.72	1.61	0.132
Treatment*Year*Period	16	101.62	6.35	0.69	0.794
Class*Treatment*Year*Period	16	98.16	6.14	0.67	0.816
Year*Period*Plot(Class Treatment)	96	878.8	9.15	3.94	0.001
Error	1296	3011.11	2.32		
Total	1619	12213.45			

¹Plot within Class and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table A-15. Repeated measures analysis of variance of weekly (period) intercellular CO₂ concentration ($\mu\text{mol CO}_2 \text{ mol air}^{-1}$) of blue grama leaves in the good and fair condition class (Class) plots by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Class	1	0	0	0.00	0.997
Treatment	2	28786	14393	1.05	0.380
Class*Treatment	2	147396	73698	5.37	0.022
Plot(Class Treatment) ¹	12	164723	13727	0.63	0.789
Year	1	23379	23379	1.37	0.265
Class*Year	1	55	55	0.00	0.956
Treatment*Year	2	4514	2257	0.13	0.878
Class*Treatment*Year	2	4667	2333	0.14	0.874
Year*Plot(Class Treatment)	12	205182	17098	0.68	0.771
Period	8	897086	112136	3.73	0.001
Class*Period	8	745132	93141	3.09	0.004
Treatment*Period	16	547187	34199	1.14	0.334
Class*Treatment*Period	16	372730	23296	0.77	0.711
Period*Plot(Class Treatment)	96	2889369	30098	1.19	0.198
Year*Period	8	751223	93903	3.71	0.001
Class*Year*Period	8	368706	46088	1.82	0.082
Treatment*Year*Period	16	424643	26540	1.05	0.414
Class*Treatment*Year*Period	16	157144	9822	0.39	0.982
Year*Period*Plot(Class Treatment)	96	2428921	25301	4.68	0.001
Error	1296	7006049	5406		
Total	1619	17166892			

¹Plot within Class and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table A-16. Repeated measures analysis of variance of weekly (period) nitrogen use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$) of blue grama leaves in the good and fair condition class (Class) plots by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Class	1	0.073	0.073	4.06	0.067
Treatment	2	0.079	0.039	2.20	0.154
Class*Treatment	2	0.045	0.022	1.25	0.322
Plot(Class Treatment) ¹	12	0.215	0.018	1.36	0.296
Year	1	0.142	0.142	11.33	0.006
Class*Year	1	0.013	0.013	1.00	0.337
Treatment*Year	2	0.010	0.005	0.40	0.677
Class*Treatment*Year	2	0.010	0.005	0.39	0.689
Year*Plot(Class Treatment)	12	0.150	0.013	3.24	0.001
Period	8	0.729	0.091	19.91	0.001
Class*Period	8	0.103	0.013	2.80	0.008
Treatment*Period	16	0.068	0.004	0.92	0.544
Class*Treatment*Period	16	0.037	0.002	0.51	0.937
Period*Plot(Class Treatment)	96	0.439	0.005	1.18	0.204
Year*Period	8	1.093	0.137	35.36	0.001
Class*Year*Period	8	0.075	0.009	2.42	0.020
Treatment*Year*Period	16	0.038	0.002	0.62	0.858
Class*Treatment*Year*Period	16	0.043	0.003	0.70	0.786
Year*Period*Plot(Class Treatment)	96	0.371	0.004	3.24	0.001
Error	1296	1.547	0.001		
Total	1619	5.279			

¹Plot within Class and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table A-17. Repeated measures analysis of variance of weekly (period) water use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) of blue grama leaves in the good and fair condition class (Class) plots by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Class	1	5.09	5.09	0.31	0.589
Treatment	2	14.94	7.47	0.45	0.647
Class*Treatment	2	71.81	35.91	2.17	0.157
Plot(Class Treatment) ¹	12	198.33	16.53	3.00	0.049
Year	1	15.82	15.82	3.72	0.078
Class*Year	1	7.36	7.36	1.73	0.213
Treatment*Year	2	0.31	0.15	0.04	0.965
Class*Treatment*Year	2	2.50	1.25	0.29	0.750
Year*Plot(Class Treatment)	12	51.05	4.25	0.51	0.902
Period	8	1221.11	152.64	16.00	0.001
Class*Period	8	201.96	25.24	2.65	0.012
Treatment*Period	16	128.83	8.05	0.84	0.634
Class*Treatment*Period	16	98.03	6.13	0.64	0.842
Period*Plot(Class Treatment)	96	916.12	9.54	1.15	0.246
Year*Period	8	1766.31	220.79	26.63	0.001
Class*Year*Period	8	166.97	20.87	2.52	0.016
Treatment*Year*Period	16	82.87	5.18	0.62	0.857
Class*Treatment*Year*Period	16	67.32	4.21	0.51	0.938
Year*Period*Plot(Class Treatment)	96	795.98	8.29	3.65	0.001
Error	1296	2945.10	2.27		
Total	1619	8757.79			

¹Plot within Class and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table A-18. Repeated measures analysis of variance of weekly (period) leaf water potential (MPa) of blue grama leaves in the good and fair condition class (Class) plots by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Class	1	2.337	2.337	2.74	0.124
Treatment	2	0.050	0.025	0.03	0.971
Class*Treatment	2	2.605	1.302	1.52	0.257
Plot(Class Treatment) ¹	12	10.253	0.854	1.23	0.360
Year	1	86.177	86.177	140.40	0.001
Class*Year	1	2.087	2.087	3.40	0.090
Treatment*Year	2	0.743	0.371	0.60	0.562
Class*Treatment*Year	2	0.196	0.098	0.16	0.854
Year*Plot(Class Treatment)	12	7.366	0.614	1.05	0.409
Period	8	120.500	15.062	22.76	0.001
Class*Period	8	10.781	1.348	2.04	0.050
Treatment*Period	16	8.283	0.518	0.78	0.702
Class*Treatment*Period	16	8.302	0.519	0.78	0.700
Period*Plot(Class Treatment)	96	63.531	0.662	1.13	0.269
Year*Period	8	343.15	42.894	73.53	0.001
Class*Year*Period	8	7.761	0.970	1.66	0.117
Treatment*Year*Period	16	9.796	0.612	1.05	0.414
Class*Treatment*Year*Period	16	4.117	0.257	0.44	0.967
Year*Period*Plot(Class Treatment)	96	55.998	0.583	4.68	0.001
Error	648	80.852	0.125		
Total	971	824.881			

¹Plot within Class and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table A-19. Repeated measures analysis of variance of weekly (period) leaf carbon content (mg g⁻¹ leaf) of blue grama (Species) leaves in the good and fair condition class (Class) plots by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Class	1	115.11	115.11	1.48	0.247
Treatment	2	256.46	128.23	1.5	0.232
Class*Treatment	2	21.84	10.92	0.14	0.870
Plot(Class Treatment) ¹	12	930.79	77.57	1.32	0.319
Year	1	968.15	968.15	17.40	0.001
Class*Year	1	0.22	0.22	0.00	0.951
Treatment*Year	2	106.02	53.01	0.95	0.413
Class*Treatment*Year	2	25.02	12.51	0.22	0.802
Year*Plot(Class Treatment)	12	667.78	55.65	1.59	0.107
Period	8	1092.14	136.52	3.58	0.001
Class*Period	8	137.82	17.23	0.45	0.887
Treatment*Period	16	343.27	21.45	0.56	0.904
Class*Treatment*Period	16	604.41	37.78	0.99	0.474
Period*Plot(Class Treatment)	96	3661.63	38.14	1.09	0.337
Year*Period	8	847.99	106.00	3.03	0.004
Class*Year*Period	8	237.753	29.69	0.85	0.563
Treatment*Year*Period	16	594.48	37.15	1.06	0.402
Class*Treatment*Year*Period	16	353.55	22.10	0.63	0.851
Error ²	96	3359.33	34.99		
Total	323	14323.52			

¹Plot within Class and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

²Residual error term includes the Year*Period*Plot(Class Treatment) variance component because insufficient error degrees of freedom.

Table A-20. Repeated measures analysis of variance of weekly (period) leaf nitrogen content (mg g^{-1} leaf) of blue grama leaves in the good and fair condition class (Class) plots by treatment (0, 11.2, and 22.4 t ha^{-1} soil removal) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Class	1	4.036	4.036	0.69	0.423
Treatment	2	14.706	7.353	1.25	0.320
Class*Treatment	2	5.992	2.996	0.51	0.612
Plot(Class Treatment) ¹	12	70.332	5.861	11.03	0.001
Year	1	4.776	4.776	9.19	0.010
Class*Year	1	0.397	0.397	0.76	0.399
Treatment*Year	2	0.852	0.426	0.82	0.464
Class*Treatment*Year	2	0.387	0.193	0.37	0.697
Year*Plot(Class Treatment)	12	6.234	0.520	1.86	0.049
Period	8	70.829	8.854	30.48	0.001
Class*Period	8	3.739	0.467	1.61	0.132
Treatment*Period	16	7.274	0.455	1.56	0.094
Class*Treatment*Period	16	2.376	0.149	0.51	0.936
Period*Plot(Class Treatment)	96	27.888	0.291	1.04	0.420
Year*Period	8	663.375	7.922	28.42	0.001
Class*Year*Period	8	3.611	0.451	1.62	0.129
Treatment*Year*Period	16	3.724	0.233	0.84	0.643
Class*Treatment*Year*Period	16	2.917	0.182	0.65	0.831
Error ²	96	26.758	0.279		
Total	323	320.202			

¹Plot within Class and Treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

²Residual error term includes the Year*Period*Plot(Class Treatment) variance component because insufficient error degrees of freedom.

Table A-21. Repeated measures analysis of variance of soil nitrogen content (mg g^{-1} soil) of the good and fair condition class (Class) plots by treatment (0, 11.2, and 22.4 t ha^{-1} soil removal) and sample depth (0-2.5, 2.5-5.0, and 5.0-10.0 cm) at the end of the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Class	1	0.081	0.081	5.05	0.031
Treatment	2	0.029	0.015	0.91	0.410
Class*Treatment	2	0.041	0.020	1.27	0.293
Sample depth	2	0.151	0.075	4.72	0.015
Class*Sample depth	2	0.003	0.001	0.09	0.917
Treatment*Sample depth	4	0.030	0.008	0.47	0.757
Class*Treatment*Sample depth	4	0.026	0.007	0.41	0.797
Plot(Class Treatment Sample depth)	36	0.575	0.016	4.87	0.001
Year	1	0.065	0.065	19.74	0.001
Class*Year	1	0.000	0.000	0.00	0.982
Treatment*Year	2	0.001	0.001	0.21	0.810
Class*Treatment*Year	2	0.024	0.012	3.62	0.29
Sample depth*Year	2	0.007	0.003	1.00	0.370
Class*Sample depth*Year	2	0.002	0.001	0.38	0.687
Treatment*Sample depth*Year	4	0.005	0.001	0.38	0.820
Class*Treatment*Sample depth*Year	4	0.002	0.000	0.16	0.956
Error2	144	0.472	0.003		
Total	215	1.513			

¹Plot within Class, Treatment, and Sample depth is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

²Residual error term includes the Year*Plot(Class Treatment Sample depth) variance component because insufficient error degrees of freedom.

Table A-22. Repeated measures analysis of variance of soil carbon content (mg g^{-1} soil) of the good and fair condition class (Class) plots by treatment (0, 11.2, and 22.4 t ha^{-1} soil removal) and sample depth (0-2.5, 2.5-5.0, and 5.0-10.0 cm) at the end of the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Class	1	4.52	4.52	3.01	0.091
Treatment	2	3.03	1.51	1.01	0.375
Class*Treatment	2	1.56	0.78	0.52	0.599
Sample depth	2	36.57	18.29	12.18	0.001
Class*Sample depth	2	0.15	0.07	0.05	0.952
Treatment*Sample depth	4	2.15	0.54	0.36	0.837
Class*Treatment*Sample depth	4	2.38	0.59	0.40	0.810
Plot(Class Treatment Sample depth)	36	54.03	0.15	5.60	0.001
Year	1	4.21	4.21	15.71	0.001
Class*Year	1	0.97	0.97	3.61	0.059
Treatment*Year	2	0.05	0.02	0.08	0.919
Class*Treatment*Year	2	0.61	0.30	1.13	0.325
Sample depth*Year	2	0.34	0.17	0.63	0.534
Class*Sample depth*Year	2	0.15	0.07	0.28	0.753
Treatment*Sample depth*Year	4	0.21	0.05	0.19	0.941
Class*Treatment*Sample depth*Year	4	0.26	0.06	0.24	0.915
Error ²	144	38.62	0.27		
Total	215	149.78			

¹Plot within Class, Treatment, and Sample depth is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

²Residual error term includes the Year*Plot(Class Treatment Sample depth) variance component because insufficient error degrees of freedom.

Table A-23. Repeated measures analysis of variance of weekly (Period) soil moisture (%) by sample depth (0-5 and 5-10 cm) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Sample depth	1	88.61	88.61	2.54	0.131
Plot(Sample depth)	16	558.14	34.88	10.61	0.001
Year	1	364.21	364.21	112.92	0.001
Sample depth*Year	1	25.05	25.05	7.77	0.013
Year*Plot(Sample depth)	16	51.61	3.23	2.42	0.003
Period	8	595.50	74.44	53.36	0.001
Sample depth*Period	8	54.43	6.80	4.88	0.001
Period*Plot(Sample depth)	128	178.55	1.40	1.05	0.398
Year*Period	8	1686.10	210.76	158.14	0.001
Sample depth*Year*Period	8	120.52	15.07	11.30	0.001
Error ²	128	170.60	1.33		
Total	323	3893.31			

¹Plot within Sample depth is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

²Residual error term includes the Year*Period*Plot(Sample depth) variance component because insufficient error degrees of freedom.

Appendix B

Chapter III Data and Statistical Outputs

Table B-1. Mean ($n = 5$) net photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), total conductance to CO_2 ($\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), intercellular CO_2 concentration ($\mu\text{mol CO}_2 \text{ mol air}^{-1}$), transpiration rate ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), ambient air temperature ($^{\circ}\text{C}$), relative humidity (%), and leaf chamber and ambient photosynthetically active radiation ($\mu\text{mol PAR m}^{-2} \text{ s}^{-1}$) by plot for bluebunch wheatgrass (Pssp) and Wyoming big sagebrush (Artr) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Week of Year	Soil Removal Level (t/ha)	Plant Species	Photo-synthesis	Conduct-ance	Intercellular CO_2 Concentration	Trans-piration	Air Temperature	Relative Humidity	Photosynthetically Active Radiation	
									Chamber	Ambient
23	0.0	Pssp	-2.12	0.154	369.8	3.04	18.5	28.5	1500	868
23	0.0	Artr	14.73	0.472	282.8	7.86	20.1	28.3	1499	1442
23	22.4	Pssp	8.53	0.190	257.2	4.54	21.9	26.8	1499	1678
23	22.4	Artr	13.46	0.374	272.8	7.14	21.4	27.7	1500	1767
23	11.2	Pssp	7.57	0.210	277.6	4.71	20.9	28.2	1500	1624
23	11.2	Artr	17.36	0.486	267.6	7.90	21.2	27.7	1499	1658
23	0.0	Pssp	8.64	0.137	236.8	3.30	21.6	26.9	1500	1439
23	0.0	Artr	11.78	0.279	264.4	5.67	21.5	26.8	1501	1575
23	11.2	Pssp	5.32	0.106	262.8	3.13	23.8	22.1	1500	1620
23	11.2	Artr	11.29	0.222	246.6	5.66	23.6	22.4	1500	1552
23	22.4	Pssp	5.60	0.115	260.4	2.89	21.9	24.6	1501	1457
23	22.4	Artr	13.12	0.271	254.8	5.96	21.7	23.4	1500	680
23	11.2	Pssp	10.64	0.182	246.2	3.51	18.2	25.4	1500	611
23	11.2	Artr	14.46	0.262	242.0	4.40	18.0	25.2	1500	1303
23	22.4	Pssp	7.79	0.134	242.8	3.43	21.5	22.2	1499	1415
23	22.4	Artr	12.74	0.330	266.2	6.55	21.4	22.9	1499	1379
23	0.0	Pssp	6.48	0.130	263.2	3.22	21.3	23.3	1500	1297
23	0.0	Artr	14.24	0.344	262.8	6.79	21.5	23.0	1500	1370
25	0.0	Pssp	3.99	0.065	235.8	3.19	33.2	21.8	1500	1364
25	0.0	Artr	12.74	0.320	263.4	11.82	32.0	22.8	1500	812
25	22.4	Pssp	5.23	0.091	241.0	4.43	32.5	22.0	1500	1326
25	22.4	Artr	9.69	0.163	235.2	7.21	32.2	22.0	1500	1593
25	11.2	Pssp	3.17	0.077	276.2	3.90	32.6	20.1	1500	1826
25	11.2	Artr	10.78	0.281	261.8	10.60	32.9	18.8	1500	1221
25	0.0	Pssp	0.76	0.065	325.2	2.91	30.2	18.2	1500	421
25	0.0	Artr	11.11	0.219	249.0	8.49	29.9	16.5	1500	682
25	11.2	Pssp	5.33	0.077	217.0	4.12	31.4	13.9	1500	1950
25	11.2	Artr	10.33	0.158	216.0	8.70	33.0	12.6	1500	1917
25	22.4	Pssp	4.28	0.056	201.4	3.27	33.3	11.9	1500	1507
25	22.4	Artr	5.56	0.140	265.4	7.14	32.5	11.8	1501	1559
25	11.2	Pssp	7.24	0.109	205.8	6.30	33.0	11.2	1500	1500
25	11.2	Artr	7.32	0.188	262.4	10.05	34.8	9.8	1500	1834
25	22.4	Pssp	3.36	0.083	262.4	5.50	35.2	9.5	1500	1916
25	22.4	Artr	6.44	0.137	249.4	7.96	35.4	9.2	1500	1424
25	0.0	Pssp	5.08	0.067	219.0	3.72	32.4	9.8	1500	762
25	0.0	Artr	9.56	0.198	247.6	8.94	32.0	9.2	1500	1082
26	0.0	Pssp	1.34	0.067	304.6	2.61	30.5	33.9	1501	743
26	0.0	Artr	10.50	0.176	237.4	5.53	29.2	34.2	1499	989
26	22.4	Pssp	7.21	0.086	213.2	3.14	28.9	31.8	1491	596
26	22.4	Artr	10.74	0.139	211.2	4.96	28.9	29.4	1501	1463
26	11.2	Pssp	3.82	0.121	293.6	4.83	29.0	26.3	1501	1242
26	11.2	Artr	12.65	0.238	242.4	7.82	29.4	25.0	1500	697
26	0.0	Pssp	2.71	0.074	280.2	3.10	29.7	23.6	1500	828
26	0.0	Artr	9.11	0.140	226.4	5.21	29.1	23.9	1500	871
26	11.2	Pssp	5.49	0.158	283.6	5.80	27.8	24.0	1497	1073
26	11.2	Artr	11.81	0.184	229.0	6.66	28.6	22.4	1500	636
26	22.4	Pssp	2.05	0.134	310.8	5.94	29.8	20.9	1503	1115
26	22.4	Artr	7.16	0.150	260.2	5.98	29.6	21.1	1501	962
26	11.2	Pssp	3.42	0.058	245.0	2.54	29.4	20.9	1507	1214
26	11.2	Artr	9.44	0.139	221.2	5.82	30.2	19.9	1489	1608
26	22.4	Pssp	1.39	0.084	304.4	3.93	30.1	20.0	1499	979
26	22.4	Artr	9.22	0.179	242.4	6.80	29.8	19.9	1501	1039

Table B-1. Continued.

