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**NUTRIENT DYNAMICS AND FIRE HISTORY IN MESQUITE
(*Prosopis spp.*)-DOMINATED DESERT GRASSLANDS OF THE
SOUTHWESTERN UNITED STATES**

by

Thomas Bachman Wilson

**A Dissertation Submitted to the Faculty of the
DEPARTMENT OF SOIL, WATER AND ENVIRONMENTAL SCIENCE**

**In Partial Fulfillment of the Requirements
For the Degree of**

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WITH A MAJOR IN SOIL AND WATER SCIENCE**

In the Graduate College

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As members of the Final Examination Committee, we certify that we have read the dissertation prepared by Thomas Bachman Wilson entitled Nutrient Dynamics and Fire History in Mesquite (Prosopis spp.)-Dominated Desert Grasslands of the Southwestern United States

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy

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SIGNED: A handwritten signature in black ink, appearing to read "James B. ...", is written over a horizontal line.

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ABSTRACT

In desert grasslands of the southwestern United States, *Prosopis velutina* (mesquite), an N-fixing legume, has proliferated from historic drainage locations into more xeric grassland plains. This expansion is forming a more heterogenous soil nutrient topography in grasslands; N-pools are becoming localized under mesquite canopies, yet the rate and extent of this sequestration remains relatively unknown. Repeated prescribed burning has been used to control *Prosopis* distribution, but effects of fires on grassland soil nutrient distribution and aboveground plant biomass are also largely unknown. I examined recent research concerning *P. velutina* natural history, emphasizing characteristics that contribute to range expansion. I also evaluated *Prosopis* management practices—which include herbicide treatment, prescribed burning, grazing reduction, and mechanical removal—and management goals—which involve complete removal, no removal, and limited removal. Of these, limited removal is the most beneficial, using an herbicide application followed by periodic prescribed burning. In 1997 I established a study area at Fort Huachuca Military Reservation in southeastern Arizona, selecting two adjacent sites with similar soil composition and topography but different fire histories. I examined spatial and seasonal changes in composition and distribution of available soil N and litterfall. My results indicated these were more spatially and temporally heterogenous on sites with low fire frequency and high *P. velutina* stand development. In 1998 I selected nine sites at Fort Huachuca on two upland surfaces located < 1 km apart, with similar soil physical characteristics and fire frequencies ranging from 0 to 5 fires/decade. I evaluated relationships between fire frequency, soil nutrient status (pH, available P, organic C, total N, and available N), and aboveground plant biomass.

including that of the non-native *Eragrostis lehmanniana* (Lehmann lovegrass). Soil pH and ammonium significantly decreased with increased fire frequency on one surface, and available P significantly decreased with increased fire frequency on the other surface. Available P and pH were significantly different between the 2 surfaces, but aboveground biomass was similar. Soil nutrient status and biomass were not related, suggesting plant-available soil nutrients may not control plant distribution or recovery following fire. *E. lehmanniana* biomass was negatively correlated with native grass and forb biomass, and tended to increase with increasing fire frequency. Surface litter and *E. lehmanniana* biomass were correlated, and may increase fire frequency, an important consideration when implementing grassland fire management practices.

CHAPTER 1

INTRODUCTION

Explanation of the Problem and its Context

In arid regions, decomposition of litter from N fixing plants is an important source of bioavailable N. Nitrogen fixing legumes such as *Prosopis* spp. (mesquite) provide a dramatic example, as their senesced leaves may contain up to 3.5% N (Killingbeck and Whitford, 1996; Appendix B, Table 3). This input, coupled with uptake of soil nutrients followed by leaf senescence and subsequent litterfall, facilitates the sequestration of soil nutrients under *Prosopis* canopies. Evaluating seasonal variation in litterfall inputs is an important step in determining the rate and extent of soil nutrient sequestration under *Prosopis* canopies. While determining seasonal variation in N fixation by *Prosopis* is hampered by considerable technical difficulties (Zitzer et al. 1996), litterfall inputs may be readily quantified, yet this information remains unpublished.

Altered climatic conditions (Polley et al., 1994) and human land use (Brown and Archer, 1989) are the main factors that have influenced the spread of *Prosopis* spp. Two species, *Prosopis glandulosa* var. *glandulosa* Torr. and *Prosopis velutina* Woot., have expanded their localized distribution within the past several decades from historic drainage locations to more xeric open grassland areas in the southwestern United States (Archer et al. 1988; Buffington and Herbel 1965; Hastings and Turner 1965; McClaran and Van Devender 1995). This has resulted in a corresponding alteration of the spatial distribution of soil nutrient concentrations (nutrient topography) as *Prosopis* becomes a major component of the plant biomass of desert grasslands (Tiedemann and Klemmedson, 1986; Klemmedson and Tiedemann, 1986; Biggs, 1997).

Repeated prescribed burning is a management tactic that has been used for limiting

Prosopis stand development and to increase forage potential (Wright et al. 1976). While this can be effective in limiting the distribution of *Prosopis* of certain size classes, it could also provide conditions which facilitate the establishment of non-native plant species better adapted than native species to cope with frequent disturbance, such as Lehmann Lovegrass (*Eragrostis lehmanniana*) (Martin 1983, Wilson et al. 1999). This is an important point to consider when attempting to restore desert grasslands to historic species compositions, and demonstrates the importance of a clearly defined long-term management strategy.

The objectives of this dissertation are to: 1) clarify causes, rate, and extent of *Prosopis* spp. range expansion within the past 150 years; 2) identify characteristics of *Prosopis* spp. that have contributed to this expansion; 3) describe *Prosopis* management strategies and identify those that are most effective; 4) evaluate seasonal and spatial variation in soil nutrient concentrations, and litterfall quantity and composition, in grassland locations containing *Prosopis* but with different fire histories; and 5) evaluate relationships among fire frequency, soil nutrient status, and aboveground biomass on sites located in close proximity but with different fire histories.

Explanation of Dissertation Format

The main body of this dissertation consists of three research manuscripts which are appended. The author of this dissertation worked closely with the coauthors of these papers. He helped direct the majority of the research presented in the manuscripts, and provided most of the intellectual content and writing. Preparation of the manuscripts was completed with assistance and guidance from his advisor and advisory committee.

CHAPTER 2

PRESENT STUDY

The literature review, methods, results, discussion, conclusions, and data of this research are presented in the manuscripts appended to this dissertation. The following is a summary of the most important findings in these manuscripts.

The relationships among fire frequency, *Prosopis* spp. (mesquite), aboveground plant biomass, and soil nutrient status are evaluated in this dissertation. The first two papers (Appendix A and Appendix B) evaluate the effects of *Prosopis* spp. range expansion on grassland soil nutrient distribution and plant communities in the southwestern United States during the past 150 years. The first manuscript (Appendix A) is a literature review that emphasizes recent research (within the past 15 years) on *Prosopis* natural history, focusing on those factors that have contributed to its range expansion, and *Prosopis* management strategies. I conclude in this paper that the most effective management strategy results in limited *Prosopis* removal by an initial herbicide application, followed by periodic prescribed burning. The second manuscript (Appendix B) took place in a desert grassland at the Fort Huachuca Military Reservation in southeastern Arizona. I evaluated spatial and temporal variations in soil nutrient concentrations and litterfall quantity and composition around *Prosopis velutina* (velvet mesquite) canopies, on adjacent sites with different fire histories, during a two-year period. The site with a lower fire frequency had greater *P. velutina* stand development, litterfall, and soil nutrient sequestration under canopies. Litterfall quantity differed significantly between seasons on both sites. Litterfall nutrient composition also differed significantly between seasons, but was similar on each site. Seasonal variations in soil nutrients were not correlated with seasonal variations in litterfall nutrient

composition. This suggests that fire frequency indirectly affects nutrient sequestration in desert grasslands containing *P. velutina*, by reducing its stand development, and suggests that studies evaluating *P. velutina* nutrient sequestration should account for seasonal variation. In the third manuscript (Appendix C), nine plots on two upland surfaces were analyzed that had reasonably uniform soil characteristics but with fire frequencies ranging from zero to five fires/decade. Soil nutrient status was not correlated with upland surface, fire frequency or aboveground biomass, suggesting that it is not an important criterion for evaluating long-term recovery of grasslands following repeated fires. Biomass of the non-native *Eragrostis lehmanniana* (Lehmann lovegrass) significantly increased with increasing fire frequency, and was negatively correlated with that of native grasses and forbs. The biomass of litter was correlated with *E. lehmanniana* biomass. These results suggest that *E. lehmanniana* biomass may be synergistically associated with increasing fire frequency.

APPENDIX A

**MECHANISMS OF RANGE EXPANSION AND REMOVAL OF MESQUITE
(*PROSOPIS SPP.*) IN DESERT GRASSLANDS OF THE SOUTHWESTERN
UNITED STATES**

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ABSTRACT (200 word)

Two species of mesquite trees in the southwestern United States have become increasingly common in what formerly was desert grassland during the past 150 years. These trees have spread from nearby watercourses onto relatively xeric upland areas, decreasing rangeland grass production. Management attempts to limit or reverse this spread have been largely unsuccessful. This paper reviews studies regarding mesquite natural history and management strategies, emphasizing studies published during the past decade. Mesquites possess a deep root system and are capable of fixing atmospheric N, rendering them capable of accessing resources unavailable to many other plants in open rangeland. Their seeds, which remain viable for decades, have a hard exocarp and require scarification before germination. Consumption by cattle provides a means of scarification and seed dispersal, and is a major factor contributing to the spread of mesquite in open rangelands. Increased atmospheric CO₂ and winter precipitation during the past century also contribute to enhanced seed germination. Mesquite removal techniques have included herbicides, prescribed burning, grazing reduction, and mechanical removal. For increased effectiveness of these techniques, management goals must be clearly articulated; these goals include complete removal, no removal, and limited removal. Of these, limited removal appears the most feasible, using an initial herbicide application followed by periodic prescribed burning.

ABSTRACT (50 word)

Mesquite populations have increased in the last 150 years in desert grasslands of the southwestern United States. We review relevant literature and identify increased seed germination, distribution by cattle, and fluctuating climate as contributing factors. Limited removal by an initial herbicide application followed by prescribed burning is the most feasible management strategy for continued rangeland productivity.

KEYWORDS

mesquite, biological invasions, rangeland ecology, soil nitrogen, rangeland management

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INTRODUCTION

Rangelands in the southwestern United States have been used for settlement, agriculture, and livestock ranching during the past 150 years. Because of the gentle topography, sufficient available water, and abundant forage, use of this rangeland—especially in southeastern Arizona and southwestern New Mexico—has been intensive. As a result, much of this area has been transformed to a mixed-phase woodland or shrubland, with no sign of this trend diminishing (Archer et al. 1988; Buffington and Herbel 1965; Hastings and Turner 1965; McClaran and Van Devender 1995). This alteration has created considerable concern as land use managers recognize a corresponding decline in available livestock forage. The mesquite tree (*Prosopis* spp.) has played a major role in this change, as it has expanded its range from more mesic desert grassland drainage systems and riparian zones to open rangelands.

While the causes that account for this altered distribution— climate change (Grover and Music 1990), livestock grazing (Archer et al. 1988; Bahr and Shelton 1993; Schlesinger et al. 1990), suppression of wildfires (Bahre 1985; Biggs 1997; Humphrey 1958), or rodent activity (Cox et al. 1993; Reynolds and Glendening 1949)— have been investigated for several decades, no single effective strategy has been offered as a means of slowing or reversing mesquite encroachment in desert grasslands. Removal tactics have included prescribed burning (Britton and Wright 1970; Wright et al. 1976), herbicides (Gibbens et al. 1986; Jacoby et al. 1982; Warren et al. 1996), and mechanical removal (Dodd and Holtz 1971). These have resulted in varying degrees of success, mainly short-term.

One key to understanding why mesquite has expanded its range, and why it may be at times impervious to attempts at removal, is through an examination of its natural history. Though this has been studied in the past, many studies concerning intraspecific competition (Ansley et al. 1998; Kramp et al. 1998), seed germination requirements (Bush and Van Auken 1990; Cox et al. 1993), root systems (Ansley et al. 1990; 1991; Stromberg 1993), and nitrogen fixation (Johnson and Mayeux 1990; Zitzer et al. 1996) have taken place only within the last 10 years.

In this review, we focus on the desert grasslands of southeastern Arizona and southwestern New Mexico (Fig. 1). Previous workers (Brown and Lowe 1980) referred to two types of grassland in this region – semidesert grassland and plains and Great Basin Desert grassland – but we prefer the simpler classification of “desert grassland” as used by McClaran and Van Devender (1995). We subdivide the desert grasslands into the desert grasslands of southeastern Arizona, which mostly surround the Santa Rita and Huachuca Mountains, and the desert grasslands of the western Chihuahuan Desert, which spans the area from the Sulfur Springs Valley of southeastern Arizona to the Bootheel of southwestern New Mexico.

The objectives of this study are to 1) describe the natural history of the mesquite species that have increased their distribution in grasslands within the southwestern United States, focusing on those attributes that could account for this range expansion, 2) review the existing research that has addressed this expansion, with an emphasis on research produced within the last decade, 3) describe management goals, practices, and results, and 4) propose a management strategy that accounts for regional differences while providing long-term effectiveness.