Week of Year	Soil Removal Level (t/ha)	Plant Species	Photo-synthesis	Conduct-ance	Intercellular CO ₂ Concentration	Trans-piration	Air Temperature	Relative Humidity	Photosynthetically Active Radiation	
									Chamber	Ambient
26	0.0	Pssp	5.21	0.083	227.0	4.10	31.0	17.5	1493	1252
26	0.0	Artr	9.69	0.190	247.8	8.37	31.9	16.0	1503	1716
28	0.0	Pssp	16.52	0.058	4.0	2.98	37.0	34.4	1500	1328
28	0.0	Artr	17.44	0.250	214.8	10.68	36.8	34.1	1500	1370
28	22.4	Pssp	-0.97	0.059	375.6	4.44	40.8	24.0	1500	1469
28	22.4	Artr	4.63	0.120	264.4	7.76	39.7	24.1	1500	1353
28	11.2	Pssp	-4.33	0.036	542.0	2.51	38.6	23.7	1500	1436
28	11.2	Artr	9.31	0.131	209.6	7.28	37.8	23.8	1500	1108
28	0.0	Pssp	-2.21	0.053	383.2	3.59	37.8	21.8	1499	1425
28	0.0	Artr	3.48	0.055	229.2	3.59	37.4	21.2	1500	1782
28	11.2	Pssp	9.53	0.051	43.2	3.81	38.3	18.8	1500	852
28	11.2	Artr	9.46	0.108	186.6	7.28	39.0	17.3	1500	750
28	22.4	Pssp	-1.55	0.047	468.0	3.87	40.4	15.4	1500	917
28	22.4	Artr	4.63	0.071	230.6	4.53	37.4	16.4	1500	469
28	11.2	Pssp	1.69	0.076	296.4	5.54	37.8	15.2	1500	1454
28	11.2	Artr	5.18	0.063	199.2	4.36	38.2	14.9	1500	1315
28	22.4	Pssp	7.05	0.055	114.3	4.26	39.0	14.2	1500	720
28	22.4	Artr	7.23	0.078	164.9	5.59	38.5	13.7	1500	1402
28	0.0	Pssp	0.85	0.025	287.0	2.34	41.3	11.4	1501	1868
28	0.0	Artr	2.19	0.033	212.0	3.06	41.6	11.0	1505	1531
29	0.0	Pssp	4.22	0.048	195.3	2.72	32.3	13.3	1500	1429
29	0.0	Artr	14.08	0.236	236.4	10.71	32.8	14.3	1499	976
29	22.4	Pssp	4.92	0.054	194.2	2.61	30.9	18.6	1499	1709
29	22.4	Artr	12.99	0.189	224.2	8.34	31.2	18.7	1500	1635
29	11.2	Pssp	6.58	0.047	176.3	2.44	31.8	18.4	1500	1728
29	11.2	Artr	10.49	0.133	208.8	6.46	32.7	16.7	1499	1727
29	0.0	Pssp	7.62	0.045	109.9	2.57	33.3	16.1	1499	1638
29	0.0	Artr	7.98	0.089	195.0	4.65	33.0	16.1	1500	1633
29	11.2	Pssp	8.26	0.062	126.4	3.51	32.9	15.2	1500	1623
29	11.2	Artr	9.66	0.111	194.4	5.90	33.4	14.4	1499	1597
29	22.4	Psp	8.05	0.063	147.8	3.68	33.6	13.6	1499	1780
29	22.4	Artr	6.30	0.072	200.8	4.11	33.6	13.2	1500	1770
29	11.2	Pssp	6.61	0.060	169.5	3.44	33.1	13.5	1500	1506
29	11.2	Artr	7.52	0.076	179.6	3.95	32.5	14.1	1500	1503
29	22.4	Pssp	-1.46	0.086	335.8	4.73	32.4	14.1	1500	1568
29	22.4	Artr	10.22	0.106	180.0	5.67	33.0	13.4	1500	1576
29	0.0	Pssp	14.48	0.062	36.6	3.87	34.5	11.6	1500	1600
29	0.0	Artr	10.49	0.116	189.0	6.48	34.6	11.2	1500	1556
30	0.0	Pssp	12.66	0.048	53.0	2.38	32.0	19.4	1500	943
30	0.0	Artr	18.20	0.313	239.4	11.12	31.6	20.7	1500	847
30	22.4	Pssp	6.82	0.056	153.7	2.60	31.6	21.8	1500	1221
30	22.4	Artr	16.58	0.212	207.8	8.66	31.8	22.5	1500	876
30	11.2	Pssp	9.37	0.041	71.5	2.16	32.8	19.9	1500	1333
30	11.2	Artr	13.62	0.138	175.2	6.98	33.9	17.5	1500	1328
30	0.0	Pssp	8.18	0.030	104.6	1.70	33.9	17.2	1500	1168
30	0.0	Artr	6.17	0.065	187.8	3.66	34.5	16.8	1500	1362
30	11.2	Pssp	5.29	0.039	171.2	2.34	35.1	17.0	1500	1417
30	11.2	Artr	8.63	0.091	178.4	5.17	35.2	17.3	1490	1380
30	22.4	Pssp	5.02	0.021	185.6	1.33	35.4	17.3	1500	1440
30	22.4	Artr	4.44	0.051	184.0	3.17	35.6	17.0	1509	1429
30	11.2	Pssp	10.10	0.058	103.8	3.84	36.2	15.0	1496	1473
30	11.2	Artr	5.50	0.054	170.2	3.42	35.9	15.1	1493	1404
30	22.4	Pssp	8.43	0.045	129.4	3.13	36.8	14.1	1490	1240
30	22.4	Artr	4.60	0.051	191.2	3.18	35.8	14.3	1489	1226
30	0.0	Pssp	7.35	0.041	145.0	2.87	36.7	13.2	1500	1459
30	0.0	Artr	7.95	0.097	197.8	6.26	37.4	12.3	1500	1429
31	0.0	Pssp	1.51	0.048	325.4	2.17	29.9	21.8	1500	1565
31	0.0	Artr	16.04	0.210	207.4	8.84	31.1	20.8	1500	1463
31	22.4	Pssp	6.49	0.031	111.6	1.76	32.9	19.3	1500	1683
31	22.4	Artr	15.86	0.154	163.8	8.31	34.4	18.0	1500	1267

Table B-1. Continued.

Week of Year	Soil Removal Level (t/ha)	Plant Species	Photo- synthesis	Conduct- ance	Intercellular CO ₂ Concentration	Trans- piration	Air Temperature	Relative Humidity	Photosynthetically Active Radiation	
									Chamber	Ambient
31	11.2	Pasp	2.57	0.058	303.4	3.04	33.3	20.3	1500	1557
31	11.2	Artr	9.77	0.082	140.2	4.23	33.5	20.0	1499	1358
31	0.0	Pasp	9.01	0.041	108.2	2.19	33.1	18.5	1499	1137
31	0.0	Artr	5.81	0.035	106.5	2.12	34.4	16.1	1500	1793
31	11.2	Pasp	12.00	0.061	58.3	3.86	35.2	15.0	1500	1694
31	11.2	Artr	9.13	0.073	125.6	4.95	36.6	14.0	1500	1743
31	22.4	Pasp	0.15	0.038	320.4	2.36	35.2	14.4	1500	1346
31	22.4	Artr	3.29	0.034	178.6	2.02	34.1	14.6	1500	753
31	11.2	Pasp	9.53	0.032	143.1	2.02	34.1	13.3	1500	1714
31	11.2	Artr	6.02	0.044	117.8	2.86	35.2	12.7	1499	1724
31	22.4	Pasp	1.53	0.031	228.4	2.19	36.7	11.7	1500	1709
31	22.4	Artr	6.66	0.068	170.0	4.50	36.7	11.8	1500	1678
31	0.0	Pasp	0.45	0.043	311.9	2.98	36.4	12.0	1500	1628
31	0.0	Artr	5.51	0.055	141.6	3.70	36.8	11.6	1499	1698
32	0.0	Artr	11.47	0.182	234.2	9.66	37.6	20.9	1500	1026
32	22.4	Artr	10.04	0.147	226.4	8.92	38.4	19.4	1500	1460
32	11.2	Artr	6.96	0.066	169.0	4.39	39.0	18.6	1500	1361
32	0.0	Artr	2.99	0.032	196.0	2.29	39.0	17.9	1500	1656
32	11.2	Artr	5.27	0.041	117.3	3.11	39.6	17.1	1500	1666
32	22.4	Artr	1.22	0.031	275.2	2.28	39.5	17.6	1500	1347
32	11.2	Artr	1.28	0.008	207.9	0.60	38.6	18.2	1501	1168
32	22.4	Artr	5.78	0.065	198.6	3.84	36.5	18.1	1500	511
32	0.0	Artr	2.01	0.038	262.4	2.11	34.5	17.6	1500	382
33	0.0	Artr	14.64	0.205	231.6	6.00	30.1	39.0	1499	1363
33	22.4	Artr	12.01	0.174	235.0	6.79	32.5	29.7	1499	1491
33	11.2	Artr	9.30	0.093	187.0	3.74	32.2	28.6	1500	1549
33	0.0	Artr	4.84	0.039	162.2	1.77	32.1	27.3	1500	1307
33	11.2	Artr	8.70	0.078	163.8	3.60	32.8	24.7	1499	1595
33	22.4	Artr	4.71	0.039	158.0	2.19	34.3	21.8	1499	1627
33	11.2	Artr	3.19	0.044	231.8	2.42	34.8	19.4	1501	837
33	22.4	Artr	7.44	0.084	207.6	3.31	30.3	21.1	1500	415
33	0.0	Artr	5.13	0.064	208.4	2.40	28.2	21.9	1500	950
34	0.0	Artr	17.78	0.341	256.4	9.75	27.3	24.1	1500	1233
34	22.4	Artr	15.02	0.262	247.0	8.99	30.4	24.3	1500	1358
34	11.2	Artr	11.92	0.145	206.0	5.51	31.1	24.8	1500	1381
34	0.0	Artr	4.76	0.065	231.4	2.61	30.6	26.7	1500	1432
34	11.2	Artr	10.29	0.114	196.8	4.42	30.9	27.2	1500	1544
34	22.4	Artr	7.07	0.056	139.9	2.47	31.9	26.0	1500	1210
34	11.2	Artr	4.84	0.049	208.0	2.15	32.7	26.0	1500	1160
34	22.4	Artr	12.21	0.128	184.8	5.35	32.9	25.2	1501	681
34	0.0	Artr	5.12	0.073	236.4	2.49	29.4	28.4	1500	809
35	0.0	Artr	13.68	0.207	226.0	7.24	28.1	20.7	1500	1227
35	22.4	Artr	9.82	0.116	201.4	4.47	28.9	21.8	1500	1131
35	11.2	Artr	9.81	0.085	153.6	3.39	29.2	22.0	1499	1179
35	0.0	Artr	4.67	0.044	175.4	1.87	29.1	22.4	1500	1314
35	11.2	Artr	7.84	0.078	180.0	3.18	29.3	22.6	1500	1011
35	22.4	Artr	2.86	0.034	207.2	1.39	28.8	22.7	1500	1566
35	11.2	Artr	6.65	0.048	117.2	2.14	30.2	21.0	1500	1337
35	22.4	Artr	10.51	0.103	173.2	4.15	29.8	21.7	1500	716
35	0.0	Artr	7.20	0.052	118.6	2.11	29.0	21.7	1500	1152
36	0.0	Artr	15.22	0.236	228.6	7.11	27.1	20.6	1500	1379
36	22.4	Artr	14.54	0.214	224.2	6.63	26.8	20.2	1500	1310
36	11.2	Artr	11.65	0.108	161.6	3.73	27.5	20.1	1500	1453
36	0.0	Artr	4.34	0.043	171.6	1.60	27.7	20.2	1500	1310
36	11.2	Artr	10.68	0.113	183.6	4.04	27.9	20.7	1500	1240
36	22.4	Artr	6.17	0.042	96.3	1.77	29.4	18.7	1500	1521
36	11.2	Artr	1.62	0.016	315.9	0.76	30.4	17.2	1499	1558
36	22.4	Artr	8.08	0.090	184.8	3.84	30.6	16.8	1500	1479
36	0.0	Artr	2.15	0.032	228.2	1.44	30.7	16.5	1500	1588

Table B-2. Mean ($n = 5$) water use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), nitrogen use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$), percent leaf carbon and nitrogen, and leaf water potential (Mpa, $n = 3$) by plot for bluebunch wheatgrass (Pssp) and Wyoming big sagebrush (Artr) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Week of Year	Soil Removal Level (t/ha)	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
23	0.0	Pssp	-0.78	-0.008	45.1	1.6	-2.4
23	0.0	Artr	1.84	0.015	48.6	2.4	-2.1
23	22.4	Pssp	2.10	0.027	45.5	2.1	-2.7
23	22.4	Artr	1.92	0.013	48.0	2.6	-1.7
23	11.2	Pssp	1.72	0.023	45.8	1.9	-2.5
23	11.2	Artr	2.19	0.020	49.1	2.2	-1.8
23	0.0	Pssp	2.67	0.028	45.5	2.0	-2.5
23	0.0	Artr	2.07	0.013	48.8	2.2	-1.8
23	11.2	Pssp	1.60	0.019	45.1	1.8	-2.5
23	11.2	Artr	2.04	0.014	48.1	2.0	-1.7
23	22.4	Pssp	1.97	0.022	45.6	1.8	-3.0
23	22.4	Artr	2.20	0.014	48.7	2.3	-1.3
23	11.2	Pssp	3.07	0.032	44.2	2.2	-3.0
23	11.2	Artr	3.28	0.016	49.3	2.2	-1.3
23	22.4	Pssp	2.32	0.024	44.3	2.1	-3.0
23	22.4	Artr	1.99	0.016	49.9	2.0	-1.3
23	0.0	Pssp	1.92	0.024	44.8	1.8	-3.0
23	0.0	Artr	2.08	0.016	49.3	2.1	-1.3
25	0.0	Pssp	1.23	0.016	43.8	1.7	-2.2
25	0.0	Artr	1.08	0.015	48.9	2.1	-2.2
25	22.4	Pssp	1.19	0.015	46.0	2.2	-3.0
25	22.4	Artr	1.33	0.012	48.6	2.1	-2.4
25	11.2	Pssp	0.69	0.013	44.1	1.6	-3.0
25	11.2	Artr	1.03	0.013	49.0	2.0	-2.4
25	0.0	Pssp	0.16	0.003	44.3	1.6	-3.4
25	0.0	Artr	1.29	0.014	49.1	1.9	-1.9
25	11.2	Pssp	1.38	0.021	44.5	1.6	-2.9
25	11.2	Artr	1.21	0.014	48.1	1.8	-1.9
25	22.4	Pssp	1.38	0.017	45.7	1.6	-3.3
25	22.4	Artr	0.77	0.007	49.1	2.1	-1.6
25	11.2	Pssp	1.31	0.026	43.5	1.8	-3.1
25	11.2	Artr	0.69	0.009	49.4	2.0	-2.3
25	22.4	Pssp	0.58	0.012	45.1	1.9	-3.0
25	22.4	Artr	0.78	0.009	50.5	1.8	-1.9
25	0.0	Pssp	1.27	0.019	44.4	1.7	-3.1
25	0.0	Artr	1.08	0.012	49.1	1.9	-2.0
26	0.0	Pssp	0.52	0.006	43.6	1.3	-2.8
26	0.0	Artr	1.88	0.013	48.8	2.0	-2.6
26	22.4	Pssp	2.15	0.028	44.7	1.6	-3.2
26	22.4	Artr	2.15	0.014	47.8	1.9	-2.7
26	11.2	Pssp	0.67	0.014	43.9	1.6	-3.2
26	11.2	Artr	1.61	0.016	50.2	1.9	-2.6
26	0.0	Pssp	0.84	0.012	44.6	1.5	-3.6
26	0.0	Artr	1.78	0.012	49.1	1.9	-2.5
26	11.2	Pssp	0.93	0.025	43.5	1.4	-3.0
26	11.2	Artr	1.78	0.016	48.0	1.8	-2.6

Table B-2. Continued.

Week of Year	Soil Removal Level (t/ha)	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
26	22.4	Pssp	0.33	0.009	44.4	1.4	-3.6
26	22.4	Artr	1.13	0.009	49.4	2.0	-3.0
26	11.2	Pssp	1.31	0.013	43.1	1.7	-2.8
26	11.2	Artr	1.61	0.013	50.1	1.8	-2.7
26	22.4	Pssp	0.40	0.005	44.4	1.4	-3.6
26	22.4	Artr	1.40	0.015	50.1	1.5	-2.5
26	0.0	Pssp	1.33	0.017	44.0	1.9	-3.3
26	0.0	Artr	1.10	0.013	49.7	1.8	-2.5
28	0.0	Pssp	26.34	0.065	43.4	1.3	-4.8
28	0.0	Artr	1.65	0.023	49.5	1.8	-2.7
28	22.4	Pssp	-0.47	-0.003	47.1	2.1	-6.5
28	22.4	Artr	0.60	0.006	49.6	1.9	-2.6
28	11.2	Pssp	-2.03	-0.017	45.4	1.6	-5.1
28	11.2	Artr	1.29	0.013	51.1	1.7	-2.6
28	0.0	Pssp	-0.54	-0.008	46.4	1.6	-5.8
28	0.0	Artr	0.96	0.005	49.9	1.7	-3.5
28	11.2	Pssp	2.47	0.036	47.1	1.7	-4.9
28	11.2	Artr	1.25	0.014	49.2	1.7	-3.0
28	22.4	Pssp	-0.62	-0.001	46.7	1.4	-6.5
28	22.4	Artr	0.97	0.006	49.8	1.8	-3.5
28	11.2	Pssp	0.24	0.006	46.5	1.5	-4.3
28	11.2	Artr	1.13	0.008	51.3	1.7	-2.7
28	22.4	Pssp	1.73	0.027	46.7	1.4	-5.6
28	22.4	Artr	1.35	0.012	51.8	1.5	-2.6
28	0.0	Pssp	0.63	0.004	46.6	1.3	-4.4
28	0.0	Artr	0.71	0.004	51.1	1.5	-2.6
29	0.0	Pssp	1.63	0.024	44.5	1.1	-3.8
29	0.0	Artr	1.30	0.020	50.6	1.8	-2.6
29	22.4	Pssp	1.92	0.017	47.5	1.6	-3.8
29	22.4	Artr	1.56	0.017	50.0	1.9	-2.8
29	11.2	Pssp	3.41	0.026	45.9	1.3	-5.8
29	11.2	Artr	1.62	0.016	51.5	1.6	-3.0
29	0.0	Pssp	2.97	0.032	46.7	1.2	-5.0
29	0.0	Artr	1.71	0.011	49.6	1.7	-3.8
29	11.2	Pssp	2.43	0.031	45.3	1.5	-4.8
29	11.2	Artr	1.65	0.015	48.3	1.6	-3.1
29	22.4	Pssp	1.91	0.026	45.0	1.5	-4.8
29	22.4	Artr	1.49	0.009	49.4	1.7	-3.6
29	11.2	Pssp	1.89	0.024	44.7	1.5	-6.1
29	11.2	Artr	1.90	0.011	50.1	1.6	-3.1
29	22.4	Pssp	0.01	-0.003	45.4	1.3	-4.9
29	22.4	Artr	1.81	0.016	51.2	1.5	-2.7
29	0.0	Pssp	4.07	0.058	44.3	1.3	-5.0
29	0.0	Artr	1.61	0.017	50.7	1.5	-2.8
30	0.0	Pssp	5.48	0.058	44.9	1.2	-4.7
30	0.0	Artr	1.64	0.027	49.7	1.6	-2.8
30	22.4	Pssp	2.59	0.023	46.7	1.6	-5.5
30	22.4	Artr	1.94	0.024	49.6	1.7	-3.1
30	11.2	Pssp	4.52	0.044	45.5	1.1	-6.4

Table B-2. Continued.

Week of Year	Soil Removal Level (t/ha)	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
30	11.2	Artr	1.95	0.022	51.3	1.6	-3.4
30	0.0	Pssp	6.15	0.035	45.1	1.3	-5.7
30	0.0	Artr	1.69	0.009	50.0	1.6	-4.2
30	11.2	Pssp	2.77	0.024	45.3	1.2	-5.7
30	11.2	Artr	1.72	0.014	48.6	1.5	-3.1
30	22.4	Pssp	4.38	0.025	45.2	1.1	-6.1
30	22.4	Artr	1.54	0.007	49.7	1.6	-4.4
30	11.2	Pssp	2.58	0.044	41.1	1.0	-6.5
30	11.2	Artr	1.62	0.009	50.8	1.5	-3.7
30	22.4	Pssp	3.23	0.034	45.2	1.3	-6.1
30	22.4	Artr	1.45	0.009	51.0	1.3	-3.1
30	0.0	Pssp	2.76	0.029	47.0	1.4	-6.4
30	0.0	Artr	1.28	0.014	50.8	1.3	-3.2
31	0.0	Pssp	0.65	0.007	45.1	1.0	-5.6
31	0.0	Artr	1.83	0.025	50.5	1.6	-3.2
31	22.4	Pssp	4.07	0.026	47.3	1.3	-6.3
31	22.4	Artr	1.91	0.025	50.4	1.6	-3.0
31	11.2	Pssp	0.36	0.010	45.9	1.1	-6.1
31	11.2	Artr	2.32	0.017	51.7	1.5	-3.5
31	0.0	Pssp	4.91	0.038	46.9	1.2	-6.3
31	0.0	Artr	2.83	0.009	51.2	1.6	-4.3
31	11.2	Pssp	4.02	0.039	45.1	1.5	-6.4
31	11.2	Artr	1.89	0.015	50.1	1.5	-3.4
31	22.4	Pssp	0.10	0.000	46.1	1.0	-6.4
31	22.4	Artr	1.64	0.005	50.9	1.5	-4.7
31	11.2	Pssp	4.49	0.042	46.0	1.2	-6.4
31	11.2	Artr	2.09	0.010	51.4	1.5	-4.2
31	22.4	Pssp	0.90	0.007	46.7	1.2	-6.1
31	22.4	Artr	1.51	0.012	52.0	1.4	-3.1
31	0.0	Pssp	0.12	0.001	47.4	1.3	-6.2
31	0.0	Artr	1.69	0.011	51.4	1.3	-3.2
32	0.0	Artr	1.18	0.018	50.1	1.6	-3.3
32	22.4	Artr	1.12	0.016	50.5	1.6	-2.8
32	11.2	Artr	1.58	0.012	52.4	1.4	-3.6
32	0.0	Artr	1.26	0.005	51.0	1.5	-4.7
32	11.2	Artr	1.82	0.010	52.5	1.3	-2.7
32	22.4	Artr	0.49	0.002	50.7	1.5	-4.2
32	11.2	Artr	2.05	0.002	52.8	1.4	-3.3
32	22.4	Artr	1.51	0.010	52.3	1.3	-3.0
32	0.0	Artr	0.92	0.004	52.0	1.4	-3.4
33	0.0	Artr	2.45	0.022	50.0	1.7	-3.4
33	22.4	Artr	1.77	0.020	50.3	1.5	-3.0
33	11.2	Artr	2.49	0.016	52.1	1.4	-3.6
33	0.0	Artr	2.65	0.008	50.9	1.6	-4.9
33	11.2	Artr	2.46	0.014	51.1	1.6	-3.1
33	22.4	Artr	2.13	0.009	52.6	1.4	-4.8
33	11.2	Artr	1.28	0.006	52.7	1.4	-3.2
33	22.4	Artr	2.23	0.014	52.2	1.3	-2.7
33	0.0	Artr	2.34	0.009	51.2	1.5	-3.9

Table B-2. Continued.

Week of Year	Soil Removal Level (t/ha)	Plant Species	Water Use Efficiency	Nitrogen Use Efficiency	Carbon	Nitrogen	Leaf Water Potential
34	0.0	Artr	1.82	0.029	50.8	1.6	-3.1
34	22.4	Artr	1.69	0.024	50.7	1.6	-2.7
34	11.2	Artr	2.20	0.020	52.8	1.4	-3.3
34	0.0	Artr	1.81	0.008	50.9	1.6	-4.4
34	11.2	Artr	2.37	0.019	53.2	1.4	-2.7
34	22.4	Artr	2.92	0.011	51.5	1.6	-4.0
34	11.2	Artr	1.91	0.009	52.9	1.3	-3.3
34	22.4	Artr	2.31	0.023	52.9	1.3	-3.1
34	0.0	Artr	2.04	0.009	52.0	1.4	-3.6
35	0.0	Artr	1.94	0.020	51.7	1.7	-3.1
35	22.4	Artr	2.22	0.016	51.6	1.6	-2.6
35	11.2	Artr	2.89	0.016	53.2	1.5	-3.7
35	0.0	Artr	2.50	0.007	52.1	1.7	-4.4
35	11.2	Artr	2.46	0.014	53.6	1.4	-2.7
35	22.4	Artr	2.07	0.004	52.1	1.7	-4.4
35	11.2	Artr	3.11	0.013	53.3	1.3	-3.0
35	22.4	Artr	2.55	0.019	53.2	1.4	-3.2
35	0.0	Artr	3.43	0.012	53.1	1.6	-4.1
36	0.0	Artr	2.15	0.022	50.8	1.8	-3.8
36	22.4	Artr	2.22	0.021	51.5	1.7	-3.4
36	11.2	Artr	3.13	0.019	53.2	1.5	-4.4
36	0.0	Artr	2.81	0.007	51.4	1.6	-5.9
36	11.2	Artr	2.65	0.018	53.7	1.5	-3.6
36	22.4	Artr	3.57	0.009	52.1	1.7	-5.5
36	11.2	Artr	0.33	0.003	53.7	1.3	-3.4
36	22.4	Artr	2.16	0.013	53.3	1.5	-4.5
36	0.0	Artr	1.49	0.004	52.7	1.5	-6.0

Table B-3. Soil carbon and nitrogen content (%) at the end of the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Year	Plot	Soil Removal Level (t/ha)	Plot Section ¹	Sample Depth (cm)	Carbon (%)	Nitrogen (%)
2000	2	0.0	A	0-2.5	1.075	0.136
			A	2.5-5.0	1.205	0.135
			A	5.0-10.0	0.774	0.083
			B	0-2.5	1.570	0.126
			B	2.5-5.0	1.860	0.143
			B	5.0-10.0	1.438	0.138
	3	22.4	A	0-2.5	0.903	0.135
			A	2.5-5.0	0.894	0.097
			A	5.0-10.0	0.897	0.107
			B	0-2.5	1.590	0.140
			B	2.5-5.0	1.415	0.137
			B	5.0-10.0	1.021	0.104
	18	11.2	A	0-2.5	1.582	0.178
			A	2.5-5.0	1.130	0.120
			A	5.0-10.0	0.988	0.105
			B	0-2.5	1.611	0.159
			B	2.5-5.0	1.301	0.117
			B	5.0-10.0	1.440	0.134
	20	0.0	A	0-2.5	0.996	0.100
			A	2.5-5.0	1.093	0.122
			A	5.0-10.0	1.109	0.112
			B	0-2.5	1.436	0.132
			B	2.5-5.0	1.241	0.121
			B	5.0-10.0	0.915	0.095
	22	11.2	A	0-2.5	0.940	0.079
			A	2.5-5.0	1.063	0.103
			A	5.0-10.0	1.254	0.124
			B	0-2.5	2.020	0.153
			B	2.5-5.0	1.668	0.140
			B	5.0-10.0	1.266	0.108
24	22.4	A	0-2.5	0.968	0.106	
		A	2.5-5.0	1.071	0.105	
		A	5.0-10.0	1.139	0.114	
		B	0-2.5	0.957	0.092	
		B	2.5-5.0	1.159	0.106	
		B	5.0-10.0	1.021	0.114	
26	11.2	A	0-2.5	1.194	0.106	
		A	2.5-5.0	1.211	0.121	
		A	5.0-10.0	1.048	0.103	
		B	0-2.5	1.157	0.121	
		B	2.5-5.0	0.854	0.086	
		B	5.0-10.0	0.966	0.084	
29	22.4	A	0-2.5	1.118	0.120	
		A	2.5-5.0	0.978	0.103	
		A	5.0-10.0	1.027	0.108	
		B	0-2.5	2.333	0.192	

Table B-3. Continued.

Year	Plot	Soil Removal Level (t/ha)	Plot Section ¹	Sample Depth (cm)	Carbon (%)	Nitrogen (%)
2000	29	22.4	B	2.5-5.0	1.543	0.125
			B	5.0-10.0	1.074	0.074
2000	30	0.0	A	0-2.5	3.396	0.283
			A	2.5-5.0	1.412	0.122
			A	5.0-10.0	1.439	0.140
			B	0-2.5	0.889	0.089
			B	2.5-5.0	1.101	0.112
			B	5.0-10.0	1.081	0.078

¹Plots were divided into upslope and downslope halves for sampling soil carbon and nitrogen; where A = upslope section and B= downslope section.

Table B-4. Weekly average (n = 9) soil moisture content by sample depth (cm) for the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Year	Week of Year	Sample Depth (cm)	Soil Water Content
2000	23	0.0-5.0	2.95
		5.0-10.0	4.87
	25	0.0-5.0	3.06
		5.0-10.0	4.14
	26	0.0-5.0	3.51
		5.0-10.0	4.74
	28	0.0-5.0	2.89
		5.0-10.0	4.67
	29	0.0-5.0	2.36
		5.0-10.0	4.21
	30	0.0-5.0	2.52
		5.0-10.0	4.63
	31	0.0-5.0	1.87
		5.0-10.0	3.39
	32	0.0-5.0	2.26
		5.0-10.0	3.71
	33	0.0-5.0	2.30
		5.0-10.0	3.70
34	0.0-5.0	4.38	
	5.0-10.0	4.56	
35	0.0-5.0	3.47	
	5.0-10.0	4.49	
36	0.0-5.0	2.73	
	5.0-10.0	4.38	

Table B-5. Repeated measures analysis of covariance of weekly (Period) net photosynthetic rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) of bluebunch wheatgrass and Wyoming big sagebrush (Species) leaves by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Adjusted Sums of Squares	Adjusted Mean Squares	F-Value	P-Value
Relative Humidity	1	646.38	17.33	17.33	1.09	0.298
Air temperature	1	579.30	126.77	126.77	7.95	0.005
Species	1	3239.91	1622.16	1622.16	14.86	0.002
Treatment	2	240.16	569.11	284.55	3.26	0.069
Species*Treatment	2	32.46	171.89	85.94	0.62	0.553
Plot (Species Treatment) ¹	12	1957.21	1650.29	137.52	2.37	0.012
Period	6	787.06	864.78	144.13	2.97	0.011
Species*Period	6	512.69	565.91	94.32	1.55	0.173
Treatment*Period	12	442.13	490.76	40.90	0.71	0.742
Species*Treatment*Period	12	405.40	409.33	34.11	0.54	0.879
Period*Plot(Species Treatment)	72	4563.49	4563.49	63.38	3.97	0.001
Error	502	8009.48	8009.48	15.96		
Total	629	21415.68				

	Coefficient	Standard Deviation	T-Value	P-Value
Constant	-45.76	32.69	-1.40	0.162
Relative Humidity	-0.69	0.66	-1.04	0.298
Air Temperature	2.07	0.73	2.82	0.005

¹Plot within species and treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table B-6. Individual repeated measures analysis of variance for Wyoming big sagebrush and analysis of covariance for bluebunch wheatgrass on weekly (Period) net photosynthetic rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Adjusted Sums of Squares	Adjusted Mean Squares	F-Value	P-Value
-----ANOVA for Big Sagebrush Only-----						
Treatment	2	34.44	34.44	17.221	0.02	0.978
Plot (Treatment)	6	4732.04	4732.04	788.67	28.07	0.001
Period	11	2071.54	2071.54	188.32	6.70	0.001
Treatment*Period	22	378.72	378.72	17.22	0.61	0.900
Period*Plot (Treatment)	66	1854.31	1854.31	28.10	4.49	0.001
Error	432	2701.06	2701.06	6.25		
Total	539	11772.12				
-----ANCOVA for Bluebunch Wheatgrass Only-----						
Relative Humidity	1	0.62	17.09	17.09	0.74	0.392
Air Temperature	1	101.81	254.94	254.94	10.97	0.001
Treatment	2	173.36	703.01	351.51	4.31	0.055
Plot (Treatment) ¹	6	300.69	739.32	123.22	1.47	0.214
Period	6	1089.35	1182.85	197.14	2.54	0.034
Treatment*Period	12	611.91	680.56	56.71	0.61	0.824
Period*Plot (Treatment)	36	3612.84	3612.84	100.36	4.32	0.001
Error	250	5810.52	5810.52	23.24		
Total	314	11701.10				
		Coefficient	Standard Deviation	T-Value	P-Value	
Constant		-95.80	48.51	-1.97	0.049	
Relative Humidity		-0.82	0.95	-0.86	0.392	
Air Temperature		3.65	1.10	3.31	0.001	