MESQUITE NATURAL HISTORY

Floristics

Three species of mesquite are currently recognized as indigenous to the southwest United States: screwbean mesquite (*Prosopis pubescens* Benth.), velvet mesquite (*Prosopis velutina* Woot.), and honey mesquite (*Prosopis glandulosa* Torr.). Two subspecies of honey mesquite are found in this area: Texas honey mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) and western honey mesquite (*Prosopis glandulosa* Torr. var. *torreyana* (L. Benson) M.C. Johnston). They are members of the legume family (Fabaceae) and are characterized by pinnate leaves, spiny branches, seedpods, and a central taproot. However, individual variation in physical characteristics as well as hybridization makes taxonomic classification at the species level problematic. In general, *P. glandulosa* can be differentiated from *P. velutina* due to glabrous leaflets up to 4 cm long; the latter has pubescent leaflets up to 1.3 cm long. The two varieties of *P. glandulosa* are distinguished by their thorns; *P. glandulosa* var. *torreyana* has paired thorns, while *P. glandulosa* var. *glandulosa* has solitary thorns (Isely 1998).

Two of these species, *P. glandulosa* and *P. velutina*, have had the most significant expansion into desert grasslands. While *P. velutina* is restricted in the United States to southern and central Arizona, *P. glandulosa* occurs from Texas to California. *P. glandulosa* var. *glandulosa* is found mainly in Texas east of the Pecos river and north into Oklahoma, while *P. glandulosa* var. *torreyana* is found west of the Pecos river, throughout southern New Mexico and adjacent Arizona, and in southern California, northwestern Arizona, southern Nevada, and southwestern Utah. *P. glandulosa* var. *glandulosa* can also be found along Interstate 10 through

New Mexico and Arizona east of Tucson due to cattle transport with subsequent seed dispersal. In this paper we assume that *Prosopis velutina* and the 2 subspecies of *P. glandulosa* are sufficiently similar in characteristics to be treated together.

Morphology

Mesquite attains its maximum height of over 12 m in riparian habitats, yet is opportunistic enough to grow on exposed desert slopes where reproductively mature individuals may only be 1.5 m tall. In xeric upland sites, their taproot may reach only 1 m in depth where solid bedrock prevents deeper penetration; however, taproots of *P. velutina* have been recorded at over 53 m depth (Philips 1963) under more favorable conditions.

While mesquite trees are characterized by a massive central taproot, they also possess an extensive lateral root system (Heitschmidt et al. 1988). For this reason they are classified as facultative phreatophytes, able to extract permanent groundwater when available but also able to extract soil moisture (Ansley et al. 1990). Ansley et al. (1990; 1991) severed the lateral roots of 4 *P. glandulosa* var. *glandulosa* trees at 2 sites in west Texas. They found that stomatal conductance was reduced during the first growing season on the site with less available subsurface water; this reduction disappeared during the second growing season, probably due to root regeneration or compensation of total leaf area.

In riparian habitats and desert grasslands, *P. glandulosa* and *P. velutina* are typically single-stemmed with a central trunk up to 35 cm in diameter. However, multi-stemmed individuals are not uncommon, especially as a result of resprouting following fire. Conversely, multi-stemmed plants are most common in more arid habitats such as the Arizona Upland regions of the Sonoran

Desert. Aboveground form also appears to be related to subsurface characteristics. For example, Stromberg et al. (1993) compared *P. velutina* aboveground characteristics to available water and found that the height of stands in riparian areas was inversely related to depth of the water table; trees were 8 m tall where the groundwater depth was greater than 15 m, but grew to 12 m where the ground water was <15 m.

Whether single or multi-stemmed, mesquite trees produce branches that may form a canopy with a diameter twice the height of the plant. Both stems and larger branches may be either smooth or rough textured with a fair degree of individual variation. Branches are typically spiny with considerable variation in thorn length (from 0.5 to over 5 cm) and density.

Finn et al. (1994) identified annual growth rings in the wood of *P. glandulosa* at 5 sites in Texas. Their samples included trees that resprouted vegetatively following cutting; for these plants they noted that ring count would signify age of regrowth, not necessarily the tree itself. They found stems ranging from 7 to 30 years in age, but their data in conjunction with Archer's (1989) growth rate study suggest that the age of tree stems may exceed 200 years. Using repeat photography, Bowers et al. (1995) documented *P. glandulosa* longevities >100 years.

Phenology and Germination

Though climatic conditions vary considerably throughout the ranges of *P. glandulosa* and *P. velutina*, their growing seasons are generally in the spring and in the late summer. This is typical of a C3 species but not the C4 grass species that dominate open rangelands. Mesquite trees are typically deciduous during the winter months, but may also lose their leaves during summer drought (Ansley et al. 1992). Leaves produced during the spring may be larger than in

late summer (Nilsen 1986), perhaps in response to light intensity and transpiration potential. These leaves form a hydrophobic waxy cuticle that can accumulate during the growing season, providing mesquite some resistance to foliar-applied herbicides (Jacoby et al. 1990c).

Flowering occurs in the late spring and typically attracts a variety of flying insect-pollinators, including bees, wasps, and beetles. Seed pods exceeding 30 cm in length are produced through the summer. The seeds have a generally high mortality rate from bruchid beetles (*Algarobius prosopis* and *Neltumius arizonensis*) which bore holes into the fruit and deposit eggs on the seed. Germination occurs in both fall and spring, coincident with peaks in annual precipitation (Brown and Archer 1987).

The seeds have a hard exocarp and must undergo scarification prior to germination. This contributes to their long-term viability, which may exceed 20 years (Martin 1948; 1970). Kramp et al. (1998) evaluated the effectiveness of deer, cattle, and coyotes as scarification agents and vectors for *P. glandulosa* var. *glandulosa* seed dispersal. They found that seeds continued to germinate in fecal samples of all species 2 years after deposition, and that an average of 7.8, 5.2, and 4.5 seedlings emerged from deer, cattle, and coyote feces, respectively. These authors concluded that cattle were most effective as seed vectors because cattle feces contained more seed. Brown and Archer (1989) found that honey mesquite had a survival rate of 74 to 97% for individuals that survived 2 weeks after germination in cattle fecal sites. Ingestion by herbivores has the added benefit of eliminating bruchid beetles from the fruit (Burkhart 1976).

Under laboratory conditions, *P. glandulosa* seedlings in a clay loam soil emerged from planting depths between 0.5 and 1.5 cm after 3 to 6 days, with a root to shoot ratio of 5:1 within

this period (Scifres and Brock 1971). In a similar study of *P. velutina* seedlings, Cox et al. (1993) found that a planting depth of 2 to 4 cm in a sandy loam resulted in the highest percent germination; they also determined that seeds planted at this depth were unaffected by fire. Brock (1986) found that unrestricted root growth is critical for the survival of velvet mesquite seedlings. In a laboratory study, he found that the greatest root development and growth rate during the first 30 days was in sandy loam and clay loam soils; after this aboveground growth exceeded root development.

Emerging seedlings readily survive losses of top-growth due to herbivory (Weltzin et al. 1998). In a growth chamber experiment, Weltzin et al. (1998) evaluated the relative tolerances of seedlings aged 18 and 33 days to repeated clipping above either the 1st or 4th nodes. They found that the younger seedlings had a 75% survival rate after repeated clipping above the 1st node, versus a 38% survival rate for older seedlings.

Insufficient light may limit the survival of emerging seedlings. Bush and Van Auken (1990) observed that seedlings rarely emerge under the canopy of mature *P. glandulosa* trees, despite elevated soil nutrient concentrations. When these authors compared seedling emergence and survival, they found that the largest seedlings were found in areas with full light and herbaceous plant exclusion, while the smallest seedlings were found under adult trees with herbaceous plant competition. Conversely, Brown and Archer (1989) found *P. glandulosa* seed germination and establishment to be independent of herbaceous biomass or moisture conditions, though their survival rate increased with supplemental watering.

Intraspecific competition can limit population densities of either seedlings or reproductively mature individuals. In a survey of establishment rates for *Prosopis glandulosa* var. *glandulosa* in cattle fecal sites in northern Texas, Kramp et al. (1998) found that all sites where mesquite had germinated eventually either a single established plant or no survivors. Ansley et al. (1998) noted that access to soil water appears to be the competitive mechanism limiting population densities and individual tree size for this species in areas where lateral root systems provide the main source of water uptake.

Mesquite and Nitrogen

Nitrogen availability is considered to be a major factor limiting plant growth in regions where mesquite occurs in the southwestern United States (West and Klemmedson 1978). However, several studies have indicated that mesquite in these regions represent a source of nitrogen rather than a sink. In a 3-year study, Barth and Klemmedson (1983) found that soil under *P. velutina* canopies accumulated 11.2 g N/m² per meter of tree height; this concentration was inversely related to distance from the trunk and decreased away from the canopy edge. Virginia and Jarrell (1983) found similar results in a study of soil properties under *P. glandulosa* var. *glandulosa* canopies; total N, NH₄⁺, NO₃⁻, organic C, plant-available P, and K were significantly ($P \leq 0.05$) higher beneath canopies than in adjacent open areas. In California, Rundel et al. (1982) found 1020 g soil total N/m² under *Prosopis glandulosa* var. *torreyana* canopies, 160 g soil total N/m² between canopies, and 45 g soil total N/m² in adjacent open areas. At the Fort Huachuca Military Reservation in southeast Arizona, shallow soil under mesquite canopies had an average of 17mg NO₃⁻-N/kg and 2.05 mg/kg in adjacent open areas (Biggs. 1997).

The main mechanism responsible for elevated soil nutrient concentrations under mesquite is biological nitrogen fixation by soil Rhizobia followed by litterfall. In a symbiotic relationship, mesquite will transport abundant C into their root systems at a high energy cost to facilitate the establishment of Rhizobia bacteria within the rhizosphere. Subsequently, the roots form nodules around the Rhizobia which proceed to convert N_2 from the soil atmosphere to a form usable by the host plant (NH_3). Eventually this fixed atmospheric N is returned to the soil via litterfall. Though plants resorb leaf nutrients to varying degrees before leaf senescence, fallen *P. glandulosa* leaves can contain 2.6% N, a retention rate of over 74% (Killingbeck and Whitford 1996). This represents an annually renewed source of soil N which is replenished mainly during the late fall when mesquite become deciduous. Rundel et al. (1982) have estimated that 25-30 kg N/ha accumulates annually under canopies of *P. glandulosa* var. *torreyana* as a result of fixation, whereas Virginia (1986) found that mesquite litterfall annually returns 135 kg N/ha to the soil. Since litter deposition occurs mainly under the mesquite canopy, adjacent open areas may remain unaffected.

Despite empirical evidence, explicit identification of N fixation by mesquite has remained elusive. Shearer et al. (1983) found significantly lower $^{15}N/^{14}N$ in leaf tissue of *P. glandulosa* var. *torreyana* compared to similar tissue of unrelated reference plants (1.08 vs. 2.98). This indicated that mesquite were using atmospheric N, which has a lower ratio of $^{15}N/^{14}N$ than mineralized soil N. However, these authors could not quantify the amount of N fixed using this method, due to lack of replication, the absence of appropriate non-N-fixing reference plants, and other logistical difficulties.

Other researchers have attempted to locate N-fixing nodules in the roots of mesquite. Johnson and Mayeux (1990) recovered brown, leathery textured nodules in the roots of *P. glandulosa* var. *glandulosa* in east Texas. They found that 11 of 19 trees possessed nodules within 10 cm of the soil surface; the average length of each nodule was 1.7 mm. These nodules increased in frequency with increasing depth below the surface to their maximum sampling depth of 3 m. The nodules were weakly attached to roots < 0.5 mm in diameter. These authors also found abundant insect frass and body parts in the vicinity of the roots and suggested that nodule predation by insects may have occurred. Virginia (1986) found that soil Rhizobia populations increased with soil depth to a maximum concentration at the upper margins of ground water. Johnson and Mayeux (1990) suggest that since soil NO₃ can inhibit N fixation, nodule formation may occur in deeper soils with lower NO₃ concentrations. Jenkins et al. (1988; 1989) found seasonally fluctuating populations of Rhizobia at 0 - 9 m depth in soil columns collected in playas, dunes, arroyos, and grasslands in California and New Mexico. Their data suggest that soil salinity, age of the host plant, and groundwater depth and fluctuations determine Rhizobia distribution and type. Presumably, the location and density of nodulation in the mesquite root zone corresponds to these populations.

Considerable logistical difficulties must be overcome for field identification of nodules, given their fragility, small size, and the depths at which they are found. Johnson and Mayeux (1990) failed to find nodules under mesquite in west Texas, New Mexico, and Arizona despite $\delta^{15}\text{N}$ analysis that suggested that these mesquite were utilizing atmospheric N. These authors speculated that they may have simply failed to locate the soil nodules since nodule formation may be of an ephemeral nature, as has been suggested by Bailey (1976) and Zitzer et al. (1996).

Conversely, mesquite seedlings can form nodules under controlled conditions. Bailey (1976) identified root nodules produced by *P. glandulosa* seedlings grown in a growth chamber. Frequency of nodulation was statistically correlated with soil texture, water, and the abundance of Rhizobia; wet sandy soils produced the most nodules, while dry clayey soils produced the least. Felker and Clark (1980) also found nodules formed when both *P. glandulosa* varieties were grown in vermiculite, furnished with a nutrient solution free of N, and inoculated with soil Rhizobia collected from the nodules of a mesquite grown in a separate nodulation experiment (Eskew and Ting 1978).

HISTORICAL RANGE EXPANSION OF MESQUITE

Much of the information on mesquite expansion in the southwestern United States comes from anecdotal observations of ranchers and other rangeland users, published reports, and repeat photography. In one of the earliest scientific reports on the subject, Griffiths (1910) reported increases in mesquite populations, due to overgrazing, on the Santa Rita Experimental Range south of Tucson, Arizona. Hastings and Turner (1965) present repeat photography that documents increases in *P. velutina* on southern Arizona rangelands. They found that much of the increase in mesquite occurred after 1880. A recent update of Hastings and Turner (1965) shows that mesquite has also increased between the mid-1960s and mid-1990s, indicating that the expansion has not ceased (R.M. Turner, written commun., 1999).