¹Plot within treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table B-7. Repeated measures analysis of covariance of weekly (Period) intercellular CO₂ concentration ($\mu\text{mol CO}_2 \text{ mol air}^{-1}$) of bluebunch wheatgrass and Wyoming big sagebrush (Species) leaves by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Adjusted Sums of Squares	Adjusted Mean Squares	F-Value	P-Value
Relative Humidity	1	262826	80	80	0.01	0.919
Air temperature	1	56595	152381	152381	19.54	0.001
Species	1	9395	81	81	0.00	0.961
Treatment	2	55206	186882	93441	3.58	0.053
Species*Treatment	2	20149	99654	49827	1.27	0.315
Plot (Species Treatment) ¹	12	299203	468189	39016	1.44	0.166
Period	6	737291	751706	125284	5.52	0.001
Species*Period	6	353133	383235	63873	2.26	0.047
Treatment*Period	12	105815	161154	13430	0.50	0.911
Species*Treatment*Period	12	117315	184844	15404	0.53	0.890
Period*Plot(Species Treatment)	72	2124833	2124833	29512	3.78	0.001
Error	502	3915752	3915752	7800		
Total	629	8057513				

	Coefficient	Standard Deviation	T-Value	P-Value
Constant	2544.4	722.8	3.52	0.001
Relative Humidity	-1.48	14.64	-0.10	0.919
Air Temperature	-71.79	16.24	-4.42	0.001

¹Plot within species and treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table B-8. Individual repeated measures analysis of variance for Wyoming big sagebrush and bluebunch wheatgrass on weekly (Period) intercellular CO₂ concentration ($\mu\text{mol CO}_2 \text{ mol air}^{-1}$) by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Adjusted Sums of Squares	Adjusted Mean Squares	F-Value	P-Value
-----ANOVA for Big Sagebrush Only-----						
Treatment	2	38936	38936	19468	1.42	0.314
Plot (Treatment)	6	82501	82501	13750	3.01	0.012
Period	11	474897	474897	43172	9.45	0.001
Treatment*Period	22	96023	96023	4365	0.96	0.529
Period*Plot (Treatment)	66	301563	301563	4569	2.73	0.001
Error	432	722261	722261	1672		
Total	539	1716181				
-----ANOVA for Bluebunch Wheatgrass Only-----						
Treatment	2	46182	46182	23091	0.50	0.628
Plot (Treatment) ¹	6	275760	275760	45960	0.89	0.515
Period	6	960184	960184	160031	3.09	0.015
Treatment*Period	12	213612	213612	17801	0.34	0.975
Period*Plot (Treatment)	36	1866944	1866944	51860	3.25	0.001
Error	250	4023570	4023570	15967		
Total	314	7386252				

¹Plot within treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table B-9. Repeated measures analysis of covariance of weekly (Period) nitrogen use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$) of bluebunch wheatgrass and Wyoming big sagebrush (Species) leaves by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Adjusted Sums of Squares	Adjusted Mean Squares	F-Value	P-Value
Relative Humidity	1	0.00032	0.00023	0.00023	1.27	0.261
Air temperature	1	0.00041	0.00225	0.00225	12.56	0.001
Species	1	0.00758	0.00853	0.00853	12.90	0.003
Treatment	2	0.00252	0.00682	0.00341	6.23	0.010
Species*Treatment	2	0.00087	0.00386	0.00193	2.38	0.135
Plot (Species Treatment) ¹	12	0.00730	0.00970	0.00081	1.19	0.307
Period	6	0.01234	0.01486	0.00248	4.37	0.001
Species*Period	6	0.00622	0.00619	0.00103	1.45	0.208
Treatment*Period	12	0.00580	0.00597	0.00050	0.73	0.716
Species*Treatment*Period	12	0.00472	0.00535	0.00045	0.61	0.831
Period*Plot(Species Treatment)	72	0.05356	0.05356	0.00074	4.16	0.001
Error	502	0.08975	0.08975	0.00018		
Total	629	0.19140				

	Coefficient	Standard Deviation	T-Value	P-Value
Constant	-0.2150	0.109	-1.96	0.050
Relative Humidity	-0.0025	0.002	-1.13	0.261
Air Temperature	0.0087	0.002	3.54	0.001

¹Plot within species and treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table B-10. Individual repeated measures analysis of variance for Wyoming big sagebrush and analysis of covariance for bluebunch wheatgrass on weekly (Period) nitrogen use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol N m}^{-2}$) by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Adjusted Sums of Squares	Adjusted Mean Squares	F-Value	P-Value
-----ANOVA for Big Sagebrush Only-----						
Treatment	2	0.000015	0.000015	0.000007	0.00	0.995
Plot (Treatment)	6	0.009606	0.009606	0.001601	22.34	0.001
Period	11	0.002574	0.002574	0.000234	3.27	0.001
Treatment*Period	22	0.00836	0.00836	0.000038	0.53	0.951
Period*Plot (Treatment)	66	0.004730	0.004730	0.000072	5.26	0.001
Error	432	0.005890	0.005890	0.000014		
Total	539	0.023650				
-----ANCOVA for Bluebunch Wheatgrass Only-----						
Relative Humidity	1	0.00011	0.0022	0.0022	0.68	0.410
Air Temperature	1	0.00026	0.0040	0.0040	12.25	0.001
Treatment	2	0.00328	0.0115	0.0057	4.93	0.042
Plot (Treatment) ¹	6	0.00328	0.0105	0.0018	1.43	0.226
Period	6	0.01916	0.0219	0.0037	3.22	0.011
Treatment*Period	12	0.01007	0.1011	0.0008	0.62	0.815
Period*Plot (Treatment)	36	0.05285	0.0528	0.0015	4.44	0.001
Error	250	0.08263	0.0826	0.0003		
Total	314	0.17209				
		Coefficient	Standard Deviation	T-Value		P-Value
Constant		-0.388	0.183	-2.12		0.035
Relative Humidity		-0.003	0.004	-0.82		0.410
Air Temperature		0.015	0.004	3.50		0.001

¹Plot within treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table B-11. Repeated measures analysis of variance of weekly (Period) transpiration rate ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) of bluebunch wheatgrass and Wyoming big sagebrush (Species) leaves by treatment (0, 11.2, and 22.4 t ha^{-1} soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Species	1	1381.536	1381.536	24.86	0.001
Treatment	2	4.203	2.101	0.04	0.963
Species*Treatment	2	70.098	35.049	0.63	0.549
Plot (Species Treatment) ¹	12	666.800	55.567	7.14	0.001
Period	6	476.474	79.412	10.21	0.001
Species*Period	6	115.681	19.280	2.48	0.031
Treatment*Period	12	71.514	5.960	0.77	0.683
Species*Treatment*Period	12	49.466	4.122	0.53	0.888
Period*Plot(Species Treatment)	72	560.239	7.781	3.57	0.001
Error	502	1098.314	2.179		
Total	629	4494.325			

¹Plot within species and treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table B-12. Individual Repeated measures analysis of variance for Wyoming big sagebrush and bluebunch wheatgrass on weekly (Period) transpiration rates ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) by treatment (0, 11.2, and 22.4 t ha^{-1} soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
-----ANOVA for Big Sagebrush Only-----					
Treatment	2	48.26	24.13	0.09	0.912
Plot (Treatment)	6	1557.13	259.52	29.60	0.001
Period	11	1348.58	122.60	13.98	0.001
Treatment*Period	22	178.96	8.13	0.93	0.561
Period*Plot (Treatment)	66	578.59	8.77	4.62	0.001
Error	432	820.54	1.90		
Total	539	4532.07			
-----ANOVA for Bluebunch Wheatgrass Only-----					
Treatment	2	33.01	16.50	5.18	0.049
Plot (Treatment) ¹	6	19.13	3.19	0.71	0.642
Period	6	120.46	20.08	4.49	0.002
Treatment*Period	12	23.78	1.98	0.44	0.934
Period*Plot (Treatment)	36	161.01	4.47	2.40	0.001
Error	250	469.74	1.86		
Total	314	827.12			

¹Plot within treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table B-13. Repeated measures analysis of variance of weekly (Period) water use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) of bluebunch wheatgrass and Wyoming big sagebrush (Species) leaves by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Species	1	51.02	51.02	2.58	0.134
Treatment	2	69.83	34.91	1.77	0.213
Species*Treatment	2	66.86	33.43	1.69	0.226
Plot (Species Treatment) ¹	12	237.33	19.78	0.58	0.854
Period	6	174.53	29.09	0.85	0.537
Species*Period	6	166.63	27.77	0.81	0.566
Treatment*Period	12	337.39	28.12	0.82	0.630
Species*Treatment*Period	12	334.93	27.91	0.81	0.636
Period*Plot(Species Treatment)	72	2470.38	34.31	1.76	0.001
Error	502	9811.42	19.47		
Total	629	13720.34			

¹Plot within species and treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table B-14. Individual Repeated measures analysis of variance for Wyoming big sagebrush and bluebunch wheatgrass on weekly (Period) water use efficiency ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} / \text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
-----ANOVA for Big Sagebrush Only-----					
Treatment	2	2.89	1.45	1.64	0.270
Plot (Treatment)	6	5.30	0.88	0.82	0.560
Period	11	119.77	10.89	10.08	0.001
Treatment*Period	22	16.85	0.77	0.71	0.814
Period*Plot (Treatment)	66	71.28	1.08	3.67	0.001
Error	432	127.07	0.29		
Total	539	343.16			
-----ANOVA for Bluebunch Wheatgrass Only-----					
Treatment	2	134.31	67.16	1.73	0.256
Plot (Treatment) ¹	6	233.27	38.88	0.57	0.751
Period	6	293.85	48.98	0.72	0.637
Treatment*Period	12	669.00	55.75	0.82	0.631
Period*Plot (Treatment)	36	2451.81	68.11	1.75	0.007
Error	250	9790.26	38.85		
Total	314	13572.50			

¹Plot within treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table B-15. Repeated measures analysis of variance of weekly (Period) leaf water potential (MPa) of bluebunch wheatgrass and Wyoming big sagebrush (Species) leaves by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Species	1	280.31	280.31	147.87	0.001
Treatment	2	1.69	0.84	0.44	0.651
Species*Treatment	2	1.92	0.96	0.51	0.616
Plot (Species Treatment) ¹	12	22.75	1.90	4.37	0.001
Period	6	374.30	62.38	143.76	0.001
Species*Period	6	53.60	8.93	20.59	0.001
Treatment*Period	12	10.16	0.85	1.95	0.042
Species*Treatment*Period	12	8.46	0.70	1.62	0.104
Period*Plot(Species Treatment)	72	31.24	0.43	2.73	0.001
Error	252	40.06	0.16		
Total	377	824.47			

¹Plot within species and treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table B-16. Individual Repeated measures analysis of variance for Wyoming big sagebrush and bluebunch wheatgrass on weekly (Period) leaf water potential (MPa) by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
-----ANOVA for Big Sagebrush Only-----					
Treatment	2	6.51	3.26	0.48	0.642
Plot (Treatment)	6	41.00	6.83	12.10	0.001
Period	11	178.27	16.21	28.70	0.001
Treatment*Period	22	13.03	0.59	1.05	0.423
Period*Plot (Treatment)	66	37.28	0.56	11.66	0.001
Error	216	10.46	0.05		
Total	323	286.54			
-----ANOVA for Bluebunch Wheatgrass Only-----					
Treatment	2	3.58	1.79	0.90	0.454
Plot (Treatment) ¹	6	11.90	1.98	4.77	0.001
Period	6	340.53	56.75	136.62	0.001
Treatment*Period	12	17.51	1.46	3.51	0.002
Period*Plot (Treatment)	36	15.00	0.42	1.50	0.052
Error	126	34.82	0.28		
Total	188	423.28			

¹Plot within treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

Table B-17. Repeated measures analysis of variance of weekly (Period) leaf carbon content (%) of bluebunch wheatgrass and Wyoming big sagebrush (Species) leaves by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Species	1	666.26	666.26	173.74	0.001
Treatment	2	5.54	2.77	0.72	0.506
Species*Treatment	2	4.55	2.28	0.59	0.568
Plot (Species Treatment) ¹	12	46.02	3.84	9.02	0.001
Period	6	63.57	10.60	24.91	0.001
Species*Period	6	7.09	1.18	2.78	0.017
Treatment*Period	12	5.35	0.45	1.05	0.416
Species*Treatment*Period	12	3.67	0.31	0.72	0.729
Error ²	72	30.62	0.43		
Total	125	832.67			

¹Plot within species and treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

²Error term contains the Period*Plot(Species Treatment) variance component because of insufficient degrees of freedom.

Table B-18. Individual Repeated measures analysis of variance for Wyoming big sagebrush and bluebunch wheatgrass on weekly (Period) leaf carbon content (%) by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
-----ANOVA for Big Sagebrush Only-----					
Treatment	2	7.68	3.84	0.61	0.572
Plot (Treatment)	6	37.50	6.25	24.76	0.001
Period	11	169.08	15.37	60.88	0.001
Treatment*Period	22	13.37	0.61	2.41	0.003
Error ²	66	16.66	0.25		
Total	107	244.29			
-----ANOVA for Bluebunch Wheatgrass Only-----					
Treatment	2	10.03	5.02	1.90	0.230
Plot (Treatment) ¹	6	15.86	2.64	3.82	0.005
Period	6	36.22	6.04	8.72	0.001
Treatment*Period	12	7.89	0.66	0.95	0.511
Error ²	36	24.92	0.69		
Total	62	94.93			

¹Plot within treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

²Error term contains the Period*Plot(Species Treatment) variance component because of insufficient degrees of freedom.

Table B-19. Repeated measures analysis of variance of weekly (Period) leaf nitrogen content (%) of bluebunch wheatgrass and Wyoming big sagebrush (Species) leaves by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Species	1	2.21	2.21	15.98	0.002
Treatment	2	0.09	0.04	0.32	0.732
Species*Treatment	2	0.09	0.05	0.33	0.727
Plot (Species Treatment) ¹	12	1.66	0.14	10.23	0.001
Period	6	7.37	1.23	90.89	0.001
Species*Period	6	0.06	0.01	0.76	0.604
Treatment*Period	12	0.27	0.02	1.69	0.088
Species*Treatment*Period	12	0.19	0.02	1.16	0.328
Error ²	72	0.97	0.01		
Total	125	12.91			

¹Plot within species and treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

²Error term contains the Period*Plot(Species Treatment) variance component because of insufficient degrees of freedom.

Table B-20. Individual Repeated measures analysis of variance for Wyoming big sagebrush and bluebunch wheatgrass on weekly (Period) leaf nitrogen content (%) by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
-----ANOVA for Big Sagebrush Only-----					
Treatment	2	0.16	0.082	0.47	0.644
Plot (Treatment)	6	1.03	0.172	36.51	0.001
Period	11	5.60	0.510	108.09	0.001
Treatment*Period	22	0.21	0.009	1.98	0.017
Error ²	66	0.31	0.005		
Total	107	7.32			
-----ANOVA for Bluebunch Wheatgrass Only-----					
Treatment	2	0.156	0.078	0.55	0.604
Plot (Treatment) ¹	6	0.853	0.142	6.42	0.001
Period	6	3.854	0.642	29.03	0.001
Treatment*Period	12	0.409	0.034	1.54	0.155
Error ²	36	0.800	0.022		
Total	62	6.069			

¹Plot within treatment is the subject term (random) in the repeated measures design, and is used to test the significance of the previous variance components.

²Error term contains the Period*Plot(Species Treatment) variance component because of insufficient degrees of freedom.

Table B-21. Analysis of variance of soil carbon and nitrogen content (%) by treatment (0, 11.2, and 22.4 t ha⁻¹ soil removal), plot section (Section) and sample depth (0-2.5, 2.5-5.0, 5.0-10.0 cm) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
-----Soil Carbon-----					
Treatment	2	0.238	0.119	0.62	0.543
Section	1	0.300	0.300	1.56	0.219
Treatment*Section	2	0.487	0.244	1.27	0.293
Sample Depth	2	0.961	0.480	2.51	0.096
Treatment*Sample Depth	4	0.072	0.018	0.09	0.984
Section*Sample Depth	2	0.66	0.033	0.17	0.843
Treatment*Section*Sample Depth	4	0.673	0.168	0.88	0.487
Error	36	6.896	0.192		
Total	53	9.693			
-----Soil Nitrogen-----					
Treatment	2	0.00102	0.00051	0.46	0.637
Section	1	0.00004	0.00004	0.04	0.849
Treatment*Section	2	0.00282	0.00141	1.26	0.295
Sample Depth	2	0.00776	0.00388	3.48	0.042
Treatment*Sample Depth	4	0.00038	0.00010	0.09	0.986
Section*Sample Depth	2	0.00049	0.00024	0.22	0.805
Treatment*Section*Sample Depth	4	0.00406	0.00101	0.91	0.469
Error	36	0.04015	0.00112		
Total	53	0.05671			

Table B-22. Repeated measures analysis of variance of weekly (Period) soil moisture content (%) by sample depth (0-5.0, 5.0-10.0 cm) during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
Sample Depth	1	0.01107	0.01107	65.45	0.001
Plot(Sample Depth)	16	0.00271	0.00017	8.28	0.001
Period	11	0.00552	0.00050	24.58	0.001
Sample Depth*Period	11	0.00134	0.00012	5.95	0.001
Error ¹	176	0.00359	0.00002		
Total	215	0.02423			

¹Error term contains the Period*Plot(Sample Depth) Variance component because of insufficient degrees of freedom.