Estimates of the rate of recent mesquite establishment in open rangelands vary widely. Hennessy et al. (1983) determined that a black grama (*Bouteloua eriopoda*) grassland on the Jornada Experimental Range in southern New Mexico was completely converted to mesquite

woodland between 1934 and 1980. Gibbens et al. (1992) compared mesquite density on the Jornada in herbicide-treated areas in 1976 and in 1988 and noted an increase from 67 to 494 plants/ha. These authors also estimated that on the College Ranch in New Mexico, *P. glandulosa* increased from 130 plants/ha in 1982 to 147 plants/ha in 1988. Using data from Glendening (1952), Gibbens et al. (1992) estimated that *P. velutina* increased in a 17-year period on the Santa Rita Experimental Range at the rate of 9.2 plants/ha/year in areas with livestock grazing, and at the rate of 15.7 plants/ha/year in areas where livestock and rodents were excluded. Felker et al. (1990) noted that *P. glandulosa* stands can regenerate to a density of 10,000 stems/ha, with an average trunk diameter of 4 cm, 10 years after land has been cleared. To predict future growth of *P. velutina* stands, Chojnacky (1991) developed a model using basal area, stems per stand, trees per stand, and average tree height data from 47 locations in southern Arizona. This model is mainly applicable to short-term projections, since it does not account for mesquite mortality. Using the model with a 30-year projection, this author noted that initial basal area was probably the most important variable influencing growth rate; for a stand with an initial basal area of 18.5 m²/ha the stand volume increased from approximately 62 to 80 m³/ha within 10 years, followed by a reduction to the initial volume in the last 20 years. Implicit in this model is the idea that mesquite stands that occur in locations with abundant resources will experience a rapid increase in size, then decline through intraspecific competition.

MECHANISMS OF MESQUITE RANGE EXPANSION

Mesquite have the ability to access groundwater using a deep root system, grow in a variety of soil types and in the variety of climatic conditions found in the southwestern United

States, and can indirectly fix atmospheric N. Therefore, mesquite can avoid the resource limitations that restrict the establishment and maintenance of competing plants in the majority of the habitats in which they are found. With this relative independence, why have mesquite moved into open grasslands from adjacent riparian or ephemeral channels only within the past century? While much research has been focused on the mechanisms of recent mesquite dispersal into open grasslands (Archer et al. 1988; Bahre 1985; Bahre and Shelton 1993; Cox et al. 1993; Grover and Musick 1990; Humphrey 1958; Reynolds and Glendening 1949; Schlesinger et al. 1990), little attention has focused on why mesquite had not occupied these areas prior to the past 150 years.

Seed Dispersal

Mechanisms of seed dispersal are likely to play a key role in the dynamics of mesquite distribution (Brown and Archer 1989). Janzen and Martin (1982) suggested that mesquite thrived in open grasslands as recently as 10,000 years ago. During the Pleistocene, horses, elephants, and ground sloths served as the primary seed-dispersal agents, ingesting mesquite fruit and subsequently depositing scarified seed at fecal sites. Martin and Burney (1999) also suggest that many of the characteristics of mesquite--sharp spines, waxy leaves, sweet-tasting fruit, and the ability to readily resprout following herbivory--evolved with ancestral megafauna. This prevented overgrazing while promoting fruit consumption and seed dispersal. With the extinction of these large mammalian herbivores, mesquite were found less frequently in open areas but persisted in drainages and riparian areas, where they were more resistant to environmental perturbations such as drought or fire, and where their seeds became dispersed through surface-water transport (Grover and Musick 1990).

Adjacent drainages and riparian areas offer more favorable growing conditions compared to open grasslands: improved moisture and nutrient availability through surface-water transport, reduced maximum air temperatures, and some protection from wind and fire. However, mesquite are currently thriving on open grasslands, and are providing an environment favorable for the establishment of other woody plants such as prickly pear cactus (*Opuntia lindheimeri*), desert hackberry (*Celtis pallida*), hog plum (*Colubrina texensis*) (Archer et al. 1988), and perennial grasses such as bush muhly (*Muhlenbergia porteri*) (Haque et al. 1991). Birds, rodents, and insects acting as seed dispersal agents for shrub species may be attracted to mesquite canopies for shade and reduced visibility, incidentally transporting seed to the soil below (Archer et al. 1988). Consequently, the shrubs germinating from these seeds might become established because areas under mesquite canopies provide most of the same resources and protection from the elements as riparian areas.

Livestock Grazing

Cattle grazing is believed to be a major cause of the contemporary range expansion of mesquite trees. Through grazing, cattle limit herbaceous competition for germinating mesquite seedlings, creating more open areas with access to sunlight. Cattle ingest mesquite fruit, consequently transporting the seed, scarifying it, then depositing it in a moist, nutrient-rich micro-environment. Brown and Archer (1987) compared seedling emergence on sites with and without cattle. They found 12 to 15 seedlings/m in the former case and no seedlings in the latter. Brown and Archer (1989) maintain that as seed dispersers, cattle are surrogate megafauna, resuming relationship between mesquite and large mammals that last existed in the latest Pleistocene.

Cattle indirectly facilitate the establishment of other shrubs under mesquite by augmenting soil nutrient concentrations. Cattle tend to congregate under the shade of mesquite trees, where they deposit abundant feces, providing supplemental N to the soil that adds to the elevated N concentrations that result from litterfall. Livestock therefore contribute to the redistribution of nutrients from open rangelands to beneath mesquite canopies.

Livestock grazing facilitates mesquite establishment in open grassland ranges but reduces the biomass of native grasses by at least three mechanisms. First, as mesquite woodlands comprise a larger portion of the above-ground biomass within an area, the grazing intensity on the remaining grasses increases because shrubs and trees are less palatable than grasses (Grover and Musick 1990). Second, mesquite woodlands can form a canopy that inhibits native grass seed germination as suitable microclimates become more spatially restricted. Third, mesquite trees sequester nutrients, making inter-tree areas relatively nutrient poor (Biggs 1997).

Eventually, mesquite growth may inhibit grazing. Archer et al. (1988) used aerial photographs taken in 1941, 1960, and 1983 to monitor closed-canopy woodlands and woody plant groupings centered around *P. glandulosa* within grasslands on the Rio Grande Plains of Texas. Within the grassland, they found that half of the groupings were <5 m apart and 95% were within 15 m. These authors predicted that these gaps would diminish as individual canopies grew because the mean area for each grouping increased from 494 m² to 717 m² (+70%) between 1941 and 1983. Seedlings, composed mainly of *P. glandulosa*, occupied 85% of the open areas (Archer et al. 1988). Eventually these trees can form an impenetrable thicket, restricting livestock traffic and increasing the cost of livestock management (Teague et al. 1997).

Mesquite stands may continue to increase in size on open ranges after cattle grazing has been eliminated (Brown 1950; Brown and Archer 1989; Glendening 1952). Once seed has been dispersed into open areas and mesquites have become established, a constantly renewed seed bank and seed viability that can last for 20 years (Martin 1970) insure that mesquite could persist on open rangelands. For example, at the Fort Huachuca Military Reservation in southeast Arizona, cattle grazing has been eliminated since the mid-1940s. However, aerial photographs of the region from 1935 to 1994 document the continued increase of mesquite in open rangeland 50 years after cattle grazing was terminated, despite periodic grassland fires which appear to affect average canopy size (Fig. 3). While maximum stand densities continue to exist within riparian areas, populations of established trees and seedlings in grasslands persist to form woodlands of greater than 80 trees/ha at Fort Huachuca (Wilson et al., unpublished data, 2000).

Fire

Mesquite range expansion has been attributed to altered land-management practices associated with cattle ranching (Bahre and Shelton 1993). Fires have been actively suppressed during the past century to minimize damage to vegetation, livestock and property; in addition, cattle grazing has reduced herbaceous fuel loads, thereby reducing fire frequency (Van Auken and Bush 1997). Before widespread settlement by Europeans, Native Americans regularly set wildfires in desert grasslands (Bahre 1985). Over long periods, these fires presumably minimized mesquite seedling establishment in open areas while allowing the continued presence of mesquite in sheltered drainage and riparian areas.

At the Fort Huachuca Military Reservation, we located three adjacent sites of different fire frequency but equivalent topography and soil type (Fig. 3). These sites are separated by a network of roads which function as firebreaks. The site with < 1 fire per decade for the past 30 years had 4.75 kg/m² of *Prosopis velutina* aboveground biomass; the site with an average of 2 fires per decade for this time period had 0.52 kg/m²; and the site with an average of 4 fires per decade had 0.078 kg/m² (Biggs 1997). The ratios of *P. velutina* biomass to grass biomass were 116:1 on the unburned site, 3:1 on the site with 2 fires per decade, and 1:2 on the site with 4 fires per decade.

Climate Fluctuations and Atmospheric Gases

An increase in the relative contribution of winter rains to annual precipitation can favor the germination and establishment of certain shrub species, including mesquite (Sala et al. 1997). Mesquite and many common shrubs in the southwestern United States have a C3 photosynthetic pathway, deciduous habit, a moderate transpiration rate, drought avoidance, low herbivory, high seed production, many germination requirements, high survival following disturbance, and slow recruitment (Diaz and Cabido 1997). Grasses in this region are C4 plants with a high leaf area, a shallow dense fine root system, a high transpiration rate, low to moderate drought resistance, moderate herbivory, moderate seed production, few germination requirements, and low survival after disturbance but rapid reestablishment. Changes in the seasonal pattern of soil-water potential is reflected in the relative abundance of C3 shrubs versus C4 grasses in a region (Sala et al. 1997). Shrubs respond favorably to winter precipitation for seed germination and vegetative growth,

while grasses are more responsive to warm-season rainfall, suggesting that variation in seasonal precipitation may drive rangeland conversions from grasses to shrubs.

Climatic variations in the southwestern United States during the 20th century have been documented (Hastings and Turner 1965) and disputed (Bahre 1991). To evaluate climatic variation in southwestern New Mexico and southeastern Arizona, we standardized seasonal precipitation using the technique of Hereford and Webb (1992). We identified the two ecological precipitation seasons of summer (July - September) and winter (November - March). For winter precipitation, November and December totals were considered part of the following year. For each climate station (Tables 1 - 2), we calculated the standardized seasonal precipitation, P_s , by

$$P_s = \sum \{ \sum [(x_{i,j} - \mu_i) / \sigma_i] / k \} / n, \quad (1)$$

where $x_{i,j}$ = monthly precipitation for climate station i in month j (mm); μ_i = the mean and σ_i = the standard deviation of monthly precipitation for climate station i (mm); k = the number of months in the season; and n = the number of climate stations with data. The value of n varies through the 20th century due to the varying number of available climate stations (e.g., Tables 1-2) and whether or not data are missing.

Annual and seasonal precipitation in southwestern New Mexico and southeastern Arizona has varied during the 20th century (Figs. 4-6). From 1980 through 1998, 15 and 12 years had above-average annual precipitation in southwestern New Mexico and southeastern Arizona, respectively. Annual precipitation from about 1940 to 1980 was generally below average, particularly in the mid-1950s. The results displayed in Figs. 4-6 confirm previous work suggesting

that annual precipitation in the southwestern United States is does not follow a fixed pattern (Hereford and Webb 1992; Webb and Betancourt 1992).

Seasonal precipitation also varies between years. Between 1900 and 1998 in southeastern Arizona, winter or summer precipitation (but not both) was above average for 51 years; of these, 28 years had above-average winter precipitation with below-average summer precipitation. The period from 1895 to 1906 included only 3 years of above-average precipitation, and those only occurred during the summer. However, 10 of the following 11 years had above-average winter precipitation, coinciding with the range expansion of mesquite observed by Griffiths (1910). These weather patterns may have significantly contributed to this expansion by optimizing environmental conditions for enhanced mesquite seed germination. In southwestern New Mexico and southeastern Arizona, 12 years had above-average winter precipitation between 1980 and 1998, compared to 12 years of above-average winter precipitation during the previous 40 years. More recent increases in winter precipitation could be manifested in an accelerated rate of mesquite establishment during the past 20 years as observed by ranchers in the southwestern United States.

The increase in atmospheric CO₂ from the beginning of the century to the present has been cited as a contributing factor in mesquite range expansion. Polley et al. (1994) observed increased nodulation and N fixation when greenhouse-grown *P. glandulosa* seedlings were exposed to elevated CO₂ concentrations. These seedlings also produced more below-ground biomass, and their N and water-use efficiencies increased linearly with increasing atmospheric CO₂ concentrations. Conversely, mesquite seedlings grown with little bluestem (*Schizachyrium*

scoparium), a C4 perennial grass, manifested none of these characteristics. The authors suggest competition with grasses attenuates the beneficial effects of increased atmospheric CO₂ on mesquite. In the absence of this competition, mesquite seedlings can establish more rapidly.

MESQUITE MANAGEMENT PRACTICES

Because of mesquite expansion into open rangelands, with resulting reductions in livestock forage, land-use managers have employed a variety of tactics--fire, herbicide, and physical removal--to completely remove existing trees and limit further spread. These practices all have something in common: logistical difficulties and side-effects potentially harmful to habitat restoration. For example, ranchers at the Waggoner Ranch (202,000 hectares) in northern Texas have attempted to remove mesquite since the 1950s without success, and it continues to regenerate in treated areas and spread further. Attempts at control have been largely terminated due to increasing costs (Teague et al. 1997).

Prescribed Burning

Fire has been used as a management tool to control mesquite distribution for decades (Humphrey 1949). However, mesquite trees can survive fire while still relatively young. Wright et al. (1976) determined that while *P. glandulosa* seedlings up to 1.5 years of age were easy to kill with medium intensity fires, 2.5-year-old trees survived with severe damage, and 3.5-year-old trees were tolerant; these authors recommended against using fire as a management tool in overgrazed areas. Archer et al. (1988) found similar results. Martin (1983) determined that within 5 years of a fire in southern Arizona *P. velutina* biomass had attained preburn levels. In these cases cattle grazing could increase mesquite survival rates by not only lowering fire frequency

through fuel removal (Van Auken and Bush 1997), but fire intensity as well. Hobbs et al. (1991) found that grazing reduced fire temperature and energy release in a tallgrass prairie.

Livestock grazing alters rangeland fire characteristics in the following ways. Consumption and trampling by livestock can lower the density and average height of herbaceous biomass. In turn, this can effect the average flame height and duration of a fire; in many cases, flames may not reach the canopies of reproductively mature mesquite (Fig. 2). After a fire, mesquite below a certain size class can be reduced in numbers; however, given the survival rate of larger reproductively mature trees, recruitment would continue as the larger trees replenish the mesquite seed bank.

Since mesquite trees appear largely impervious to individual fires, repeated burning has been recommended (Wright et al. 1976). In this case, the fires would need to occur at a frequency that would prevent the recovery from damage inflicted by previous fires, and it assumes that sufficient fuel would accumulate in the periods between fires. While this might provide an effective management tool to limit the distribution of mesquite of certain size classes, it could also provide the conditions which facilitate the establishment of exotic plant species better adapted than native grass species to cope with frequent fires, such as Lehmann Lovegrass (*Eragrostis lehmanniana*) (Martin 1983; Wilson et al. 1999). This is an important point to consider when attempting to restore desert grasslands to historic species compositions.

Herbicide Application

Herbicides have also been employed to control the spread of mesquite. In a 3-year study, aircraft applied 1.12 kg/ha of 3,6-dichloropicolinic acid (clopyralid) (Jacoby et al. 1981). Subsequent monitoring over a 2-year period showed that this agent was significantly more effective at killing mesquite than 2,4,5-T and picloram applied at the same rate, with 60-68% mortality. Jacoby et al. (1981) observed that clopyralid was not effective in killing associated shrub and succulent plants such as saltbush (*Atriplex* sp.) or prickly pear (*Opuntia* sp.). In another study, Jacoby et al. (1982) determined that dead mesquite serves to protect germinating forage plants from grazing, allowing significant increases in forage production.

Subsequent studies have attempted to quantify the effects of herbicide treatment based upon mesquite morphology. Jacoby et al. (1990b) determined that mesquite with multiple stems were significantly more resistant to mortality from a variety of herbicides including clopyralid, triclopyr, picloram, and 2,4,5-T. Though they determined that clopyralid was the most effective herbicide, mortality decreased from 55% for single-stemmed trees, 35% for 3 to 5-stemmed trees, and 19% for trees with greater than 5 stems. These authors suggest that the greater canopy coverage for multiple-stemmed trees is more effective in preventing herbicides from penetrating the soil under the canopies. In contrast, they did not find a significant relationship between tree height and herbicide-induced mortality (Jacoby et al. 1990a).

The epicuticular wax found on mesquite leaves can minimize the effects of foliage-absorbed herbicides. Mayeux and Wilkinson (1990) suggest that herbicides applied in an oil spray are more effective than aqueous sprays. Jacoby et al. (1990c) found that leaf epicuticular wax increased

through the growing season, then stabilized or decreased in late summer. These authors also found individual differences in the amount of leaf epicuticular wax within populations and suggest that over time these trees could represent a greater portion of the population as the selective pressure of foliage-absorbed herbicide applications eliminated trees with less leaf epicuticular wax.

Jacoby and Ansley (1991) evaluated the effects of herbicide applications during various seasons. They found the most effective herbicide--clopyralid-- induced the greatest mortality (92%) when applied during September. These authors suggested that herbicide applications during the late summer are most effective, and nearby agricultural areas are less susceptible to treatment effects at that time.

One negative effect of herbicide treatment is the potentially deleterious effects on the environment and biodiversity within open rangeland. Nolte and Fulbright (1997) monitored plant and animal biomass for 2 years following treatment of mesquite with a mixture of picloram and triclopyr. They found no differences in vegetation, rodent, and avian species richness between control plots and treatment areas, although they noted that annual precipitation was 16% above average during this period, possibly attenuating the deleterious effects of the herbicide.

This study and the ones previously mentioned (Jacoby et al. 1981; 1982; 1990a; 1990b; 1990c; 1991) were conducted within a 10-year period or less, and only the effects of a single herbicide application were monitored. To completely remove mesquite or at least limit its spread in open rangeland using herbicides only, multiple treatments are required; otherwise, the long-term viability of mesquite seeds and their abundance within the seedbank would ensure continual recruitment.

These multiple applications could create adverse side effects to certain rangeland species that would not be discernible from the results of a single treatment. In a study that evaluated impacts of repeated herbicide applications on biodiversity, Gibbens et al. (1986) applied 2,4,5-T to *Prosopis glandulosa* within dunelands in southern New Mexico during 3 consecutive years. They found mesquite mortality to be 54%, without specifying if any specific age class of mesquite were particularly susceptible. These authors also determined that residual 2,4,5-T in the soil dissipated rapidly, and was not detected 131 days after treatment. While they found lower indices of microbial activity on treated areas, they attributed this to lower carbon availability as the mesquite trees were defoliated. Overall, the authors found a decrease in avian species diversity on treated areas but no differences in arthropod or rodent diversity. Since this was a 3-year study, no data were presented on the rate of mesquite recruitment following the herbicide treatment. Although these results appear promising, mesquite mortality after 3 consecutive years of herbicide applications accounted for just over half of the trees in the study area. This implies that these treatments would have to continue at a fairly regular interval for many years to create a significant long term reduction in mesquite populations. With the attendant costs of herbicides and aerial application over large areas, a viable long-term management strategy using only herbicides may be impractical.

Mechanical Removal

Physical removal of mesquite is another management tactic. Roller chopping and shredding can reduce plant density, stature, and canopy cover immediately following treatment, but subsequent basal resprouting can create greater stem densities (Dodd and Holtz 1971). Other

techniques include root-plowing, chaining, and dozing. While these tactics may kill existing mesquite, the woody debris is often left in place, therefore impeding navigation through these areas and limiting available space for livestock forage (McPherson and Wright 1986). In addition, mechanical removal may negatively affect other plant and animal species. For example, driving large mechanical equipment through rangeland can cause soil compaction, crush animals, destroy animal burrows, and uproot desirable plant species such as perennial grasses. The extent of these effects remains unknown.

MESQUITE MANAGEMENT OBJECTIVES

This paper has mainly discussed the negative impacts of mesquite population expansion onto open rangeland. However, mesquite wood is prized as a material for furniture, and the wood is also used for cooking, with an estimated value of \$400/ton as barbeque chips (Felker 1996). Some characteristics of the wood, such as hardness and shrinkage, are considered equivalent or superior to mahogany, oak, and walnut (Felker et al. 1990), with lower rates of expansion and contraction due to changes in ambient humidity. While still nascent, the mesquite lumber industry in Texas generates \$5 to 10 million per year (Felker 1996).

Mesquite seed pods are high in carbohydrates, providing a rich energy source for wildlife, livestock, and humans (Felker 1998). Mesquite trees also provide habitat for birds, small mammals, reptiles, and insects, increasing biodiversity and recreational opportunities (McPherson 1997). Therefore, completely removing mesquite trees from open rangeland may not only be an unrealistic objective, it may actually lower the profitability of this rangeland to land use managers.

For this reason, management objectives and their implications should be clearly articulated when formulating a management strategy.

For example, if the management objective is the complete removal of mesquite trees from open rangeland, the long-term commitment of resources to this task might not be a realistic goal for many land-use managers. Instead, a compromise may have to be reached, whereby the density of mesquite stands are reduced to the point that land-use activities such as cattle ranching may be efficiently practiced, while recognizing that these trees will continue to exist on open rangeland. Periodic burning of this open rangeland may therefore not entirely remove mesquite, but will lower its density to the point that cattle may find sufficient forage, and ranchers can more easily navigate their land. Overall, land-use managers have a choice of three management objectives. They are described as follows, with the specific procedure or combination of procedures that may be most effective.

Objective 1. Complete Mesquite Removal from Desert Grassland.

This option is considered by those who wish to restore desert grasslands to their historic (within the past 150 years) species compositions. To completely remove mesquite trees, two points need consideration. First, one has to consider the prodigious commitment of resources in terms of personnel, materials, time, and expense. Second, complete removal of mesquite does not necessarily result in the restoration of desert grassland. If mesquite range expansion represents a form of disturbance to the grassland plant community, then efforts to remove it represent another. Exotic plant species better adapted to various disturbance regimes may have a competitive advantage over native grasses in exploiting this disturbance. For this reason, a management

strategy would have to include continual monitoring and persistent removal of mesquite, and other undesirable plant species. Where possible, documentation of the rate and extent of mesquite spread in the management area could help determine the extent of management efforts necessary for removal. This documentation would include dated aerial photographs and interviews with local residents.

A suggested management tactic is a combination of mechanical removal and/or herbicide treatment followed by prescribed burning. If prescribed burning is scheduled after allowing the mechanically displaced woody debris to dry sufficiently for combustion, then this may allow the surviving mesquite to resprout. These resprouts could then be killed back by the subsequent fire. McPherson and Wright (1986) recommended that areas to be burned should be suspended from livestock grazing for at least a previous growing season so that herbaceous dry matter could accumulate. They also recommended conducting a small test burn to verify the efficacy of a prescribed burn within a given time period. Over time, periodic prescribed fires could be used to destroy emerging mesquite seedlings. The rate of mesquite re-establishment in this area would depend on the size of the existing seed bank, the density and distribution of mesquite stands in adjacent areas, and the mechanisms of seed dispersal from those adjacent areas.

To satisfy this objective, land-use managers could identify and protect rangelands that are currently devoid of mesquite, such as the desert grassland north of Sonoita in southeastern Arizona (Fig. 1). Since the seedbank in these areas would be largely devoid of mesquite, potential seed dispersers would have to be monitored and controlled. Due to the high rate of mesquite establishment in rangelands, these mesquite-free areas are becoming more limited in size.

Preventing mesquite establishment is less difficult than removing it, though this may be unrealistic in areas that contain livestock.

Objective 2. Continued Mesquite Establishment in Desert Grassland.

This objective may be implemented by ranchers who lack the resources necessary for range control or by researchers who wish to study the current and future rate and extent of mesquite establishment on open rangelands. Because the N-fixing capability of mesquite can elevate soil N concentrations within the rangeland, exotic plants that have higher N requirements could become established. Even a management objective of non-intervention would have to include continued monitoring of rangeland for potentially invasive species.

The implementation of any of the other management objectives will become more difficult with time as the mesquite alter soil-nutrient concentrations and create a long-lasting seed bank. Therefore, a long-range forecast of land use in these rangelands is advisable before implementing this objective.

Objective 3. Limited Mesquite Removal from Desert Grassland.

This objective is probably the most feasible alternative for most land use managers, including those who have limited resources for rangeland control, and/or those who wish to profit from the beneficial aspects of limited mesquite establishment on rangeland. Prescribed fires combined with limited grazing and an initial herbicide application are recommended management tactics in this case. Ansley et al. (1996) determined that while intense fires may kill all aboveground portions of mesquite, basal resprouting may quickly produce an impenetrable grove.

These authors suggested that lower intensity fires may kill small mesquite while allowing larger individuals to survive with intact upper canopies; this can create a park effect with enhanced visibility beneath stand canopies. Since the main stems of the larger mesquite remain intact, resprouting would be minimized.

By minimizing multi-stemmed resprouting, the average stem diameter of mesquite stands would be larger, increasing the commercial lumber value. Ansley et al. (1998) thinned sections of a dense mesquite woodland from 300 to 80 trees/ha; within 5 years of thinning, trees within this section had significantly greater basal stem diameters, canopy diameters, and leaf area. Felker et al. (1990) have suggested that limited removal of mesquite from rangeland may actually increase its value as lumber, as stands below maximum density tend to produce larger individuals with thicker main stems. They predicted that a spacing of 10 meters per tree would produce an optimum yield. Limited grazing intensity would slow the rate of mesquite seed establishment and would also allow grasses to retain viable populations between mesquite canopies.

The park-like stands resulting from periodic prescribed fires would become more aesthetically appealing, creating opportunities for recreation and tourism while maintaining an increased biodiversity of wildlife. Ultimately, this land management system could increase the commercial value of rangeland for ranchers; commercial utilization of these areas for mesquite lumber and tourism and recreation would offset any losses in revenue from limited livestock grazing. Since this management tactic is relatively inexpensive to implement (Teague et al. 1997), it can be used over a long period to insure that these thinned mesquite stands remain stable in density.

CONCLUSIONS

After European settlement in rangelands of the southwestern United States, mesquite has moved from predominantly riparian and ephemeral-channel locations to adjacent xeric grasslands. The exact causes for this range expansion are complex and may never be fully determined. Although mesquite is native to the geographic region, its expansion into more xeric habitats resembles that of non-native invasive species, and warrants an inspection of its life history strategies, as discussed in this paper.

Although many plant species lack common features which determine whether they are invasive or potentially invasive, mesquite is uniquely qualified to occupy areas that are resource-limited to many other C3 plants. As C3 plants, they can utilize winter precipitation that is unused by C4 grasses, and their deep root system insures that they have access to soil moisture unavailable to shallow-rooted grasses. Mesquite can indirectly access atmospheric N, a resource that is severely limited in xeric environments.