Appendix C

Chapter IV Data and Statistical Output

Table C-1. Mean (n = 6) total and bare soil efflux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and plant respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) rates during the 1999 and 2000 growing seasons at the Central Plains Experimental Range research area.

Year	Week of Year	Treatment	Condition Class	Plot	Bare Soil Efflux	Total Soil Efflux	Plant Respiration ¹		
1999	24	22.4	Good	1	3.64	7.63	3.99		
		0.0	Good	5	4.18	5.24	1.05		
		11.2	Good	6	3.22	5.51	2.29		
		22.4	Good	10	4.49	6.85	2.36		
		11.2	Fair	12	4.26	6.81	2.55		
		0.0	Fair	56	5.44	8.29	2.91		
		0.0	Fair	15	3.30	6.30	3.01		
		22.4	Fair	20	3.18	6.70	3.52		
		22.4	Fair	23	3.12	6.69	3.56		
		22.4	Fair	24	3.74	6.28	2.54		
		0.0	Fair	25	3.31	6.76	3.44		
		11.2	Fair	30	3.51	7.05	3.54		
		11.2	Fair	33	3.80	7.20	3.40		
		11.2	Good	54	4.51	7.18	2.67		
		11.2	Good	45	4.74	6.87	2.13		
		22.4	Good	43	3.90	6.75	2.85		
		0.0	Good	47	5.06	6.79	1.76		
		0.0	Good	40	3.16	6.81	3.65		
		1999	25	22.4	Good	1	2.95	5.49	2.54
				0.0	Good	5	3.84	4.53	0.69
11.2	Good			6	3.40	5.28	1.89		
22.4	Good			10	3.38	6.23	2.86		
11.2	Fair			12	3.28	6.23	2.95		
0.0	Fair			56	4.28	8.24	3.97		
0.0	Fair			15	3.36	5.61	2.25		
22.4	Fair			20	3.70	6.45	2.75		
22.4	Fair			23	4.67	5.77	1.79		
22.4	Fair			24	3.78	6.54	2.75		
0.0	Fair			25	4.00	5.97	1.97		
11.2	Fair			30	3.75	6.67	2.91		
11.2	Fair			33	3.98	6.49	2.51		
11.2	Good			54	3.76	5.72	1.96		
11.2	Good			45	4.01	6.00	2.00		
22.4	Good			43	4.63	6.62	1.99		
0.0	Good			47	3.63	5.42	1.79		
0.0	Good			40	2.63	3.96	1.33		
1999	30			22.4	Good	1	3.36	4.68	1.32
				0.0	Good	5	4.36	4.65	0.38
		11.2	Good	6	3.69	5.24	1.55		
		22.4	Good	10	4.19	7.51	3.33		
		11.2	Fair	12	4.38	7.12	2.74		
		0.0	Fair	56	5.02	7.52	2.50		
		0.0	Fair	15	4.42	6.04	1.62		
		22.4	Fair	20	4.84	7.64	2.80		
		22.4	Fair	23	4.49	6.82	2.32		

Table C-1. Continued.

Year	Week of Year	Treatment	Condition Class	Plot	Bare Soil Efflux	Total Soil Efflux	Plant Respiration ¹		
1999	30	22.4	Fair	24	4.34	6.68	2.34		
		0.0	Fair	25	3.78	6.11	2.33		
		11.2	Fair	30	3.87	5.82	1.95		
		11.2	Fair	33	5.57	7.81	2.24		
		11.2	Good	54	5.04	7.19	2.15		
		11.2	Good	45	5.69	6.97	1.34		
		22.4	Good	43	5.78	7.60	1.83		
		0.0	Good	47	4.70	6.17	1.47		
		0.0	Good	40	3.63	4.19	0.66		
		1999	31	22.4	Good	1	2.38	7.96	5.58
				0.0	Good	5	2.30	6.28	3.98
				11.2	Good	6	3.57	6.60	3.03
				22.4	Good	10	3.87	8.80	4.94
				11.2	Fair	12	4.07	7.51	3.44
0.0	Fair			56	4.10	8.17	4.07		
0.0	Fair			15	4.34	7.06	2.72		
22.4	Fair			20	2.17	7.15	4.99		
22.4	Fair			23	4.01	7.44	3.43		
22.4	Fair			24	3.06	7.79	4.72		
0.0	Fair			25	4.90	6.88	1.99		
11.2	Fair			30	3.92	7.97	4.05		
11.2	Fair			33	4.53	8.35	3.82		
11.2	Good			54	5.77	8.23	2.46		
11.2	Good	45	6.32	8.78	2.46				
22.4	Good	43	5.51	8.34	2.83				
0.0	Good	47	5.20	8.44	3.24				
0.0	Good	40	4.10	8.65	4.56				
1999	32	22.4	Good	1	2.86	4.31	1.45		
		0.0	Good	5	4.87	5.52	0.72		
		11.2	Good	6	3.52	5.26	1.74		
		22.4	Good	10	4.23	7.70	3.48		
		11.2	Fair	12	5.64	7.88	2.50		
		0.0	Fair	56	5.10	6.72	1.64		
		0.0	Fair	15	3.65	4.83	1.18		
		22.4	Fair	20	6.51	4.91	0.19		
		22.4	Fair	23	4.52	5.10	0.70		
		22.4	Fair	24	4.03	4.93	1.18		
		0.0	Fair	25	4.54	4.81	0.42		
		11.2	Fair	30	3.35	5.54	2.20		
		11.2	Fair	33	4.63	5.19	1.17		
		11.2	Good	54	4.30	5.82	1.52		
11.2	Good	45	5.18	5.34	1.13				
22.4	Good	43	6.00	4.92	0.00				
0.0	Good	47	3.87	6.17	2.30				
0.0	Good	40	3.74	6.64	2.90				
1999	33	22.4	Good	1	3.08	4.85	1.77		
		0.0	Good	5	4.03	4.31	0.32		
		11.2	Good	6	3.27	4.43	1.16		

Table C-1. Continued.

Year	Week of Year	Treatment	Condition Class	Plot	Bare Soil Efflux	Total Soil Efflux	Plant Respiration ¹		
1999	33	22.4	Good	10	3.51	5.26	1.75		
		11.2	Fair	12	3.73	5.73	2.01		
		0.0	Fair	56	3.89	5.25	1.36		
		0.0	Fair	15	3.36	5.06	1.69		
		22.4	Fair	20	3.70	6.12	2.43		
		22.4	Fair	23	3.97	5.18	1.23		
		22.4	Fair	24	4.15	5.34	1.20		
		0.0	Fair	25	3.89	4.61	0.84		
		11.2	Fair	30	3.65	5.44	1.79		
		11.2	Fair	33	4.65	6.19	1.54		
		11.2	Good	54	3.88	6.79	2.91		
		11.2	Good	45	4.63	5.84	1.22		
		22.4	Good	43	4.61	5.84	1.29		
		0.0	Good	47	4.22	5.32	1.10		
		0.0	Good	40	3.53	5.38	1.84		
		1999	34	22.4	Good	1	2.60	5.96	3.36
				0.0	Good	5	3.30	3.90	0.60
11.2	Good			6	2.56	4.43	1.87		
22.4	Good			10	2.88	6.17	3.29		
11.2	Fair			12	3.58	6.01	2.49		
0.0	Fair			56	2.88	5.76	2.89		
0.0	Fair			15	2.64	5.10	2.46		
22.4	Fair			20	3.32	5.40	2.08		
22.4	Fair			23	3.16	4.74	1.58		
22.4	Fair			24	3.12	4.87	1.76		
0.0	Fair			25	3.02	4.30	1.29		
11.2	Fair			30	3.02	5.05	2.03		
11.2	Fair			33	3.47	5.30	1.83		
11.2	Good			54	3.35	5.72	2.38		
11.2	Good			45	3.50	4.88	1.39		
22.4	Good			43	3.57	5.02	1.45		
0.0	Good			47	3.17	4.83	1.66		
0.0	Good	40	3.24	4.76	1.72				
1999	35	22.4	Good	1	1.63	8.82	7.19		
		0.0	Good	5	2.87	5.61	2.74		
		11.2	Good	6	2.08	6.02	3.95		
		22.4	Good	10	2.81	8.42	5.61		
		11.2	Fair	12	3.93	7.28	3.35		
		0.0	Fair	56	4.14	7.05	2.90		
		0.0	Fair	15	2.39	6.37	3.98		
		22.4	Fair	20	1.63	8.14	6.51		
		22.4	Fair	23	2.86	7.35	4.49		
		22.4	Fair	24	2.42	6.57	4.15		
		0.0	Fair	25	4.31	5.96	1.65		
		11.2	Fair	30	3.35	6.23	2.89		
		11.2	Fair	33	3.71	6.86	3.15		
		11.2	Good	54	3.98	7.68	3.70		
		11.2	Good	45	6.49	6.52	0.74		

Table C-1. Continued.

Year	Week of Year	Treatment	Condition Class	Plot	Bare Soil Efflux	Total Soil Efflux	Plant Respiration ¹
1999	35	22.4	Good	43	4.50	5.55	1.05
		0.0	Good	47	3.15	5.47	2.31
		0.0	Good	40	3.40	7.41	4.01
1999	36	22.4	Good	1	2.18	3.41	1.23
		0.0	Good	5	3.00	2.97	0.07
		11.2	Good	6	2.33	3.22	0.89
		22.4	Good	10	2.68	4.04	1.36
		11.2	Fair	12	2.99	4.26	1.26
		0.0	Fair	56	3.34	4.05	0.71
		0.0	Fair	15	2.69	3.92	1.23
		22.4	Fair	20	3.23	4.47	1.24
		22.4	Fair	23	3.21	4.61	1.40
		22.4	Fair	24	2.92	4.69	1.77
		0.0	Fair	25	3.10	4.03	0.93
		11.2	Fair	30	2.95	4.66	1.70
		11.2	Fair	33	3.94	5.72	1.78
		11.2	Good	54	3.44	5.54	2.10
		11.2	Good	45	4.00	5.26	1.26
2000	24	22.4	Good	43	3.84	4.90	1.11
		0.0	Good	47	3.54	5.01	1.47
		0.0	Good	40	3.15	4.48	1.33
		22.4	Good	1	0.92	1.08	0.17
		0.0	Good	5	1.55	1.95	0.41
		11.2	Good	6	1.13	1.77	0.65
		22.4	Good	10	1.34	3.47	2.13
		11.2	Fair	12	1.44	3.04	1.60
		0.0	Fair	56	1.32	3.22	1.90
		0.0	Fair	15	1.41	2.20	0.79
		22.4	Fair	20	1.80	3.22	1.42
		22.4	Fair	23	1.80	2.70	0.90
		22.4	Fair	24	0.85	2.51	1.67
		0.0	Fair	25	1.35	2.18	0.83
		11.2	Fair	30	1.53	2.05	0.71
		11.2	Fair	33	1.04	2.31	1.27
		11.2	Good	54	1.99	1.88	0.07
		11.2	Good	45	2.21	2.66	0.72
		22.4	Good	43	3.07	2.40	0.00
		0.0	Good	47	1.66	2.37	0.70
		0.0	Good	40	1.44	1.54	0.10
2000	25	22.4	Good	1	0.60	0.59	0.03
		0.0	Good	5	0.81	0.83	0.11
		11.2	Good	6	0.94	0.99	0.06
		22.4	Good	10	0.80	1.15	0.35
		11.2	Fair	12	0.79	1.27	0.48
		0.0	Fair	56	0.67	0.87	0.22
		0.0	Fair	15	1.11	1.31	0.20
		22.4	Fair	20	0.77	1.35	0.57
		22.4	Fair	23	0.99	1.22	0.22

Table C-1. Continued.

Year	Week of Year	Treatment	Condition		Bare Soil Efflux	Total Soil Efflux	Plant Respiration ¹		
			Class	Plot					
2000	25	22.4	Fair	24	0.84	0.89	0.12		
		0.0	Fair	25	0.54	0.88	0.34		
		11.2	Fair	30	0.59	0.83	0.24		
		11.2	Fair	33	1.16	1.56	0.40		
		11.2	Good	54	0.91	1.57	0.65		
		11.2	Good	45	1.18	2.18	1.00		
		22.4	Good	43	0.95	1.69	0.74		
		0.0	Good	47	1.43	1.10	0.02		
		0.0	Good	40	0.63	1.23	0.60		
		2000	30	22.4	Good	1	1.73	2.98	1.25
				0.0	Good	5	1.76	2.65	0.88
				11.2	Good	6	1.71	3.00	1.30
				22.4	Good	10	2.24	4.67	2.44
				11.2	Fair	12	2.08	3.93	1.85
0.0	Fair			56	1.21	2.46	1.25		
0.0	Fair			15	2.20	3.70	1.51		
22.4	Fair			20	2.54	4.81	2.27		
22.4	Fair			23	2.54	4.18	1.63		
22.4	Fair			24	2.64	4.29	1.66		
0.0	Fair			25	2.47	3.38	0.91		
11.2	Fair			30	2.40	3.54	1.14		
11.2	Fair			33	3.29	4.68	1.39		
11.2	Good			54	2.95	4.57	1.62		
11.2	Good	45	2.99	4.37	1.38				
22.4	Good	43	3.31	4.28	1.07				
0.0	Good	47	3.19	4.36	1.17				
0.0	Good	40	2.61	3.63	1.15				
2000	31	22.4	Good	1	1.65	2.33	0.68		
		0.0	Good	5	1.38	1.92	0.54		
		11.2	Good	6	1.44	2.32	0.88		
		22.4	Good	10	1.82	4.39	2.57		
		11.2	Fair	12	1.16	2.35	1.19		
		0.0	Fair	56	0.99	1.84	0.85		
		0.0	Fair	15	1.83	3.48	1.65		
		22.4	Fair	20	1.31	3.94	2.63		
		22.4	Fair	23	1.90	3.28	1.38		
		22.4	Fair	24	2.10	2.93	0.89		
		0.0	Fair	25	1.57	3.05	1.48		
		11.2	Fair	30	1.36	3.07	1.72		
		11.2	Fair	33	2.60	4.47	1.88		
		11.2	Good	54	2.52	3.65	1.14		
11.2	Good	45	2.26	3.36	1.10				
22.4	Good	43	2.45	3.64	1.19				
0.0	Good	47	2.96	3.79	0.84				
0.0	Good	40	1.94	2.94	0.99				
2000	32	22.4	Good	1	1.18	1.32	0.18		
		0.0	Good	5	0.99	1.23	0.24		
		11.2	Good	6	0.99	1.57	0.58		

Table C-1. Continued.

Year	Week of Year	Treatment	Condition Class	Plot	Bare Soil Efflux	Total Soil Efflux	Plant Respiration ¹		
2000	32	22.4	Good	10	1.38	3.27	1.89		
		11.2	Fair	12	0.91	1.67	0.76		
		0.0	Fair	56	0.78	1.54	0.76		
		0.0	Fair	15	1.19	2.27	1.08		
		22.4	Fair	20	1.09	2.58	1.49		
		22.4	Fair	23	1.52	2.69	1.17		
		22.4	Fair	24	1.43	1.87	0.53		
		0.0	Fair	25	1.11	1.90	0.79		
		11.2	Fair	30	0.97	1.67	0.71		
		11.2	Fair	33	1.74	2.81	1.09		
		11.2	Good	54	1.68	3.80	2.12		
		11.2	Good	45	1.90	2.35	0.82		
		22.4	Good	43	1.37	3.10	1.73		
		0.0	Good	47	3.04	2.95	0.07		
		0.0	Good	40	1.34	2.90	1.56		
		2000	33	22.4	Good	1	1.37	4.23	2.86
				0.0	Good	5	1.86	4.46	2.60
				11.2	Good	6	1.97	4.18	2.21
				22.4	Good	10	2.44	5.96	3.52
				11.2	Fair	12	1.91	3.81	1.90
0.0	Fair			56	1.82	4.70	2.89		
0.0	Fair			15	1.82	3.93	2.11		
22.4	Fair			20	2.49	5.68	3.20		
22.4	Fair			23	2.01	4.87	2.86		
22.4	Fair			24	2.48	5.31	2.83		
0.0	Fair			25	2.59	3.88	1.29		
11.2	Fair			30	2.07	3.86	1.80		
11.2	Fair			33	2.88	4.14	1.26		
11.2	Good			54	3.32	3.69	0.39		
11.2	Good			45	3.01	4.11	1.10		
22.4	Good			43	3.47	4.75	1.28		
0.0	Good			47	4.31	5.11	0.80		
0.0	Good			40	3.12	6.63	3.52		
2000	34			22.4	Good	1	2.29	3.34	1.05
				0.0	Good	5	2.78	3.42	0.65
		11.2	Good	6	2.40	3.00	0.61		
		22.4	Good	10	2.78	3.95	1.17		
		11.2	Fair	12	2.57	3.64	1.07		
		0.0	Fair	56	2.70	3.56	0.88		
		0.0	Fair	15	2.41	3.74	1.33		
		22.4	Fair	20	2.86	4.72	1.86		
		22.4	Fair	23	2.51	4.31	1.81		
		22.4	Fair	24	2.75	4.41	1.66		
		0.0	Fair	25	2.69	3.88	1.20		
		11.2	Fair	30	2.27	3.98	1.71		
		11.2	Fair	33	3.41	4.93	1.57		
		11.2	Good	54	3.18	4.00	0.82		
		11.2	Good	45	3.29	4.52	1.34		

Table C-1. Continued.