Two interdependent factors may account for increased mesquite distribution in open rangelands within the last 150 years. Seed dispersal has increased due to ingestion by livestock, and to a lesser extent by rodents. Germination and establishment of seeds has been enhanced by increases in winter precipitation, particularly within the past 40 years, and decreases in interspecific competition due to livestock grazing. Ultimately, mesquite stands may increase until mesquites are only competing with each other for resources. In the absence of a land-management strategy, intraspecific competition may be the main mechanism limiting their densities in this habitat.

It is ironic that livestock grazing is one of the main dispersal mechanisms for seed, while at the same time increasing mesquite stand densities limit future grazing potential of this region. For continued use of these areas for livestock grazing, a land-management strategy is therefore mandated. This strategy must contain clearly defined objectives after determining how these areas will be used.

Of the three management objectives offered, complete removal of mesquite from open rangelands would be the most difficult to accomplish and to maintain. In contrast, non-intervention would be the easiest to implement. However, this could have undesirable consequences as exotic plant species may become established, and the biodiversity of native plants become diminished. Limited removal of mesquite from these rangelands is potentially the most realistic objective for most land use managers, as it may be relatively cheap to implement (Teague et al. 1997), while actually increasing the commercial potential of this landscape.

REFERENCES

- Ansley, R.J. 1991. Brush management and water. pp. 23-30 In: T.G. Welch (ed.) Proceedings: Brush Management Symposium, 7-8 May 1991, Abilene, TX. Texas Agric. Extension Service, Texas A&M Univ., College Station. 73 p.
- Ansley, R.J.; Jacoby, P.W.; Cuomo, G.J. 1990. Water relations of honey mesquite following severing of lateral roots: Influence of location and amount of subsurface water. *Journal of Range Management*. 43: 436-442.
- Ansley, R.J.; Jacoby, P.W.; Hicks, R. 1991. Leaf and whole plant transpiration in honey mesquite following severing of lateral roots. *Journal of Range Management*. 44: 577-583.
- Ansley, R.J.; Jacoby, P.W.; Meadors, C.H.; Lawrence, B.K. 1992. Soil and leaf water relations of differentially moisture-stressed honey mesquite (*Prosopis glandulosa* Torr). *Journal of Arid Environments* 22: 147-159.

Ansley, R.J.; Cadenhead, J.F.; Kramp, B.A. 1996. Mesquite savanna: A brush management option. *The Cattleman*. 82: 10-12.

Ansley, R.J.; Trevino, B.A.; Jacoby, P.W. 1998. Intraspecific competition in honey mesquite: Leaf and whole plant responses. *Journal of Range Management*. 51: 345-352.

Archer, S.; Scifres, C.; Bassham, C.R.; Maggio, R. 1988. Autogenic succession in a subtropical savanna: Conversion of grassland to thorn woodland. *Ecological Monographs*. 52: 111-127.

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? *American Naturalist*. 134: 545-561.

Bahre, C.J. 1985. Wildfire in southeastern Arizona between 1850 and 1890. *Desert Plants*. 7(4): 190-194.

Bahre, C.J. 1991. *A legacy of change: Historic impact on vegetation in the Arizona borderlands*. University of Arizona Press, Tucson.

Bahre, C.J.; Shelton, M.L. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *Journal of Biogeography*. 20: 489-504.

Bailey, A.W. 1976. Rate of nitrogen fixation in honey mesquite seedlings. *Journal of Range Management*. 29: 479-481.

Barth, R.C.; Klemmedson, J.O. 1982. Amount and distribution of dry matter, nitrogen, and organic carbon in soil-plant systems of mesquite and palo verde. *Journal of Range Management*. 35: 412-418.

Biggs, T.H. 1997. Fire frequency, nutrient concentrations and distributions, and ¹³C of soil organic matter and plants in southeastern Arizona grassland. PhD dissertation, University of Arizona. 193 pp.

Biggs, T.H.; Webb, R.H.; Quade, J. 1999. Fire frequency and spatial variability of soil biogeochemistry and plant biochemistry in a southeastern Arizona desert grassland. in *Toward integrated research, land management, and ecosystem protection in the Malpai borderlands: conference summary*; 6-8 January 1999; Douglas AZ. Compiled by G. J. Gottfried, L.G. Eskew, C.G. Curtin, and C.B. Edminster. *Proceedings RMRS-P-10*. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 77-80.

Britton, C.M. ; Wright, H.A. 1971. Correlation of weather variables to mesquite damage by fire. *Journal of Range Management*. 24: 136-141.

Brock, J.H. 1986. Velvet mesquite seedling development in three southwestern soils. *Journal of Range Management*. 39: 331-334.

- Brown, A.L. 1950. Shrub invasion of southern Arizona desert grassland. *Journal of Range Management*. 3: 172-177.
- Brown, D.E.; Lowe, C.H. 1980. Biotic communities of the southwest. U.S. Department of Agriculture, Fort Collins Colorado, RM-78.
- Brown, J.R.; Archer, S. 1987. Woody plant seed dispersal and gap formation in a North American subtropical savanna woodland: the role of domestic herbivores. *Vegetatio*. 73: 73-80.
- Brown, J.R.; Archer, S. 1989. Woody plant invasion of grasslands: Establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia*. 80: 19-26.
- Bowers, J.E.; Webb, R.H.; Rondeau, R.J. 1995. Longevity, recruitment and mortality of desert plants in Grand Canyon, Arizona, USA. *Journal of Vegetation Science* 6: 551-564.
- Buffington, L.C.; Herbel, C.H. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs*. 35: 139-164.
- Burkhardt, A. 1976. A monograph of the Genus *Prosopis* (Leguminosae Subfam. Mimosoideae) *Journal of the Arnold Arboretum*. 57: 219-249.
- Bush, J.K.; Van Auken, O.W. 1990. Growth and survival of *Prosopis glandulosa* seedlings associated with shade and herbaceous competition. *Botanical Gazette*. 151: 234-239.
- Chojnacky, D.C. 1991. Growth prediction for Arizona's mesquite (*Prosopis velutina*) woodlands. *Forest Ecology and Management*. 42: 293-310.
- Cox, J.R.; Alba-Avila, A.; Rice, R.W.; Cox, J.N. 1993. Biological and physical factors influencing *Acacia constricta* and *Prosopis velutina* establishment in the Sonoran Desert. *Journal of Range Management*. 46: 43-48.
- Diaz, S.; Cabido, M. 1997. Plant functional types and ecosystem function in relation to global change. *Journal of Vegetation Science*. 8: 463-474.
- Dodd, J.D.; Holtz, S.T. 1971. Integration of burning with mechanical manipulation of south Texas grassland. *Journal of Range Management*. 24: 130-136.
- Eskew, D.L.; Ting, I.P. 1978. Nitrogen fixation by legumes and blue-green algal-lichen crusts in a Colorado desert environment. *American Journal of Botany*. 65: 850-856.
- Felker, P.; Clark, P.R. 1980. Nitrogen fixation (acetylene reduction) and cross inoculation in 12 *Prosopis* (Mesquite) species. *Plant and Soil*. 57: 177-186.

- Felker, P.; Meyer, J. M.; Gronski, S. J. 1990. Application of self-thinning in mesquite (*Prosopis glandulosa* vs. *glandulosa*) to range management and lumber production. *Forest Ecology and Management*. 31: 225-232.
- Felker, P. 1996. Commercializing mesquite, leucaena, and cactus in Texas. p. 133-137. In: J. Janick (ed.), *Progress in new crops*. ASHS Press, Alexandria, VA.
- Felker, P. 1998. The value of mesquite for the rural southwest: fine lumber and soil improvement. *Journal of Forestry* 96: 16-20.
- Finn, R.C.; Archer, S.; Boutton, T.W.; Harlan, T. 1994. Identification of annual rings in an arid-land woody plant, *Prosopis glandulosa*. *Ecology*. 75: 850-853.
- Gibbens, R.P.; Herbel, C.H.; Morton, H.L.; Lindemann, W.C.; Ryder-White, J.A.; Richman, D.B.; Huddleston, E.W.; Conley, W.H.; Davis, C.A.; Reitzel, J.A. 1986. Some impacts of 2,4,5-T on a mesquite duneland ecosystem in southern New Mexico: A synthesis. *Journal of Range Management*. 39: 320-325.
- Gibbens, R.P.; Beck, R.F.; McNeely, R.P.; Herbel, C.H. 1992. Recent rates of mesquite establishment in the northern Chihuahuan Desert. *Journal of Range Management*. 45: 585-588.
- Glendening, G.E. 1952. Some quantitative data on the increase of mesquite and cactus on a desert grassland range in southern Arizona. *Ecology*. 33: 319-328.
- Griffiths, David. 1910. A protected stock range in Arizona. U.S. Department of Agriculture, Bureau of Plant Industry Bulletin 177.
- Grover, H.D.; Musick, H.B. 1990. Shrubland encroachment in southern New Mexico, U.S.A.: An analysis of desertification processes in the American southwest. *Climatic Change*. 17: 305-330.
- Haque, Z.; Younga, A.; McDaniel, K.C.; Pieper, R.D. 1991. Two-Phase pattern in mesquite-herbland vegetation in southern New Mexico. *Southwestern Naturalist*. 36: 54-59.
- Hastings, J.R.; Turner, R.M. 1965. *The changing mile: an ecological study of vegetation change with time in the lower mile of an arid and semi-arid region*. Tucson: University of Arizona Press.
- Heitschmidt, R.K.; Ansley, R.J.; Dowhower, S.L.; Jacoby, P.W.; Price, D.L. 1988. Some observations from the excavation of honey mesquite root systems. *Journal of Range Management*. 41: 227-231.
- Hennessy, J.T.; Gibbens, R.P.; Tromble, J.M.; Cardenas, M. 1983. Vegetation changes from 1935 to 1980 in mesquite dunelands and former grasslands of southern New Mexico. *Journal of Range Management*. 36: 370-374.

Hereford, Richard; Webb, R.H. 1992. Historic variation in warm-season rainfall on the Colorado Plateau, U.S.A. *Climatic Change*. 22: 239-256.

Hobbs, N.T.; Schimel, D.S.; Owensby, C.E.; Ojima, D.S. 1991. Fire and grazing in the tallgrass prairie: contingent effects on nitrogen budgets. *Ecology*. 72: 1374-1382.

Humphrey, R.R. 1949. Fire as a means of controlling velvet mesquite, burroweed, and cholla on southern Arizona ranges. *Journal of Range Management*. 2: 175-182.

Humphrey, R.R. 1958. The desert grasslands: a history of vegetational change and an analysis of causes. *Botanical Review*. 24: 193-252.

Isely, D. 1998. Native and naturalized Leguminosae (Fabaceae) of the United States. Provo: Brigham Young University. 1007 pp.

Jacoby, P.W.; Meadors, C.H.; Foster, M.A. 1981. Control of honey mesquite (*Prosopis juliflora* var. *glandulosa*) with 3,6-Dichloropicolinic Acid. *Weed Science*. 29: 376-378.

Jacoby, P.W.; Meadors, C.H.; Foster, M.A.; Hartmann, F.S. 1982. Honey mesquite control and forage response in Crane County, Texas. *Journal of Range Management*. 35: 424-426.

Jacoby, P.W.; Meadors, C.H.; Ansley, R.J. 1990a. Control of honey mesquite with herbicides: Influence of plant height. *Journal of Range Management*. 43: 33-35.

Jacoby, P.W.; Ansley, R.J.; Meadors, C.H.; Huffman, A.H. 1990b. Control of honey mesquite with herbicides: Influence of stem number. *Journal of Range Management*. 43: 36-38.

Jacoby, P.W.; Ansley, R.J.; Meadors, C.H.; Huffman, A.H. 1990c. Epicuticular wax in honey mesquite: Seasonal accumulation and intraspecific variation. *Journal of Range Management*. 43: 347-350.

Jacoby, P.W.; Ansley, R.J. 1991. Mesquite: Classification, distribution, ecology, and control. Chap. 36, pp. 364-376. In: *Noxious range weeds*. Ed. by L.F. James, J.O. Evans, M.H. Ralphs, and D.R. Child: Westview Press, Boulder, CO. 466 pp.

Janzen, D.H.; Martin, P.S. 1982. Neotropical anachronisms: The fruits the Gomphotheres ate. *Science*. 215: 19-27.

Jenkins, M.B.; Virginia, R.A.; Jarrell, W.M. 1988. Depth distribution and seasonal populations of mesquite-nodulating Rhizobia in warm desert ecosystems. *Soil Science Society of America Journal*. 52: 1644-1650.

Jenkins, M.B.; Virginia, R.A.; Jarrell, W.M. 1989. Ecology of fast-growing and slow-growing mesquite-nodulating Rhizobia in Chihuahuan and Sonoran Desert ecosystems. *Soil Science Society of America Journal*. 53: 543-549.

- Johnson, H.B.; Meyeux Jr., H.S. 1990. *Prosopis glandulosa* and the nitrogen balance of rangelands: Extent and occurrence of nodulation. *Oecologia*. 84: 176-185.
- Killingbeck, K.T.; Whitford, W.G. 1996. High foliar nitrogen in desert shrubs: An important ecosystem trait or defective desert doctrine? *Ecology*. 77(6): 1728-1737.
- Kramp, B.A.; Ansley, R.J.; Tunnell, T.T. 1998. Mesquite seedling survival following emergence from cattle and wildlife feces. *Southwestern Naturalist*. 43: 300-312.
- Martin, S.C. 1948. Mesquite seeds remain viable after 44 years. *Ecology*. 3: 393.
- Martin, S.C. 1970. Longevity of velvet mesquite in the soil. *Journal of Range Management*. 23: 69-70.
- Martin, S.C. 1983. Responses of semidesert grasses and shrubs to fall burning. *Journal of Range Management*. 36: 604-610.
- Martin, P.S.; Burney, D.A. 1999. Bring back the elephants! *Wild Earth*. 9: 57-64.
- Mayeux, H.S.; Wilkinson, R.E. 1990. Composition of epicuticular wax on *Prosopis glandulosa* leaves. *Botanical Gazette*. 151: 240-244.
- McClaran, M.P.; Van Devender, T.R. 1995. The desert grassland. Tucson: University of Arizona Press. 346 pp.
- McPherson, G.R.; Wright, H.A. 1986. Threshold requirements for burning downed honey mesquite. *Journal of Range Management*. 39: 327-330.
- McPherson, G. 1997. Ecology and management of North American savannas. Tucson: University of Arizona Press. 208 pp.
- Nilsen, E.T.; Sharifi, M.R.; Rundel, P.W.; Virginia, R.A. 1986. Influences of microclimatic conditions and water relations on seasonal leaf dimorphism of *Prosopis glandulosa* var. *torreyana* in the Sonoran Desert, California. *Oecologia* (Berlin). 69: 95-100.
- Nolte, K.R.; Fulbright, T.E. 1997. Plant, small mammal, and avian diversity following control of honey mesquite. *Journal of Range Management*. 50: 205-212.
- Phillips, W.S. 1963. Depth of roots in soil. *Ecology*. 44: 424.
- Polley, H.W.; Johnson, H.B.; Mayeux, H.S. 1994. Increasing CO₂: Comparative responses of the C₄ grass *Schizachyrium* and grassland invader *Prosopis*. *Ecology*. 75: 976-988.

- Reynolds, H.G.; Glendening, G.E. 1949. Merriam kangaroo rat a factor in mesquite propagation on southern Arizona rangelands. *Journal of Range Management*. 2: 193-197.
- Rundel, P.W.; Nilsen, E.T.; Sharifi, M.R.; Virginia, R.A.; Jarrell, W.M.; Kohl, K.H.; Shearer, G.B. 1982. Seasonal dynamics of nitrogen cycling for a *Prosopis* woodland in the Sonoran Desert. *Plant and Soil*. 67: 343-353.
- Sala, O.E.; Lauenroth, W.K.; Golluscio, R.A. 1997. Plant functional types in temperate semi-arid regions. in *Plant functional types*. Ed. by T.M. Smith, H.H. Shugart, and F.I. Woodward. Cambridge: Cambridge University Press. 217-233.
- Schlesinger, W.H.; Reynolds, J.F.; Cunningham, G.L.; Huenneke, L.F.; Jarrell, W.M.; Virginia, R.A.; Whitford, W.E. 1990. Biological feedbacks in global desertification. *Science*. 247: 1043-1048.
- Scifres, C.J.; Brock, J.H. 1971. Emergence of honey mesquite seedlings relative to planting depth and soil temperature. *Journal of Range Management*. 24: 217-219.
- Shearer, G.; Kohl, D.H.; Virginia, R.A.; Bryan, B.A.; Skeeters, J.L.; Nilsen, E.T.; Sharifi, M.R.; Rundel, P.W. 1983. Estimates of N₂-fixation from variation in the natural abundance of ¹⁵N in Sonoran Desert ecosystems. *Oecologia*(Berlin). 56: 365-373.
- Stromberg, J.C.; Wilkins, S.D.; Tress, J.A. 1993. Vegetation-hydrology models: Implications for management of *Prosopis velutina* (velvet mesquite) riparian ecosystems. *Ecological Applications*. 3: 307-314.
- Teague, R.; Borchardt, R.B.; Ansley, J.; Pinchak, B.; Cox, J.; Foy, J.; McGrann, J. 1997. Sustainable management strategies for mesquite rangelands: The Waggoner Kite Project. *Rangelands*. 194-198.
- Van Auken, O.W.; Bush, J.K. 1990. Importance of grass density and time of planting on *Prosopis glandulosa* seedling growth. *Southwestern Naturalist*. 35: 411-415.
- Van Auken, O.W.; Bush, J.K. 1997. Growth of *Prosopis glandulosa* in response to changes in aboveground and belowground interference. *Ecology*. 78: 1222-1229.
- Virginia, R.A.; Jarrell, W.M. 1983. Soil properties in a mesquite-dominated Sonoran Desert ecosystem. *Soil Science Society of America Journal*. 47: 138-144.
- Virginia, R.A. 1986. Soil development under legume tree canopies. *Forest Ecology Management*. 16: 69-79.
- Warren, A.; Holeshek, J.; Cardenas, M. 1996. Honey mesquite influences on Chihuahuan Desert vegetation. *Journal of Range Management* 49: 46-52.

- Webb, R.H.; Betancourt, J.L. 1992. Climatic variability and flood frequency of the Santa Cruz River, Pima County, Arizona. U.S. Geological Survey Water-Supply Paper 2379. 40 p.
- Weltzin, J.F.; Archer, S.; Heitschmidt, R.K. 1998. Defoliation and woody plant (*Prosopis glandulosa*) seedling establishment: Potential vs. realized herbivory tolerance. *Plant Ecology*. 138: 127-135.
- West, N.E.; Klemmedson, J.O. 1978. Structural distribution of nitrogen in desert ecosystems. in *Nitrogen in desert ecosystems*. Ed. by N.E. West and J.J. Skujins. IBP Synthesis Series 9. Pennsylvania: Dowden, Hutchinson & Ross, Inc. 1-16.
- Wilson, T.B.; Webb, R.H.; Thompson, T.L. 1999. Fire frequency and soil nutrient status on the Southern Gunnery Range at Fort Huachuca military reservation, Arizona. in *Toward integrated research, land management, and ecosystem protection in the Malpai borderlands: conference summary; 6-8 January 1999; Douglas AZ*. Compiled by G. J. Gottfried, L.G. Eskew, C.G. Curtin, and C.B. Edminster. Proceedings RMRS-P-10. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 81-82.
- Wright, H.A.; Bunting, S.C.; Neuenschwander, L.F. 1976. Effect of fire on honey mesquite. *Journal of Range Management*. 29: 461-471.
- Zitzer, S.F.; Archer, S.R.; Boutton, T.W. 1996. Spatial variability in the potential for symbiotic N₂ fixation by woody plants in a subtropical savanna ecosystem. *Journal of Applied Ecology*. 33: 1125-1136.

FIGURE CAPTIONS

Figure 1. Map showing biotic communities of the region of southwestern New Mexico and southeastern Arizona that contain desert grasslands (from Brown and Lowe 1980).

This area includes what we refer to as Sonoran and Chihuahuan desert grasslands, defined by Brown and Lowe (1980) as semidesert grassland and plains and Great Basin grassland.

Figure 2. (June 1999). Effect of rangeland fire on *Prosopis velutina* woodland on eastern foothills of the Huachuca Mountains, southeastern Arizona. Note the mesquite tree (*P. velutina*) in the right foreground appears to be largely undamaged by fire. (photograph by Thomas Wilson)

Figure 3. Aerial photographs of Woodcutter's Canyon in the southeastern gunnery ranges at Fort Huachuca Military Reservation in southeastern Arizona. Note that the road system changes through time but the topography is consistent among these photos. The letters A, B, and C refer to plots intensively studied by Biggs (1997), Biggs et al. (1999), and Wilson et al. (1999) for the effects of fire frequency on soil-nutrient concentrations and mesquite stand densities.

A. (1935). Individual mesquite (*P. velutina*) are mostly confined to washes at the upper right, center, and lower left. A prominent line from upper right to middle left is a fence line, a residual of livestock grazing in the area that ended in the early 1940s.

Note that no mesquite occur on sites A, B, and C.

B. (November 17, 1956). By 1956, mesquite trees are scattered throughout the view, although large sections of grasslands remain without trees, particularly at right. The modern road system, which also serves as a fire-break system, was established just before this time. The stand density of mesquite on sites A, B, and C is approximately equal; all three sites had disturbances related to World War II training exercises.

C. (January 18, 1975). Mesquite stands have become quite dense in some portions of the view, particularly at lower left. Mesquites have continued to increase on Site A, which did not burn in the 20th century. Site C burned shortly before this photograph, resulting in its light color in this photograph, and mesquite trees are not very visible on this site in 1975.

D. (January 20, 1985). Mesquite stand densities are highest in 1985, particularly in the rangelands at left. Site C, which had a fire frequency of 4 fires per decade between the early 1970s and 1989 (Biggs 1997), remains free of significant mesquite. In the same period, Site B had a fire frequency of 2 fires per decade, and mesquite trees are scattered uniformly at a lower density than sites at lower left. Mesquite density on Site A continued to increase because of lack of fires. The difference between the burned sites and Site A is reflected by differences in albedo.

E. (March 31, 1994). Because of wildfires set during military exercises, mesquite stand densities may be significantly lower on much of the rangeland, particularly at lower left. However, the size of individual plants is much lower, reflecting resprouting of trees damaged by fires. Because of the lack of fires, Site A consequently has a high

stand density and large size of individual mesquite trees (Biggs et al. 1999). For these reasons, Site A clearly is distinguishable from sites B and C as well as the rest of the rangeland. For these reasons, the Southern Gunnery Range at Fort Huachuca serves as a good example of our management objective C, the limited control of mesquite on rangelands.

Figure 4. Standardized anomalies of annual precipitation. A. Grasslands of the western Chihuahuan desert. B. Grasslands of southeastern Arizona.

Figure 5. Standardized anomalies of seasonal precipitation in grasslands of the western Chihuahuan desert (Table 1). A. Summer precipitation (July-September). B. Winter precipitation (November-March).

Figure 6. Standardized anomalies of seasonal precipitation in the desert grasslands of southeastern Arizona (Table 2). A. Summer precipitation (July-September). B. Winter precipitation (November-March).

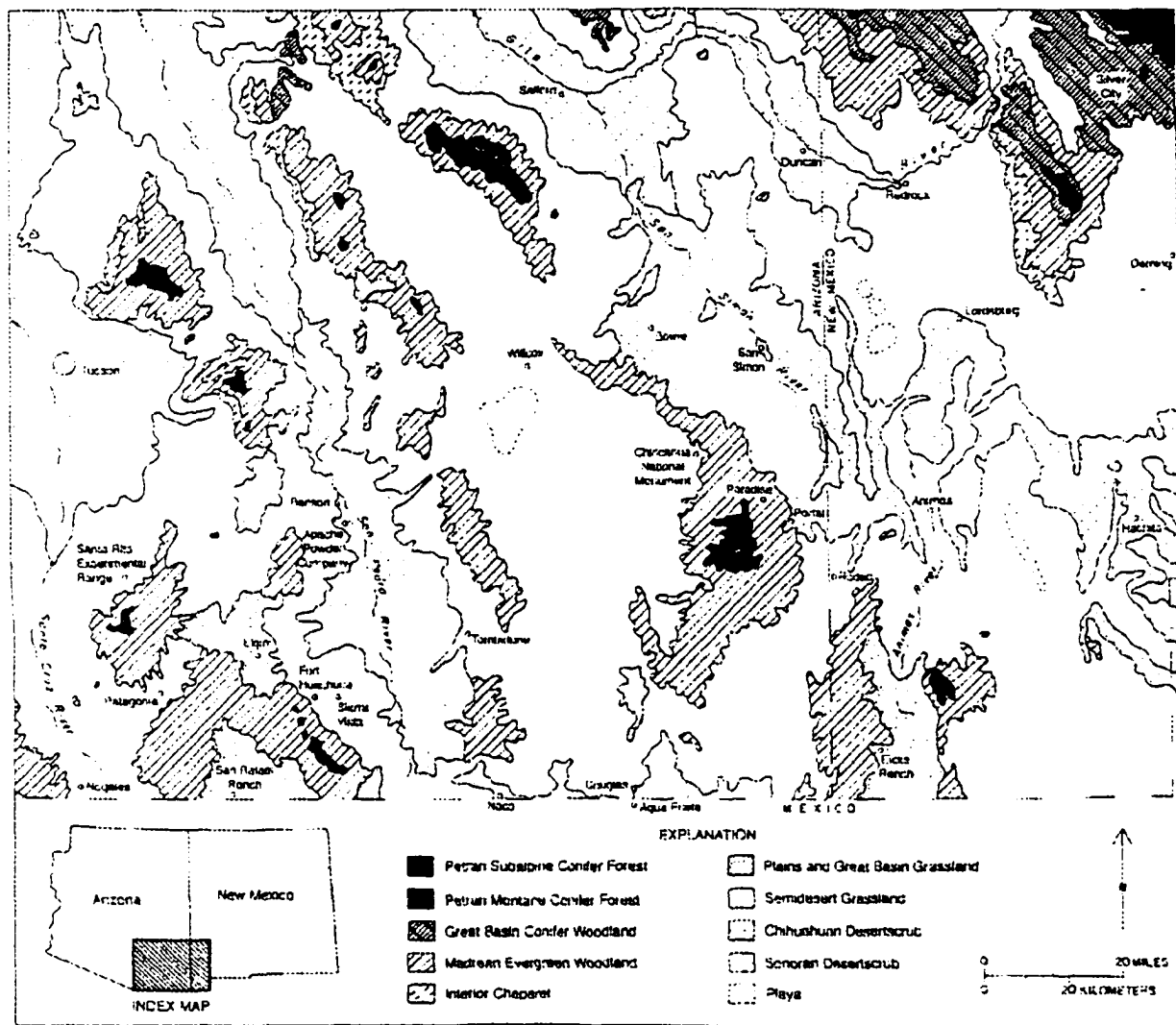


Figure 1.



Figure 2.



Figure 3a. Woodcutter's Canyon (1935).



Figure 3b. Woodcutter's Canyon (1956).



Figure 3c. Woodcutter's Canyon (1975).



Figure 3d. Woodcutter's Canyon (1985).



Figure 3e. Woodcutter's Canyon (1994).