Year	Week of Year	Treatment	Condition Class	Plot	Bare Soil Efflux	Total Soil Efflux	Plant Respiration ¹
2000	34	22.4	Good	43	3.69	4.55	1.05
		0.0	Good	47	2.99	4.75	1.76
		0.0	Good	40	2.66	4.02	1.37
2000	35	22.4	Good	1	1.90	2.56	0.70
		0.0	Good	5	2.16	2.63	0.47
		11.2	Good	6	1.78	2.57	0.79
		22.4	Good	10	2.10	4.39	2.29
		11.2	Fair	12	2.20	4.16	1.96
		0.0	Fair	56	2.20	3.50	1.30
		0.0	Fair	15	2.10	3.44	1.34
		22.4	Fair	20	2.40	4.22	1.82
		22.4	Fair	23	2.48	3.78	1.30
		22.4	Fair	24	2.62	3.78	1.16
		0.0	Fair	25	2.08	3.13	1.05
		11.2	Fair	30	1.73	3.56	1.84
		11.2	Fair	33	2.75	3.48	0.80
		11.2	Good	54	2.40	3.49	1.10
		11.2	Good	45	2.31	3.42	1.12
		2000	36	22.4	Good	43	2.18
0.0	Good			47	2.84	4.07	1.23
0.0	Good			40	2.03	4.46	2.43
22.4	Good			1	1.69	1.92	0.47
0.0	Good			5	1.98	1.44	0.00
11.2	Good			6	1.55	1.62	0.23
22.4	Good			10	1.77	2.66	0.89
11.2	Fair			12	2.35	2.22	0.14
0.0	Fair			56	1.55	1.51	0.16
0.0	Fair			15	1.11	1.69	0.63
22.4	Fair			20	3.02	2.00	0.40
22.4	Fair			23	1.85	1.94	0.52
22.4	Fair			24	1.70	2.48	0.78
0.0	Fair			25	1.58	2.17	0.58
11.2	Fair			30	1.41	2.18	0.76
11.2	Fair			33	2.44	2.22	0.12
11.2	Good	54	1.39	1.98	0.59		
11.2	Good	45	1.98	2.28	0.49		
22.4	Good	43	2.01	2.85	0.84		
0.0	Good	47	1.52	2.71	1.20		
0.0	Good	40	1.41	2.94	1.53		

¹Plant respiration is the difference between total and bare soil efflux.

Table C-2. Weekly mean (n = 6) chamber relative humidity (%), soil and ambient air temperature (°C) for the total and bare soil efflux measurements during the 1999 and 2000 growing seasons at the Central Plains Experimental Range research area.

Year	Week of Year	Treatment	Condition Class	Plot	Bare Soil			Total				
					Relative Humidity	Soil Temperature	Air Temperature	Relative Humidity	Soil Temperature	Air Temperature		
1999	24	22.4	Good	1	62.21	19.77	25.49	58.73	19.64	25.34		
		0.0	Good	5	62.01	20.72	24.90	50.53	20.30	25.51		
		11.2	Good	6	47.02	20.78	26.82	62.31	20.64	26.45		
		22.4	Good	10	54.49	25.60	27.77	64.44	25.94	26.87		
		11.2	Fair	12	52.68	20.95	26.68	47.21	21.43	28.05		
		0.0	Fair	56	39.53	22.03	29.62	39.11	21.53	29.96		
		0.0	Fair	15	42.14	21.62	29.74	51.88	21.98	28.65		
		22.4	Fair	20	55.93	22.01	26.93	62.47	23.07	26.51		
		22.4	Fair	23	48.36	23.73	26.90	39.26	22.60	28.29		
		22.4	Fair	24	52.64	20.96	29.23	51.10	22.66	30.32		
		0.0	Fair	25	51.07	23.32	30.32	55.62	23.27	30.36		
		11.2	Fair	30	56.38	22.54	30.38	60.43	23.66	30.81		
		11.2	Fair	33	50.10	25.27	30.30	49.25	24.25	30.70		
		11.2	Good	54	45.07	24.94	30.50	58.92	25.11	31.07		
		11.2	Good	45	48.91	25.69	30.86	72.57	25.58	29.26		
		22.4	Good	43	56.09	25.70	28.82	45.10	24.82	30.05		
		0.0	Good	47	30.90	26.52	30.17	42.22	26.26	29.92		
		0.0	Good	40	34.84	25.38	28.91	44.32	26.96	29.10		
		1999	25	22.4	Good	1	21.64	24.81	35.17	23.41	25.04	36.53
				0.0	Good	5	13.93	26.54	37.61	21.30	28.84	38.04
11.2	Good			6	19.44	26.05	38.13	28.05	29.21	39.39		
22.4	Good			10	19.76	24.92	39.22	48.12	27.64	39.66		
11.2	Fair			12	22.41	28.01	39.55	35.12	28.09	39.33		
0.0	Fair			56	21.29	26.62	40.41	50.56	28.19	40.49		
0.0	Fair			15	22.83	28.44	40.32	41.55	28.31	40.14		
22.4	Fair			20	19.53	28.16	39.66	37.58	28.85	39.97		
22.4	Fair			23	23.31	31.67	39.81	48.63	29.52	39.46		
22.4	Fair			24	23.77	28.27	39.03	47.41	29.84	38.78		
0.0	Fair			25	22.53	30.93	38.54	38.43	31.03	39.22		
11.2	Fair			30	28.02	30.22	38.98	40.15	29.87	39.24		
11.2	Fair			33	28.58	31.17	39.07	40.21	30.37	39.51		
11.2	Good			54	17.81	30.68	39.62	33.49	30.69	40.01		
11.2	Good			45	14.57	31.39	40.81	46.29	32.01	40.87		
22.4	Good			43	18.52	32.02	40.49	36.70	32.32	40.58		
0.0	Good			47	16.40	34.11	41.20	23.55	34.60	42.01		
0.0	Good			40	7.49	37.23	41.64	22.31	35.67	43.22		
1999	30			22.4	Good	1	19.24	25.24	35.21	32.20	26.22	33.81
				0.0	Good	5	27.76	26.04	34.02	22.55	26.81	35.48
		11.2	Good	6	26.11	28.08	35.95	42.69	27.72	36.35		
		22.4	Good	10	30.06	27.06	36.48	41.74	26.56	37.47		
		11.2	Fair	12	33.08	28.69	37.47	42.89	27.91	38.51		
		0.0	Fair	56	30.76	29.46	38.66	42.84	27.22	39.28		
		0.0	Fair	15	23.14	28.94	40.30	49.15	28.33	39.32		
		22.4	Fair	20	26.19	29.82	38.65	43.30	28.67	39.42		
		22.4	Fair	23	25.02	29.98	38.74	38.87	28.56	38.26		
		22.4	Fair	24	23.73	28.21	38.71	32.08	30.05	38.90		

Table C-2. Continued.

Year	Week of Year	Treatment	Condition Class	Plot	Bare Soil			Total		
					Relative Humidity	Soil Temperature	Air Temperature	Relative Humidity	Soil Temperature	Air Temperature
1999	30	0.0	Fair	25	24.47	32.00	38.92	44.71	30.24	38.48
		11.2	Fair	30	35.13	30.58	37.35	40.11	30.75	37.41
		11.2	Fair	33	32.42	32.07	37.97	35.24	30.09	38.75
		11.2	Good	54	17.34	29.62	39.57	40.55	31.42	39.85
		11.2	Good	45	28.26	32.42	37.89	58.69	32.02	35.57
		22.4	Good	43	30.49	30.53	34.35	44.22	31.11	33.86
		0.0	Good	47	30.10	32.51	33.48	42.24	31.16	33.36
		0.0	Good	40	34.52	33.08	32.73	38.62	33.78	32.49
1999	31	22.4	Good	1	43.12	22.59	32.78	38.96	22.61	34.42
		0.0	Good	5	42.47	23.90	34.48	43.59	25.23	34.10
		11.2	Good	6	58.17	24.39	32.95	47.09	24.81	33.12
		22.4	Good	10	46.30	24.29	34.59	45.08	26.42	35.35
		11.2	Fair	12	52.01	25.83	34.94	43.82	25.64	35.33
		0.0	Fair	56	61.71	25.96	33.97	47.75	24.76	33.91
		0.0	Fair	15	59.63	25.24	33.40	53.11	25.50	33.12
		22.4	Fair	20	65.34	26.09	32.83	46.23	25.95	33.39
		22.4	Fair	23	54.72	26.24	33.39	51.06	25.93	33.58
		22.4	Fair	24	48.36	24.62	34.09	43.47	26.64	34.56
		0.0	Fair	25	42.50	25.51	35.46	33.87	26.07	37.06
		11.2	Fair	30	37.21	26.06	38.23	36.01	26.89	39.12
		11.2	Fair	33	50.18	27.96	38.77	42.16	26.84	39.25
		11.2	Good	54	48.18	28.72	39.27	36.01	27.59	40.30
		11.2	Good	45	45.38	28.58	40.12	34.81	27.85	40.29
		22.4	Good	43	45.17	27.76	40.04	50.90	28.26	39.65
0.0	Good	47	56.24	29.20	38.93	47.33	29.73	37.95		
0.0	Good	40	32.97	30.43	38.17	28.86	30.37	39.99		
1999	32	22.4	Good	1	39.78	21.24	29.90	38.20	20.69	30.21
		0.0	Good	5	67.35	21.49	29.73	49.83	21.48	29.63
		11.2	Good	6	45.71	21.60	29.53	52.31	21.97	29.58
		22.4	Good	10	54.67	23.01	29.57	48.42	23.01	30.31
		11.2	Fair	12	55.41	22.83	30.06	52.33	22.54	30.01
		0.0	Fair	56	57.96	22.95	30.19	39.47	22.12	31.24
		0.0	Fair	15	37.17	22.91	30.97	45.03	22.83	31.40
		22.4	Fair	20	54.66	24.47	30.94	42.46	22.44	31.39
		22.4	Fair	23	46.16	24.76	30.09	60.20	22.75	29.18
		22.4	Fair	24	52.39	22.08	28.39	49.89	23.32	28.24
		0.0	Fair	25	39.25	23.63	27.94	52.46	22.42	27.96
		11.2	Fair	30	45.22	23.48	27.70	56.23	22.88	27.58
		11.2	Fair	33	45.99	24.95	28.16	48.65	23.54	28.47
		11.2	Good	54	40.30	24.30	29.63	50.76	23.39	30.08
		11.2	Good	45	44.22	24.53	29.19	54.15	24.11	28.76
		22.4	Good	43	71.10	24.97	27.97	45.83	23.95	28.41
0.0	Good	47	38.77	24.84	28.94	34.11	24.42	30.54		
0.0	Good	40	25.09	25.85	32.68	32.43	26.13	33.73		
1999	33	22.4	Good	1	27.07	23.32	31.68	37.79	23.53	32.69
		0.0	Good	5	26.23	24.20	33.43	33.19	24.07	34.31
		11.2	Good	6	24.78	23.24	34.85	34.12	24.15	35.27
		22.4	Good	10	26.29	24.36	34.90	35.82	24.02	35.15
		11.2	Fair	12	26.17	24.86	35.07	42.99	24.29	35.10

Table C-2. Continued.

Year	Week of Year	Treatment	Condition Class	Plot	Bare Soil			Total		
					Relative Humidity	Soil Temperature	Air Temperature	Relative Humidity	Soil Temperature	Air Temperature
1999	33	0.0	Fair	56	25.50	25.09	35.10	38.32	23.94	35.20
		0.0	Fair	15	24.34	26.63	34.82	37.56	25.06	34.70
		22.4	Fair	20	23.41	26.58	34.61	51.27	25.34	34.64
		22.4	Fair	23	30.60	26.51	33.85	44.02	25.48	33.77
		22.4	Fair	24	25.95	25.15	33.49	36.68	26.15	34.01
		0.0	Fair	25	20.96	26.80	34.55	38.47	27.63	34.89
		11.2	Fair	30	23.41	26.53	35.19	40.05	27.12	35.64
		11.2	Fair	33	26.96	26.98	35.71	32.68	26.38	36.25
		11.2	Good	54	18.35	26.80	36.28	38.83	26.45	36.67
		11.2	Good	45	25.06	29.04	36.07	44.22	27.38	35.81
		22.4	Good	43	22.45	28.74	35.33	37.59	27.90	35.17
		0.0	Good	47	23.23	29.89	35.17	34.36	28.90	35.53
		0.0	Good	40	18.66	28.80	35.74	35.94	29.91	36.49
		1999	34	22.4	Good	1	40.87	20.02	33.52	41.20
0.0	Good			5	35.31	21.29	34.58	25.38	22.48	35.31
11.2	Good			6	35.04	20.84	36.03	39.78	21.65	36.74
22.4	Good			10	35.95	22.60	37.44	39.83	21.74	38.60
11.2	Fair			12	32.80	23.39	38.56	33.35	22.82	39.28
0.0	Fair			56	27.21	23.08	40.41	31.43	23.24	41.31
0.0	Fair			15	27.76	24.76	41.58	49.47	23.39	40.45
22.4	Fair			20	44.53	24.54	37.85	53.20	23.23	36.36
22.4	Fair			23	40.74	24.46	35.53	53.94	24.71	34.90
22.4	Fair			24	49.68	23.85	29.04	57.50	23.29	26.55
0.0	Fair			25	50.20	23.15	25.12	57.74	23.93	24.47
11.2	Fair			30	53.02	23.44	24.14	56.43	23.06	23.96
11.2	Fair			33	54.69	23.66	24.02	55.41	23.48	24.17
11.2	Good			54	48.04	23.90	24.45	52.73	23.96	24.70
11.2	Good	45	50.89	24.69	24.72	54.49	24.01	24.63		
22.4	Good	43	41.04	24.51	24.74	52.85	23.98	24.61		
0.0	Good	47	45.03	24.93	25.34	51.45	24.53	25.50		
0.0	Good	40	44.02	24.53	26.21	37.60	24.54	28.12		
1999	35	22.4	Good	1	44.15	19.69	29.94	42.19	19.75	32.53
		0.0	Good	5	47.05	22.24	33.01	42.21	22.43	33.47
		11.2	Good	6	43.57	20.52	34.18	43.50	21.11	34.45
		22.4	Good	10	53.35	22.64	34.00	48.11	22.73	34.24
		11.2	Fair	12	53.47	24.42	34.14	50.07	23.18	33.99
		0.0	Fair	56	53.15	23.91	33.87	43.86	23.10	33.87
		0.0	Fair	15	52.50	23.43	33.50	43.96	23.49	33.21
		22.4	Fair	20	55.69	25.02	33.14	54.06	25.04	33.86
		22.4	Fair	23	54.17	26.05	33.36	38.76	25.07	33.56
		22.4	Fair	24	57.03	23.88	34.14	48.52	25.40	34.33
		0.0	Fair	25	51.97	26.06	34.07	55.92	25.31	33.35
		11.2	Fair	30	82.30	25.89	31.72	61.00	25.58	32.36
		11.2	Fair	33	63.60	27.25	32.60	54.68	26.27	32.58
		11.2	Good	54	60.05	26.16	32.57	70.52	27.41	32.96
11.2	Good	45	57.30	28.81	33.36	41.33	27.17	33.66		
22.4	Good	43	45.43	26.34	29.32	41.82	24.18	29.93		
0.0	Good	47	65.97	25.54	29.51	50.85	24.48	29.03		
0.0	Good	40	43.66	24.49	29.94	32.19	24.75	31.32		

Table C-2. Continued.