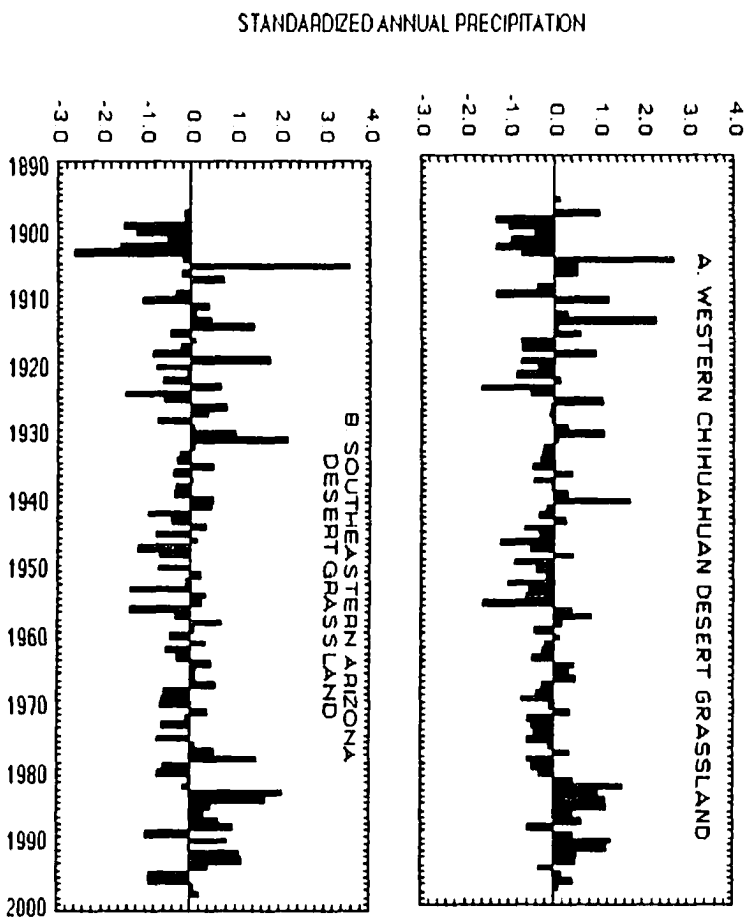


Figure 4.

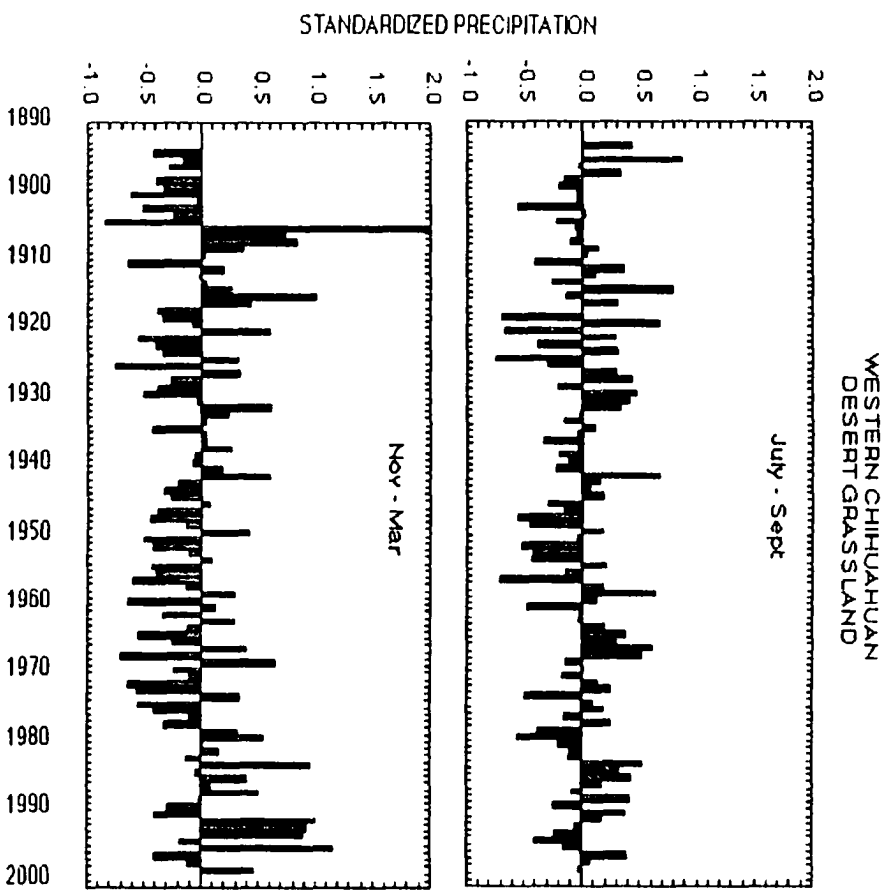


Figure 5.

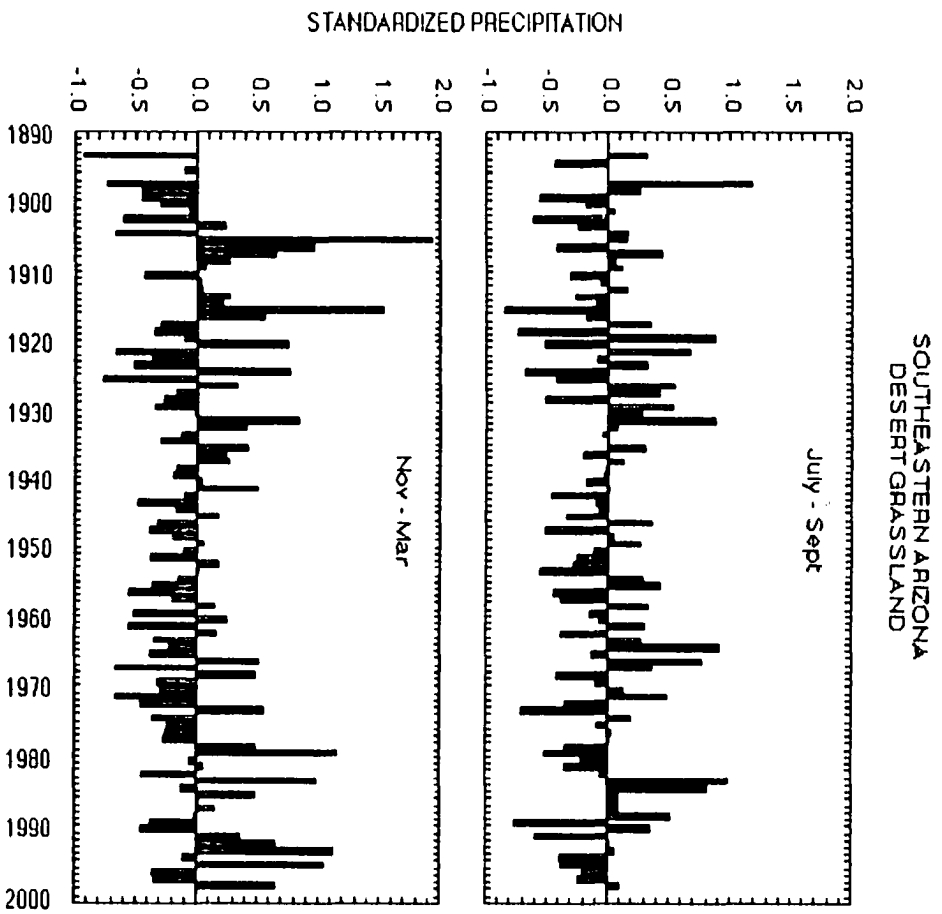


Figure 6.

Table 1. Climate stations in the western Chihuahuan desert grassland

| State | Location | Elevation (m) | Period of Record | Annual Precipitation (mm) |
|------------|------------------------------|------------------|------------------------|---------------------------------|
| Arizona | Bowie | 1149 | 1-1-1899 to 12-31-1998 | 273 |
| | Chiricahua National | | | |
| Arizona | Monument | 1616 | 1-1-1909 to 12-31-1998 | 493 |
| Arizona | Clifton | 1058 | 1-1-1893 to 12-31-1998 | 328 |
| Arizona | Douglas | 1232 | 7-1-1948 to 2-28-1994 | 371 |
| Arizona | Douglas FAA Airport | 1250 | 7-2-1948 to 12-31-1998 | 333 |
| Arizona | Douglas Smelter | 1210 | 12-1-1903 to 3-20-1973 | 312 |
| | | | 5-21-1901 to | |
| Arizona | Duncan | 1116 | 12-31-1998 | 276 |
| Arizona | Paradise | 1655 | 1-1-1906 to 8-31-1937 | 484 |
| Arizona | Portal | 1524 | 1-1-1914 to 3-31-1955 | 442 |
| Arizona | Portal 4SW | 1643 | 3-1-1965 to 12-31-1998 | 546 |
| Arizona | Safford | 884 | 8-1-1998 to 6-30-1973 | 226 |
| Arizona | Safford Agricultural Station | 899 | 8-1-1948 to 12-31-1998 | 234 |
| Arizona | San Simon | 1101 | 3-1-1898 to 12-31-1998 | 244 |
| Arizona | San Simon 9ESE | 1183 | 7-19-1962 to 7-31-1986 | 251 |
| Arizona | Willcox | 1274 | 6-1-1898 to 12-31-1998 | 311 |
| New Mexico | Animas | 1345 | 9-1-1923 to 12-31-1998 | 280 |
| New Mexico | Columbus | 1268 | 1-1-1925 to 12-31-1998 | 242 |
| New Mexico | Deming | 1311 | 1-1-1914 to 12-31-1998 | 240 |
| New Mexico | Eicks Ranch | 1619 | 1-1-1933 to 10-31-1961 | 373 |
| New Mexico | Hachita | 1375 | 1-1-1914 to 12-31-1998 | 269 |
| New Mexico | Lordsburg | 1296 | 1-1-1914 to 12-31-1998 | 275 |
| New Mexico | Redrock | 1265 | 1-1-1914 to 12-31-1998 | 324 |
| New Mexico | Rodeo | 1256 | 1-1-1914 to 12-31-1998 | 285 |
| | | | 11-1-1948 to | |
| New Mexico | White Signal | 1851 | 12-31-1998 | 381 |

Table 2. Climate Stations in the southeastern Arizona desert grassland.

| State | Location | Elevation (m) | Period of Record | Annual Precipitation (mm) |
|---------|-------------------------|------------------|-------------------------|---------------------------------|
| Arizona | Apache Powder Company | 1125 | 7-1-1923 to 4-30-1990 | 335 |
| Arizona | Arivaca | 1105 | 1-1-1956 to 12-31-1998 | 455 |
| Arizona | Benson | 1119 | 6-1-1894 to 5-31-1975 | 288 |
| Arizona | Elgin | 1494 | 10-1-1912 to 12-31-1969 | 383 |
| Arizona | Fort Huachuca | 1424 | 2-1-1900 to 12-31-1981 | 397 |
| Arizona | Nogales | 1162 | 7-1-1948 to 6-30-1983 | 421 |
| Arizona | Nogales 6N | 1085 | 10-1-1952 to 12-31-1999 | 450 |
| Arizona | Old Nogales | 1189 | 12-1-1892 to 6-30-1948 | 399 |
| Arizona | Patagonia | 1233 | 7-1-1921 to 12-31-1998 | 454 |
| Arizona | San Rafael Ranch | 1445 | 12-1-1892 to 3-31-1968 | 439 |
| | Santa Rita Experimental | | | |
| Arizona | Station | 1311 | 7-1-1916 to 12-31-1998 | 566 |
| Arizona | Sierra Vista | 1402 | 3-1-1982 to 12-31-1998 | 374 |
| Arizona | Tombstone | 1405 | 7-1-1893 to 12-31-1998 | 354 |
| Sonora | Agua Prieta | 1189 | 2-1-1961 to 12-31-1986 | 379 |
| Sonora | Cananea | 1607 | 1-1-1923 to 10-31-1991 | 539 |
| Sonora | Naco | 1404 | 1-1-1923 to 12-1-1995 | 368 |

APPENDIX B

**Nutrient Topographies of Mesquite-Dominated Desert Grasslands:
Changes in Time and Space**

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ABSTRACT

Mesquite trees in desert grasslands create altered resource distributions of soil N, C, and P, through N fixation and subsequent litterfall. Over time, these resources become localized under mesquite canopies. Fires may reverse this process, but the degree to which this occurs is poorly understood. Seasonal fluctuations in mesquite litterfall mass, nutrient content, and adjacent soil N concentrations are also largely unknown. We selected two adjacent locations in Woodcutter's Canyon at Fort Huachuca in southeastern Arizona with similar soil and climate but different fire histories. We sampled velvet mesquite (*Prosopis velutina*) litterfall monthly and soil seasonally during 1997 and 1998. We found significantly greater litterfall under trees at the less disturbed location, and single-trunked mesquites contributed more litterfall than multiple-stemmed trees which resprouted following fire at the more disturbed location. Most litterfall occurred during the winter; significantly greater litterfall C accumulated during the winter, while greater N and P accumulated during the summer. Litterfall C:N ratios ranged from 12:1 during the summer to 23:1 during the winter of each year. Seasonal variation of soil inorganic N was not significant, but the frequently burned site contained significantly lower inorganic N concentrations throughout the sampling period. Soil inorganic N, total N, total organic carbon (TOC), and available P were positively correlated with mesquite tree location, with greater concentrations under single-trunked mesquites. Comparing intercanopy locations between sites, greater concentrations of total N, TOC, and available P were found at the frequently burned location, indicating that these nutrients were less localized at this site. These results show that when mesquites survive fire, their multiple-stemmed growth form reduces nutrient sequestration. Furthermore, seasonal variation in litterfall mass and N, C, and P concentrations were significant, but were not directly related to variation in soil inorganic N concentrations.