Year	Week of Year	Treatment	Condition Class	Plot	Bare Soil			Total				
					Relative Humidity	Soil Temperature	Air Temperature	Relative Humidity	Soil Temperature	Air Temperature		
1999	36	22.4	Good	1	29.50	15.45	28.07	30.47	16.36	29.89		
		0.0	Good	5	20.30	17.63	31.12	26.50	17.34	31.71		
		11.2	Good	6	18.90	16.57	32.27	30.07	17.86	32.80		
		22.4	Good	10	23.03	18.11	32.49	31.39	18.19	32.78		
		11.2	Fair	12	23.79	18.22	32.10	33.94	16.91	32.37		
		0.0	Fair	56	20.96	18.36	32.71	31.66	18.53	33.54		
		0.0	Fair	15	25.43	19.56	27.06	43.60	18.53	25.03		
		22.4	Fair	20	26.51	20.74	27.73	42.58	21.43	30.54		
		22.4	Fair	23	22.71	22.13	31.66	33.46	20.68	32.40		
		22.4	Fair	24	23.47	18.38	33.34	30.39	19.00	34.37		
		0.0	Fair	25	18.84	22.40	34.67	37.51	20.02	34.93		
		11.2	Fair	30	23.89	20.65	34.66	42.00	21.66	34.71		
		11.2	Fair	33	27.33	22.71	34.20	41.27	21.65	34.16		
		11.2	Good	54	24.10	25.39	33.92	52.16	23.73	34.46		
		11.2	Good	45	19.49	25.09	34.35	35.54	24.69	34.56		
		22.4	Good	43	14.07	27.53	33.88	28.07	24.29	34.15		
		0.0	Good	47	20.79	25.90	33.95	37.18	24.80	33.90		
		0.0	Good	40	20.39	25.16	33.76	28.58	26.87	34.12		
		2000	24	22.4	Good	1	19.52	18.12	26.55	23.47	20.18	26.08
				0.0	Good	5	23.23	19.85	26.39	30.92	20.66	27.07
11.2	Good			6	22.52	20.37	26.97	23.38	22.05	27.13		
22.4	Good			10	22.11	22.05	28.15	30.10	21.12	28.59		
11.2	Fair			12	19.68	22.91	28.39	25.05	22.17	28.34		
0.0	Fair			56	19.33	22.65	28.58	29.48	22.60	28.99		
0.0	Fair			15	21.76	24.34	28.85	30.93	22.91	28.70		
22.4	Fair			20	19.19	24.55	29.42	30.12	23.47	30.17		
22.4	Fair			23	16.12	25.89	29.64	25.07	24.72	29.44		
22.4	Fair			24	14.16	24.68	29.78	20.43	25.11	30.28		
0.0	Fair			25	11.97	27.32	29.97	16.12	25.54	30.24		
11.2	Fair			30	15.26	26.71	30.63	18.68	26.96	30.99		
11.2	Fair			33	15.79	26.47	30.37	25.18	25.70	30.60		
11.2	Good			54	16.60	26.88	30.02	25.23	24.14	29.65		
11.2	Good			45	15.86	27.68	29.72	21.89	26.60	30.08		
22.4	Good			43	19.49	28.05	29.62	24.60	26.89	29.75		
0.0	Good			47	14.88	29.23	30.06	21.23	28.14	30.19		
0.0	Good			40	15.03	29.16	29.94	26.86	29.37	29.33		
2000	25			22.4	Good	1	46.66	19.94	18.40	44.04	20.05	19.40
				0.0	Good	5	46.57	20.46	19.10	48.04	20.82	19.48
		11.2	Good	6	51.93	20.55	18.95	52.06	20.75	19.27		
		22.4	Good	10	35.70	21.11	20.52	38.09	21.13	21.76		
		11.2	Fair	12	47.29	21.36	20.53	49.08	21.55	19.41		
		0.0	Fair	56	40.26	21.86	19.88	53.13	21.43	19.26		
		0.0	Fair	15	50.75	21.40	18.59	54.64	21.46	18.68		
		22.4	Fair	20	51.33	21.31	18.87	85.94	21.41	18.18		
		22.4	Fair	23	60.42	20.10	20.37	66.79	20.23	20.20		
		22.4	Fair	24	61.65	20.28	19.90	58.34	20.58	20.18		
		0.0	Fair	25	44.74	20.37	21.40	40.63	20.77	22.57		
		11.2	Fair	30	40.29	20.59	23.78	41.37	21.15	24.94		
		11.2	Fair	33	40.24	20.83	24.91	42.78	21.23	25.47		

Table C-2. Continued.

Year	Week of Year	Treatment	Condition Class	Plot	Bare Soil			Total		
					Relative Humidity	Soil Temperature	Air Temperature	Relative Humidity	Soil Temperature	Air Temperature
2000	25	11.2	Good	54	28.63	21.12	26.91	43.46	21.10	27.81
		11.2	Good	45	26.01	21.61	29.06	26.35	21.51	30.07
		22.4	Good	43	21.13	23.03	30.23	28.63	24.04	30.66
		0.0	Good	47	48.21	27.96	29.28	57.62	25.29	26.09
		0.0	Good	40	50.84	24.51	23.65	126.57	25.49	21.36
2000	30	22.4	Good	1	20.75	22.99	33.12	28.69	24.41	33.14
		0.0	Good	5	21.50	25.17	33.32	26.87	26.34	33.36
		11.2	Good	6	18.62	25.26	33.45	27.90	25.64	33.57
		22.4	Good	10	21.85	25.08	33.56	36.24	25.35	33.63
		11.2	Fair	12	20.26	25.42	33.58	34.85	25.80	33.64
		0.0	Fair	56	19.07	26.31	33.73	27.96	26.60	33.84
		0.0	Fair	15	20.23	26.51	33.80	36.83	26.69	33.75
		22.4	Fair	20	18.26	26.82	33.68	41.14	26.21	33.83
		22.4	Fair	23	20.07	28.02	33.78	36.51	26.53	33.90
		22.4	Fair	24	19.79	26.68	34.12	33.17	26.60	34.25
		0.0	Fair	25	17.23	27.83	34.94	40.82	26.77	34.96
		11.2	Fair	30	22.31	28.35	33.51	34.33	29.13	33.52
		11.2	Fair	33	22.53	28.66	33.40	38.86	27.53	33.35
		11.2	Good	54	20.05	28.15	33.39	46.10	26.55	33.48
		11.2	Good	45	19.93	29.46	33.43	37.82	29.11	33.50
22.4	Good	43	17.43	29.10	33.36	35.31	28.36	33.33		
0.0	Good	47	23.95	30.20	33.22	35.54	29.56	33.22		
0.0	Good	40	23.65	30.67	33.10	38.01	29.17	32.97		
2000	31	22.4	Good	1	28.83	24.39	31.20	30.02	24.92	31.51
		0.0	Good	5	24.16	27.03	31.73	29.85	27.50	31.91
		11.2	Good	6	24.69	27.51	32.21	28.45	28.11	32.53
		22.4	Good	10	23.34	27.37	32.42	38.43	26.71	32.56
		11.2	Fair	12	18.37	28.67	32.47	27.16	28.85	32.96
		0.0	Fair	56	18.41	29.62	33.13	25.44	28.48	33.44
		0.0	Fair	15	18.61	28.88	33.38	27.72	29.06	33.34
		22.4	Fair	20	16.43	29.51	33.01	38.98	29.45	33.28
		22.4	Fair	23	20.87	29.68	33.33	36.43	28.80	33.30
		22.4	Fair	24	20.46	29.18	33.86	28.44	28.35	34.01
		0.0	Fair	25	17.73	29.13	34.13	28.99	30.15	34.34
		11.2	Fair	30	19.44	29.70	34.32	37.47	30.23	33.88
		11.2	Fair	33	29.62	30.98	31.75	44.75	30.02	31.25
		11.2	Good	54	30.96	29.44	30.90	49.18	28.83	30.66
		11.2	Good	45	31.95	31.12	30.42	42.88	30.05	30.36
22.4	Good	43	33.71	30.35	30.32	44.40	30.43	30.26		
0.0	Good	47	39.27	31.25	30.22	49.67	30.33	30.19		
0.0	Good	40	38.20	31.04	30.17	47.96	30.70	30.19		
2000	32	22.4	Good	1	33.03	25.89	30.51	35.58	24.32	30.62
		0.0	Good	5	33.92	24.48	30.72	31.35	24.44	30.96
		11.2	Good	6	33.22	24.57	31.02	31.95	25.55	31.08
		22.4	Good	10	24.97	24.99	31.12	37.76	25.56	31.26
		11.2	Fair	12	25.20	25.39	31.42	21.23	25.72	31.42
		0.0	Fair	56	25.92	25.65	31.57	28.97	25.38	31.69
		0.0	Fair	15	26.14	25.08	31.66	31.21	25.09	31.65
		22.4	Fair	20	22.18	27.43	31.64	25.62	27.57	31.70

Table C-2. Continued.

Year	Week of Year	Treatment	Condition Class	Plot	Bare Soil			Total				
					Relative Humidity	Soil Temperature	Air Temperature	Relative Humidity	Soil Temperature	Air Temperature		
2000	32	22.4	Fair	23	22.41	27.67	31.75	32.52	27.37	31.90		
		22.4	Fair	24	18.51	25.71	32.27	27.71	26.13	32.47		
		0.0	Fair	25	19.93	26.07	33.04	31.63	27.43	33.42		
		11.2	Fair	30	19.70	27.41	33.72	25.85	28.68	34.41		
		11.2	Fair	33	17.06	29.38	33.95	24.19	28.49	34.21		
		11.2	Good	54	16.21	28.79	33.97	42.99	26.86	34.32		
		11.2	Good	45	17.74	30.53	34.61	28.65	30.13	34.83		
		22.4	Good	43	10.94	31.34	35.04	22.08	30.53	35.23		
		0.0	Good	47	18.09	30.55	35.53	22.74	29.55	35.94		
		0.0	Good	40	11.87	32.17	35.93	28.55	31.18	36.67		
		2000	33	22.4	Good	1	49.06	19.28	25.61	38.44	19.00	26.87
				0.0	Good	5	44.93	18.96	27.72	40.38	19.19	28.30
				11.2	Good	6	49.76	19.56	28.77	46.35	19.42	28.47
				22.4	Good	10	56.01	20.17	27.75	46.25	19.85	28.22
11.2	Fair			12	58.05	20.43	28.03	44.62	20.54	28.13		
0.0	Fair			56	57.99	20.22	27.97	43.34	20.49	28.30		
0.0	Fair			15	47.70	20.23	29.20	35.01	20.45	29.72		
22.4	Fair			20	53.60	21.23	29.23	46.43	20.87	29.64		
22.4	Fair			23	54.21	21.91	30.57	43.19	21.76	30.54		
22.4	Fair			24	56.35	20.96	29.65	46.31	21.26	29.09		
0.0	Fair			25	53.23	21.76	28.61	46.82	21.84	27.88		
11.2	Fair			30	54.17	22.27	26.87	53.16	22.22	26.58		
11.2	Fair			33	62.02	22.10	26.51	44.19	21.90	27.03		
11.2	Good			54	44.63	22.04	28.13	45.30	21.81	28.97		
11.2	Good	45	53.37	23.56	29.82	45.05	22.86	29.93				
22.4	Good	43	43.28	22.82	30.59	34.81	22.92	31.91				
0.0	Good	47	55.13	23.69	32.31	40.87	22.55	30.97				
0.0	Good	40	56.78	23.18	30.92	53.54	23.48	30.77				
2000	34	22.4	Good	1	31.99	21.01	28.71	38.66	21.06	29.74		
		0.0	Good	5	34.40	22.10	30.13	45.07	22.07	30.14		
		11.2	Good	6	36.51	22.03	30.11	44.73	22.06	30.13		
		22.4	Good	10	41.75	22.11	30.10	58.29	22.13	30.03		
		11.2	Fair	12	43.32	21.81	29.94	58.21	22.02	29.85		
		0.0	Fair	56	36.16	22.20	30.16	35.48	21.86	30.64		
		0.0	Fair	15	24.03	22.90	31.06	39.46	23.28	31.18		
		22.4	Fair	20	26.48	23.95	31.35	33.76	23.57	31.63		
		22.4	Fair	23	25.29	23.66	31.63	43.63	23.66	31.69		
		22.4	Fair	24	22.54	22.40	31.72	38.05	22.13	31.63		
		0.0	Fair	25	23.49	24.62	31.59	37.88	23.65	31.79		
		11.2	Fair	30	23.39	24.70	31.96	39.33	24.56	31.79		
		11.2	Fair	33	29.02	24.34	31.47	53.69	24.27	31.01		
		11.2	Good	54	28.83	24.28	30.91	29.30	23.76	31.15		
11.2	Good	45	16.44	25.48	31.64	41.15	24.58	31.81				
22.4	Good	43	29.96	24.91	31.50	48.87	25.04	31.43				
0.0	Good	47	28.28	25.60	31.19	50.83	25.48	30.84				
0.0	Good	40	38.14	26.51	30.44	47.66	26.28	30.26				
2000	35	22.4	Good	1	43.22	20.29	26.09	44.99	20.11	27.05		
		0.0	Good	5	36.69	21.26	28.32	39.08	21.63	29.33		
		11.2	Good	6	28.64	20.75	30.63	35.72	21.14	31.38		

Table C-2. Continued.

Year	Week of Year	Treatment	Condition Class	Plot	Bare Soil			Total				
					Relative Humidity	Soil Temperature	Air Temperature	Relative Humidity	Soil Temperature	Air Temperature		
2000	35	22.4	Good	10	29.84	21.38	30.66	48.47	21.13	30.64		
		11.2	Fair	12	34.83	21.44	30.50	52.32	21.54	30.52		
		0.0	Fair	56	41.72	22.04	30.44	46.70	22.01	30.69		
		0.0	Fair	15	35.76	22.52	30.73	50.77	23.03	30.69		
		22.4	Fair	20	32.03	23.53	30.72	62.59	23.11	30.70		
		22.4	Fair	23	33.78	24.24	30.79	62.39	23.83	30.78		
		22.4	Fair	24	34.37	21.56	30.89	51.50	21.66	30.88		
		0.0	Fair	25	33.73	23.03	30.73	46.24	23.13	30.85		
		11.2	Fair	30	36.42	23.40	30.64	50.01	23.45	30.74		
		11.2	Fair	33	28.89	23.27	30.98	42.90	23.45	31.10		
		11.2	Good	54	25.06	24.26	31.13	48.37	23.34	31.06		
		11.2	Good	45	32.05	24.60	30.79	60.60	24.06	30.60		
		22.4	Good	43	29.92	24.55	30.58	40.82	24.69	30.84		
		0.0	Good	47	31.17	25.33	31.04	37.41	23.92	31.22		
		0.0	Good	40	26.74	25.77	31.41	50.78	25.07	31.56		
		2000	36	22.4	Good	1	22.39	18.57	24.11	33.06	18.64	25.13
				0.0	Good	5	25.20	19.63	25.46	38.63	19.91	25.78
11.2	Good			6	25.76	19.21	25.91	33.61	19.04	26.75		
22.4	Good			10	23.44	19.07	27.68	40.64	19.35	28.37		
11.2	Fair			12	22.73	19.66	28.13	38.56	19.52	28.52		
0.0	Fair			56	24.15	20.25	28.67	30.53	20.64	29.19		
0.0	Fair			15	18.88	19.97	29.07	21.91	20.27	30.43		
22.4	Fair			20	20.38	20.99	30.62	46.14	20.43	30.01		
22.4	Fair			23	19.56	20.55	30.10	29.10	20.57	30.30		
22.4	Fair			24	20.85	19.99	30.45	32.28	19.79	30.64		
0.0	Fair			25	16.75	20.67	31.12	39.63	20.35	30.54		
11.2	Fair			30	20.40	21.14	31.41	35.52	21.32	32.34		
11.2	Fair			33	24.47	21.82	31.44	54.12	21.16	30.30		
11.2	Good			54	24.77	21.74	28.73	47.30	20.84	28.31		
11.2	Good			45	19.21	22.29	29.23	31.80	22.34	29.80		
22.4	Good			43	22.84	22.45	30.20	40.14	22.38	30.85		
0.0	Good			47	25.19	23.60	30.29	41.24	23.91	30.51		
0.0	Good	40	23.40	24.28	30.90	44.46	23.60	31.31				

Table C-3. Mean (n = 6) total and bare soil efflux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and plant respiration (total - bare soil; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) rates during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Year	Week of Year	Treatment	Plot	Bare Soil Efflux	Total Soil Efflux	Plant Respiration ¹		
2000	24	0.0	2	0.98	1.52	0.54		
		22.4	3	1.01	2.29	1.27		
		11.2	18	0.97	1.82	0.85		
		0.0	20	0.99	2.11	1.12		
		11.2	22	1.07	1.54	0.47		
		22.4	24	1.01	1.77	0.76		
		11.2	26	0.85	2.02	1.17		
		22.4	29	0.88	1.23	0.36		
		0.0	30	0.80	1.29	0.48		
		2000	25	0.0	2	0.97	1.34	0.37
22.4	3			1.04	1.98	0.94		
11.2	18			0.83	1.37	0.55		
0.0	20			0.72	2.05	1.33		
11.2	22			1.17	1.71	0.54		
22.4	24			1.37	1.85	0.48		
11.2	26			0.91	2.35	1.44		
22.4	29			0.95	1.40	0.45		
0.0	30			0.98	1.76	0.78		
2000	26			0.0	2	0.93	1.79	0.86
		22.4	3	0.94	1.92	0.99		
		11.2	18	0.84	1.45	0.61		
		0.0	20	0.73	1.71	0.98		
		11.2	22	1.05	1.46	0.41		
		22.4	24	1.09	1.70	0.64		
		11.2	26	0.80	2.12	1.32		
		22.4	29	0.89	1.35	0.46		
		0.0	30	0.89	1.46	0.57		
		2000	28	0.0	2	0.96	1.69	0.72
22.4	3			0.88	1.67	0.79		
11.2	18			0.87	1.31	0.44		
0.0	20			0.64	1.51	0.87		
11.2	22			0.98	1.25	0.26		
22.4	24			0.90	1.85	0.95		
11.2	26			0.73	1.79	1.05		
22.4	29			0.90	1.17	0.27		
0.0	30			0.75	0.99	0.24		
2000	29			0.0	2	0.60	0.78	0.18
		22.4	3	0.56	1.34	0.78		
		11.2	18	0.57	0.83	0.26		
		0.0	20	0.52	0.79	0.29		
		11.2	22	0.59	0.84	0.24		
		22.4	24	0.46	0.90	0.44		
		11.2	26	0.41	1.15	0.74		
		22.4	29	0.55	0.69	0.14		
		2000	31	0.0	30	0.44	0.52	0.12
				0.0	2	0.69	0.88	0.19
22.4	3			0.63	1.08	0.45		

Table C-3. Continued.

Year	Week of Year	Treatment	Plot	Bare Soil Efflux	Total Soil Efflux	Plant Respiration ¹
2000	31	11.2	18	0.51	0.67	0.16
		0.0	20	0.42	0.74	0.33
		11.2	22	0.61	0.73	0.12
		22.4	24	0.53	0.82	0.28
		11.2	26	0.41	1.03	0.63
		22.4	29	0.54	0.67	0.13
		0.0	30	0.52	0.55	0.15
2000	32	0.0	2	0.75	1.09	0.35
		22.4	3	0.65	1.09	0.44
		11.2	18	0.51	0.66	0.15
		0.0	20	0.41	0.78	0.37
		11.2	22	0.59	0.72	0.13
		22.4	24	0.54	0.77	0.23
		11.2	26	0.37	0.97	0.60
		22.4	29	0.55	0.66	0.11
		0.0	30	0.35	0.49	0.14

¹Plant respiration is the difference between total and bare soil efflux.

Table C-4. Weekly mean (n = 6) chamber relative humidity (%), and soil and ambient air temperature (°C) for the total and bare soil efflux measurements during the 2000 growing season at the Arapaho National Wildlife Refuge research area.

Year	Week of Year	Treatment	Plot	Bare Soil			Total		
				Relative Humidity	Soil Temperature	Air Temperature	Relative Humidity	Soil Temperature	Air Temperature
2000	24	0.0	2	8.49	20.42	30.62	22.00	16.58	28.95
		22.4	3	12.24	24.51	31.02	29.06	23.18	32.26
		11.2	18	12.01	19.03	31.52	26.48	22.89	31.11
		0.0	20	11.13	25.56	29.84	24.85	24.28	30.02
		11.2	22	11.80	25.09	28.38	27.26	28.25	29.27
		22.4	24	14.81	26.91	27.95	23.84	24.61	27.70
		11.2	26	9.45	25.10	27.51	39.18	26.71	27.08
		22.4	29	7.95	21.47	29.78	26.17	24.29	28.25
		0.0	30	12.30	24.79	29.10	18.67	22.13	30.09
		2000	25	0.0	2	20.33	16.05	27.08	32.51
22.4	3			20.07	17.49	29.08	37.05	17.00	28.50
11.2	18			21.92	15.98	29.86	28.46	19.28	30.37
0.0	20			11.32	22.44	33.90	26.12	18.68	29.85
11.2	22			9.84	21.12	35.06	28.93	21.79	35.21
22.4	24			13.80	23.39	34.96	18.22	19.34	34.08
11.2	26			10.38	22.78	35.21	29.56	21.54	34.51
22.4	29			13.23	22.04	36.16	22.73	26.29	35.55
2000	26	0.0	30	11.72	21.98	35.71	24.36	21.17	34.79
		0.0	2	10.50	15.59	28.85	13.84	14.04	27.42
		22.4	3	11.65	19.11	32.27	28.92	17.51	30.82
		11.2	18	13.93	15.35	32.22	22.33	18.23	32.97
		0.0	20	7.69	22.79	34.91	20.43	18.05	31.32

Table C-4. Continued.

Year	Week of Year	Treatment	Plot	Bare Soil			Total		
				Relative Humidity	Soil Temperature	Air Temperature	Relative Humidity	Soil Temperature	Air Temperature
2000	26	11.2	22	7.58	22.43	35.71	16.73	21.64	34.54
		22.4	24	9.79	21.35	35.28	14.15	20.86	35.60
		11.2	26	8.77	21.83	34.09	24.49	23.86	33.55
		22.4	29	7.99	19.80	35.41	20.97	22.77	34.11
		0.0	30	7.24	21.85	35.71	14.12	21.93	35.13
2000	28	0.0	2	12.54	19.74	34.51	14.86	17.97	33.45
		22.4	3	8.73	21.79	38.09	16.64	21.07	35.98
		11.2	18	16.94	19.38	31.48	19.68	21.97	34.43
		0.0	20	9.66	24.32	32.26	22.87	22.67	31.46
		11.2	22	12.43	24.49	33.12	24.66	23.79	32.61
		22.4	24	9.33	23.96	34.34	11.63	28.07	33.52
		11.2	26	10.39	27.08	33.93	24.63	23.99	34.14
		22.4	29	13.22	24.24	33.40	28.03	26.97	32.51
		0.0	30	16.47	26.95	31.38	24.60	27.62	31.88
2000	29	0.0	2	12.46	20.06	35.22	23.39	18.31	34.44
		22.4	3	15.97	22.47	31.35	29.89	21.45	31.91
		11.2	18	17.17	18.91	30.96	23.41	20.52	31.40
		0.0	20	7.46	24.41	31.87	17.65	21.53	30.78
		11.2	22	6.71	25.74	31.35	21.58	24.41	31.51
		22.4	24	8.01	27.18	31.42	11.08	26.85	31.17
		11.2	26	6.65	25.81	31.20	21.31	27.24	30.91
		22.4	29	7.46	24.89	30.87	16.63	25.83	31.07
2000	31	0.0	30	7.75	29.04	30.95	14.49	25.93	30.81
		0.0	2	12.99	20.37	33.06	24.05	18.72	30.23
		22.4	3	14.65	22.75	33.58	22.84	21.20	32.67
		11.2	18	14.14	20.36	34.24	16.11	23.95	34.19
		0.0	20	7.79	26.26	36.06	13.73	22.05	33.24
		11.2	22	7.97	24.93	32.66	19.46	26.78	34.14
		22.4	24	8.40	25.00	33.28	12.34	24.80	32.00
		11.2	26	7.18	25.40	34.35	18.01	26.34	33.66
		22.4	29	17.17	24.34	31.10	19.10	28.36	34.43
		0.0	30	21.09	26.57	30.86	36.05	28.32	30.05
		2000	32	0.0	2	12.82	18.84	32.46	17.26
22.4	3			12.49	23.30	30.95	24.83	19.58	31.06
11.2	18			15.74	19.58	30.67	13.42	20.45	31.11
0.0	20			11.60	23.46	31.60	12.62	21.95	31.13
11.2	22			9.47	22.82	31.76	16.44	23.58	31.46
22.4	24			7.57	22.40	31.68	10.31	23.97	31.52
11.2	26			6.69	25.68	31.61	14.78	23.30	31.47
22.4	29			10.07	22.15	31.84	14.65	24.28	31.66
0.0	30			7.63	25.09	31.86	13.40	22.09	31.52

Table C-5. Pearson correlations matrix showing correlations (r, P-value) among total and bare soil efflux ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) rates and soil moisture (0-5 and 5-10 cm), soil and ambient air temperature ($^{\circ}\text{C}$), and relative humidity (%) at both the Central Plains Experimental Range and Arapaho National Wildlife Refuge research areas.

Variable	Central Plains Experimental Range		Arapaho National Wildlife Refuge	
	Total Soil Efflux	Bare Soil Efflux	Total Soil Efflux	Bare Soil Efflux
Soil Moisture				
0 - 5 cm	0.28 (P < 0.001)	0.22 (P < 0.001)	0.47 (P < 0.001)	0.56 (P < 0.001)
5 - 10 cm	0.47 (P < 0.001)	0.45 (P < 0.001)	0.17 (P = 0.001)	0.23 (P < 0.001)
Temperature ($^{\circ}\text{C}$)				
Soil	0.23 (P < 0.001)	0.29 (P < 0.001)	-0.17 (P = 0.001)	-0.30 (P < 0.001)
Air	0.49 (P < 0.001)	0.44 (P < 0.001)	0.00 (P = 1.0)	0.08 (P = 0.147)
Relative Humidity	0.26 (P < 0.001)	0.25 (P < 0.001)	0.43 (P < 0.001)	0.18 (P = 0.001)

Table C-6. Repeated measures analysis of variance for weekly (Period) total and bare soil efflux, and plant respiration rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for both the Central Plains Experimental Range and Arapaho National Wildlife Refuge research areas (Site) during the 2000 growing season.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
-----Total Soil Efflux-----					
Site	1	603.78	603.78	56.14	0.001
Treatment	2	2.44	1.22	0.11	0.894
Site*Treatment	2	0.75	0.38	0.04	0.966
Plot (Site Treatment)	12	129.05	10.75	40.80	0.001
Period	6	163.32	27.22	30.01	0.001
Site*Period	6	379.66	63.28	69.75	0.001
Treatment*Period	12	14.52	1.21	1.33	0.219
Site*Treatment*Period	12	12.83	1.07	1.18	0.315
Period*Plot (Site Treatment)	72	65.31	0.91	3.44	0.001
Error	630	166.04	0.26		
Total	756	1537.71			

Table C-6. Continued.

Source of Variance	DF	Sums of Squares	Mean Squares	F-Value	P-Value
-----Bare Soil Efflux-----					
Site	1	317.55	317.55	43.13	0.001
Treatment	2	0.32	0.17	0.02	0.978
Site*Treatment	2	2.34	1.17	0.16	0.855
Plot (Site Treatment)	12	88.34	7.36	108.19	0.001
Period	6	63.89	10.65	21.41	0.001
Site*Period	6	117.85	19.64	39.49	0.001
Treatment*Period	12	3.28	0.27	0.55	0.874
Site*Treatment*Period	12	2.64	0.22	0.44	0.941
Period*Plot (Site Treatment)	72	35.81	0.50	7.31	0.001
Error	630	42.87	0.07		
Total	756	674.88			
-----Plant Respiration-----					
Site	1	53.43	53.43	10.34	0.007
Treatment	2	4.63	2.31	0.45	0.649
Site*Treatment	2	5.01	2.51	0.49	0.627
Plot (Site Treatment)	12	61.97	5.16	16.78	0.001
Period	6	30.86	5.14	4.09	0.001
Site*Period	6	80.97	13.50	10.73	0.001
Treatment*Period	12	13.86	1.16	0.92	0.533
Site*Treatment*Period	12	10.47	0.87	0.69	0.752
Period*Plot (Site Treatment)	72	90.56	1.26	4.09	0.001
Error	630	193.90	0.31		
Total	756	545.66			

Table C-7. Repeated measures analysis of covariance for weekly (Period) total and bare soil efflux, and plant respiration rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) among the soil removal treatments (Treatments, 0, 11.2, and 22.4 t ha^{-1} soil removal) for the good and fair condition classes (Class) during the 1999 and 2000 growing seasons (Year) at the Central Plains Experimental Range research area.

Source of Variance	DF	Sums	Adjusted	Mean Squares	F	P
		of Squares	Sums of Squares			
-----Total Soil Efflux-----						
Air Temperature	1	2000.19	21.84	21.84	32.95	0.001
Class	1	0.41	1.30	1.30	0.23	0.641
Treatment	2	70.30	76.78	38.39	5.71	0.017
Class*Treatment	2	11.93	18.57	9.28	1.25	0.322
Plot (Class Treatment)	12	173.75	94.30	7.86	1.78	0.171
Year	1	2774.74	7.17	7.17	10.06	0.002
Class*Year	1	4.82	1.52	1.52	0.34	0.571
Treatment*Year	2	13.26	15.55	7.78	1.70	0.224
Class*Treatment*Year	2	21.41	10.08	5.04	1.16	0.347
Year*Plot (Class Treatment)	12	47.28	53.15	4.43	2.24	0.015
Period	8	846.93	737.32	92.17	48.53	0.001
Class*Period	8	30.10	42.87	5.36	2.79	0.008
Treatment*Period	16	33.27	42.81	2.68	1.34	0.190
Class*Treatment*Period	16	29.10	33.94	2.12	1.06	0.406
Period*Plot (Class Treatment)	96	183.04	197.73	2.06	1.00	0.506
Year*Period	8	879.08	894.62	111.83	58.66	0.001
Class*Year*Period	8	18.05	26.73	3.34	1.73	0.099
Treatment*Year*Period	16	35.13	46.99	2.94	1.47	0.128
Class*Treatment*Year*Period	16	24.45	36.18	2.26	1.12	0.346
Year*Period*Plot (Class Treatment)	96	198.38	198.38	2.07	3.12	0.001
Error	1615	1070.43	1070.43	0.66		
Total	1939	8466.02				
Term		Coefficient		SD	T	P
Constant		-11.819		2.85	-4.15	0.001
Air Temperature		0.513		0.09	5.74	0.001

Table C-7. Continued.

Source of Variance	DF	Sums of Squares	Adjusted Sums of Squares	Mean Squares	F	P
Bare Soil Efflux						
Air Temperature	1	648.65	0.01	0.01	0.04	0.838
Class	1	14.12	3.26	3.26	0.41	0.534
Treatment	2	7.66	10.65	5.32	0.49	0.625
Class*Treatment	2	0.86	2.21	1.10	0.10	0.909
Plot (Class Treatment)	12	215.64	153.20	12.77	3.09	0.040
Year	1	1177.09	38.73	38.73	119.71	0.001
Class*Year	1	2.34	2.88	2.88	0.68	0.427
Treatment*Year	2	8.87	9.25	4.62	0.99	0.401
Class*Treatment*Year	2	7.28	6.47	3.24	0.84	0.454
Year*Plot (Class Treatment)	12	54.38	53.10	4.43	2.95	0.002
Period	8	169.33	119.89	14.99	12.81	0.001
Class*Period	8	16.34	14.77	1.85	1.54	0.152
Treatment*Period	16	23.17	23.17	1.45	1.16	0.316
Class*Treatment*Period	16	17.57	17.23	1.08	0.86	0.618
Period*Plot (Class Treatment)	96	130.13	123.96	1.29	0.82	0.838
Year*Period	8	334.13	334.45	41.81	29.31	0.001
Class*Year*Period	8	11.57	11.68	1.46	1.00	0.438
Treatment*Year*Period	16	28.90	27.80	1.74	1.14	0.332
Class*Treatment*Year*Period	16	16.07	12.69	0.79	0.52	0.934
Year*Period*Plot (Class Treatment)	96	151.75	151.75	1.58	7.07	0.001
Error	1615	361.17	361.16	0.22		
Total	1939	3396.98				
Term		Coefficient		SD	T	P
Constant		3.124		1.26	2.48	0.013
Air Temperature		-0.008		0.04	-0.21	0.838
Plant Respiration						
Air Temperature	1	359.83	10.85	10.85	15.00	0.001
Class	1	15.35	2.75	2.75	0.25	0.623
Treatment	2	85.78	81.23	40.61	3.15	0.079
Class*Treatment	2	12.58	18.22	9.11	0.63	0.547

Table C-7. Continued.

Source of Variance	DF	Sums	Adjusted	Mean Squares	F	P
		of Squares	Sums of Squares			
Plot (Class Treatment)	12	178.53	182.20	15.18	4.07	0.32
Year	1	354.59	0.25	0.25	0.32	0.574
Class*Year	1	0.60	0.002	0.002	0.00	0.984
Treatment*Year	2	9.90	14.14	7.07	1.49	0.265
Class*Treatment*Year	2	6.24	5.23	2.62	0.58	0.576
Year*Plot (Class Treatment)	12	61.29	55.20	4.60	1.75	0.068
Period	8	450.21	445.05	55.63	32.54	0.001
Class*Period	8	28.14	31.51	3.94	2.28	0.027
Treatment*Period	16	52.22	58.39	6.65	2.04	0.017
Class*Treatment*Period	16	21.35	21.65	1.35	0.75	0.733
Period*Plot (Class Treatment)	96	168.14	176.44	1.84	0.66	0.977
Year*Period	8	433.53	438.43	54.80	21.62	0.001
Class*Year*Period	8	16.65	20.67	2.58	1.01	0.436
Treatment*Year*Period	16	70.21	76.98	4.81	1.80	0.042
Class*Treatment*Year*Period	16	37.39	37.97	2.37	0.88	0.592
Year*Period*Plot (Class Treatment)	96	265.77	265.77	2.77	3.83	0.001
Error	1615	1168.40	1168.40	0.72		
Total	1939	3796.69				
Term		Coefficient		SD	T	P
Constant		-9.810		2.98	-3.30	0.001
Air Temperature		0.361		0.09	3.87	0.001

Table C-8. Repeated measures analysis of covariance for weekly (Period) total and bare soil efflux, and plant respiration rates ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) among the soil removal treatments (Treatments, 0, 11.2, and 22.4 t ha⁻¹ soil removal) during 2000 growing season at the Arapaho National Wildlife Refuge research area.

Source of Variance	DF	Sums of Squares	Mean Squares	F	P
-----Total Soil Efflux-----					
Treatment	2	0.90	0.45	0.16	0.856
Plot (Class Treatment)	6	16.99	2.83	13.88	0.001
Period	6	66.72	11.12	54.50	0.001
Treatment*Period	12	0.71	0.06	0.29	0.987
Period*Plot (Class Treatment)	36	7.35	0.20	1.09	0.345
Error	315	59.22	0.19		
Total	377	151.89			
-----Bare Soil Efflux-----					
Treatment	2	0.49	0.24	0.63	0.563
Plot (Class Treatment)	6	2.32	0.39	8.42	0.001
Period	6	15.08	2.51	54.79	0.001
Treatment*Period	12	0.38	0.03	0.69	0.753
Period*Plot (Class Treatment)	36	1.65	0.05	3.26	0.001
Error	315	4.44	0.01		
Total	377	24.36			
-----Plant Respiration-----					
Treatment	2	0.20	0.10	0.03	0.972
Plot (Class Treatment)	6	20.88	3.48	22.14	0.001
Period	6	18.13	3.02	19.23	0.001
Treatment*Period	12	1.42	0.12	0.75	0.692
Period*Plot (Class Treatment)	36	5.66	0.16	0.78	0.816
Error	315	63.48	0.20		
Total	377	109.77			