Keywords: fire frequency, seasonality, litterfall, nitrogen, phosphorus, carbon, soils

INTRODUCTION

During the last century, increases in mesquite (*Prosopis glandulosa* and *P. velutina*) distribution in areas of the southwestern United States has been the focus of numerous studies (Cable and Martin 1971, Cox et al., 1993, Glendening 1952, Grover and Musick 1990, Hastings and Turner 1965, Humphrey 1958, Reynolds and Glendening 1949, Klemmedson and Tiedemann 1986, Tiedemann and Klemmedson 1986). The causes that may account for this altered distribution--climate change (Grover and Musick, 1990), livestock grazing and seed distribution (Archer et al. 1988, Bahre and Shelton 1993, Schlesinger et al. 1990), suppression of wildfires (Bahre 1985, Humphrey 1958), or rodent seed distribution (Cox et al. 1993, Reynolds and Glendening 1949)--have been investigated for several decades. The effects that *Prosopis* may have on desert grassland soils and biogeochemical cycling of N, C, and P are less understood.

One of the effects of mesquite occupation of grasslands has been a concentration of plant-available soil nutrients under *Prosopis* canopies (Barth and Klemmedson 1983). For example, Schlesinger et al. (1990) found a coefficient of variation for soil total N to be four times higher in *P. glandulosa*-dominated areas than in black grama grassland at the Jornada Experimental Range in New Mexico. Tiedemann and Klemmedson (1986a) studied the effects of *Prosopis* removal and found a 34% decline in soil N in the upper 4.5 cm after 13 years. In southern California, Virginia and Jarrell (1983) found that concentrations of soil total N and organic C (TOC), and available NH_4^+ , NO_3^- , P, and K^+ were significantly higher under *P. glandulosa* than in adjacent open areas. Biggs (1997) found similar results for NH_4^+ , NO_3^- , P, and TOC under *P. velutina* canopies in southeastern Arizona.

Litterfall is a major mechanism for transferring N from N-fixing plants to the soil system

(Klemmedson et al. 1990), though resorption of nutrients before leaf senescence has not been well documented for deciduous plants in general (Gower and Son 1992) or for *Prosopis* in particular. However, Killingbeck (1996) found that among 89 plant species, N-fixing plants were significantly less efficient in leaf-N resorption than were non-fixing plants. Rundel et al. (1982) found a green-leaf N content of about 2.8% for *P. glandulosa*, virtually identical to that for *P. velutina* (Klemmedson 1974); in neither case were these values compared to the N concentration in senesced leaves. Killingbeck and Whitford (1996) found green-leaf and leaf-litter N contents for *P. glandulosa* of 3.5% and 2.6%, respectively, though their study does not indicate whether these values change seasonally.

The period of maximum contribution by *Prosopis* to soil fertility may be correlated with the period of maximum litterfall. According to Sharifi et al. (1983), *P. glandulosa* has growing seasons in March and August; leaf abscission occurs abruptly prior to the onset of the next years' growth in March, and is strongly correlated with soil moisture potential at 400 cm depth. This implies that the maximum deposition of leaf litter occurs during winter, which we hypothesize results in a significant increase in soil N, C, and P through mineralization during the following spring. Measuring seasonal fluctuations in litterfall nutrient content and soil plant-available N and P will increase our understanding of spatial and temporal effects of mesquite trees on desert grassland biogeochemical cycling.

Previous studies have shown that fire may aid in the redistribution of nutrients (DeBell and Ralston 1970, Raison 1979, Smith 1970), and has been used as a management technique for controlling mesquite populations, with limited success. According to Cable (1973), larger specimens of *P. velutina* are more resistant to fire; in his study at the Santa Rita Experimental

Range in southeastern Arizona, *Prosopis* mortality from fires ranged from 60% for trees with a 1.25 cm stem diameter at the base to 11% for trees with a basal stem diameter > 12.7 cm.

Following a fire, burned mesquites often resprout from the base into a multiple-stemmed growth form (Ansley et al. 1996).

The effects of seasonal variations in soil nutrient concentrations under *Prosopis* and their relationship to fire history are unknown. In addition, the relationship between spatial distribution of soil nutrients and *Prosopis* needs to be elucidated. Determining seasonal changes in soil nutrient topography under *Prosopis* versus open grassland, and the interrelation among season, fire, and biogeochemical cycling can be used to design prescribed burning practices to control or reverse *Prosopis* encroachment in rangelands. We define nutrient topography as the relationship between soil nutrient concentrations and their spatial distribution, to the depth of sampling.

To study the effects of fire history upon *Prosopis* nutrient sequestration, factors such as climate, soil type, and land use history should be held as constant as possible. Under these circumstances a detailed study of temporal and spatial variations in *Prosopis* litterfall, and adjacent soil nutrient topography, can be implemented on sites of different fire history. These conditions exist on the Fort Huachuca army base in the Huachuca Mountains in southeastern Arizona, which contains two adjacent sites with the same soil, topography, and land use history; however, each possesses a different fire frequency.

In this study our objectives are to 1) characterize spatial and seasonal variation in mesquite litterfall mass and C, N, and P content; 2) characterize the spatial distribution of soil inorganic N, total N, total organic C (TOC), and available P relative to mesquite locations; 3) characterize seasonal variation in plant-available N.

Our hypotheses are: 1) mesquite litterfall varies significantly between seasons in quantity and concentrations of total N, C, and P, and results in significant seasonal differences in soil N, C, and P through mineralization, 2) mesquite litterfall remains localized under canopies, limiting the distribution of litterfall N, C, and P, 3) the soil nutrient topography in desert grasslands containing mesquite trees is spatially and temporally more heterogenous in less frequently burned locations.

METHODS AND MATERIALS

Site Description

The study sites are located on the Fort Huachuca Army Base in the Huachuca Mountain Range in southeastern Arizona, on a uniform 4% eastward-facing slope, at 1,490 m elevation. No cattle grazing has occurred on the sites since the late 1940's (Biggs 1997). The vegetation community is semidesert grassland (Brown and Lowe 1980), and the soil is classified as a fine loamy, mixed, thermic Ustollic Haplargid (Hendricks 1985). These soils have formed in Holocene age granitic parent material, from 0.5 to 1.0 m deep, overlying a Pleistocene age buried soil. The surface A horizon ranges from 10 - 25 cm in thickness and is a very dark brown to very dark grayish brown sandy loam. The subsurface horizon is a dark brown sandy clay loam extending to a depth of 50 to 100 cm, which abruptly changes to a buried argillic horizon with a clay loam texture.

Two adjacent sites were identified possessing a similar land-use history, but different fire histories due to a road junction which functioned as a firebreak. Inspection of aerial photographs of this location revealed no discernible disturbances to these sites, other than fire, for the past 30 years. Site A has a low fire frequency. The date of the most recent fire is unknown, but probably

no later than the 1940's. It is dominated by dense stands of large, single-trunked *P. velutina*. Though Site A is located approximately 75 m from a watercourse containing an ephemeral stream (Fig. 1), it contains no riparian plant species (Biggs 1997). Site B had recorded fires in February 1981, July 1983, May 1986, February 1988, and February 1989 (Biggs 1997). It is dominated by both *Eragrostis lehmanniana*, an African grass, and *Eriogonum wrightii*. It also contains isolated *P. velutina* that are small and multiple-stemmed. When we compared spatial differences within each site and season, our study did not contain replicate study sites and was not pseudoreplicated, as defined by Hurlbert (1984) and Heffner et al. (1996). However, when we compared seasonal differences within each site, we treated all sampling locations within a single season as replicate units.

We established sampling coordinates in each site. Soil sampling locations were selected using a geostatistics computer program developed by Warrick and Myers (1987) to optimize the representative value of comparisons made between each distance class within each study site for variogram calculations. For each site, 75 samples were collected, 25 within an evenly-spaced grid distributed throughout the site, and 50 from points assigned using the geostatistics program. Sampling at Site A took place in a 60 m by 60 m square, and sampling at Site B in a 80 m by 80 m square. Site B was larger than Site A to incorporate a similar number of mesquite trees. Five trees from Site A and 5 trees from Site B were selected for litterfall sampling.

Tree Mapping

Mesquite trunk locations were assigned coordinates each site. The canopy radius of each tree was measured from various points around the trunk, then averaged. Mesquite locations and corresponding canopy coverages were plotted using Surfer 3.2 Software (Keckler, 1997).

Litterfall Sampling and Chemical Analysis

Inverted cone-shaped leaf litterfall traps were constructed and placed under 5 selected *Prosopis* on each site. Trees were selected to represent all of the size classes found at each site. Similar to the design described by Hughes et al. (1987), each trap consisted of a woven plastic mesh grain feed bag configured to an inverted cone shape, to allow for free water drainage and litter retention. Each trap was 40 cm deep, with a mouth 50 cm in diameter and 50 cm above the ground. The bag was supported by 9-gauge galvanized wire, bent into a hoop and supported by two interlocked hoops, which formed the legs of the trap. The intersection of these hoops was wired to two wooden stakes placed 30 cm deep.

Eight traps were positioned around the base of each tree forming two rings of four traps each; each trap corresponded to a cardinal direction. The inner ring of four traps were positioned at a distance of one half the canopy radius from the center of each tree; the outer ring was positioned at the canopy edge. The traps were sampled at the beginning of each month for two yr. Each sample was dried for 24 hrs at 65°C and sorted to remove extraneous material before weighing.

Litterfall was grouped by season. Litterfall samples were ground using a Wiley mill, then analyzed for total P using a colorimetric procedure (Olsen and Sommers 1982). TOC and total N were analyzed using dry combustion (Nelson and Sommers 1982).

Soil Sampling and Chemical Analysis

Soil samples (0-10 cm) were collected seasonally for two yr, from Mar. 1997 to Jan. 1999, from each site. Soil NH_4^+ and NO_3^- were extracted with 2M KCl and analyzed using steam distillation (Keeney and Nelson, 1982). The winter 1998 samples were analyzed for available P

using the Olsen extraction (Olsen and Sommers 1982), and colorimetric analysis. These samples were also analyzed for TOC and N in the manner described above.

Data Analysis

A combination of Analysis of Variance (ANOVA), parametric, and nonparametric statistics were used to determine whether differences existed between the two sites, between seasons, between trees at each site, and between individual litterfall traps. A Wilk-Shapiro/Rankit plot was used to determine if the data were normally distributed. Grouped data were analyzed using a 1-way ANOVA, and Pearson's Correlation Coefficient was used to determine the relationship between mesquite litter mass, litter nutrient concentrations, and canopy diameter. Tukey's Mean Separation Test was used to identify relationships between trap locations. Nonparametric data were analyzed using a Friedman 2-way ANOVA without replication. The null hypothesis of no differences was rejected at significance levels of $P \leq 0.05$. These analyses were performed using STATISTIX software (Analytical Software, Tallahassee FL, 1998).

Variograms were calculated for ammonium and nitrate concentrations for each season, and for total N, TOC, and P from the winter, 1998 sampling, using GEO-EAS software (Englund and Sparks 1991). These were plotted as distances between sampling points:

$$\gamma(h) = 0.5[Z(u+h) - Z(u)]^2, \quad (1)$$

where γ = semi-variance, u = sampling point, h = distance between sampling points, and Z = nutrient concentration at u . To extrapolate the values made at each sampling point to the entire site, Gaussian, linear, and spherical models were used. These models were evaluated using the GEO-EAS program X-VALID, which generated a Z-score that compared estimated soil N concentrations with experimental values.

Contour maps were generated using Surfer 3.2 Software (Keckler 1997) which performed a kriging function after the model, nugget, and sill values were entered. These contour maps were configured using a minimum search radius for pair comparisons that still allowed full coverage of each site. The total volume of each map was calculated and converted to kg/ha for both NH_4^+ and NO_3^- using bulk density values for each site calculated by Biggs (1997).

A combination of parametric and nonparametric statistics using Analysis of Variance (ANOVA) were used to determine whether differences existed between the two sites and between seasons. Data grouped by site were analyzed using a 1-way ANOVA. Tukey's Mean Separation Test was used to identify relationships between seasons. Nonparametric data were analyzed using a Friedman 2-way ANOVA without replication. The null hypothesis of no differences was rejected at $P \leq 0.05$. These analyses were performed using STATISTIX software.

RESULTS AND DISCUSSION

Tree Mapping

Forty two mesquite trees existed on Site A; of these, no more than 5 had multiple stems. Total canopy coverage was 29%, with a mean canopy diameter of 4.58 ± 1.95 m. Mesquites tended to group together on this site, with open areas between (Fig. 1). Forty mesquites were identified on Site B; all trees on this site had multiple stems. Total canopy coverage was 2%, significantly lower than coverage for Site A, and the mean canopy diameter was 1.85 ± 0.65 m. Mesquites on this site were uniformly distributed through the site, with little grouping (Fig. 1).

Litterfall Sampling

One of 5 sampled trees at Site A had multiple stems, as did all trees at Site B (Table 1). Multiple stemmed trees contributed significantly less litterfall on all sites; the average monthly

litterfall for these trees was 3.13 ± 2.84 g, compared to 10.51 ± 12.63 g for the trees with single trunks. Litterfall mass accumulation displayed a positive relationship with canopy diameter. For all grouped sites and seasons, litterfall mass vs. canopy diameter had a correlation coefficient of 0.92 ($P \leq 0.05$) in 1997, and 0.90 in 1998.

For both sites and years, litterfall accumulation was greatest during the winter months (Table 2). In 1997 the maximum average litterfall for the 8 traps of each tree was 20.49 ± 15.81 g, occurring in December; this was followed in January by the peak for 1998, 27.58 ± 24.51 g. The minimum litterfall at each site occurred during the spring. Though greater litterfall occurred for each site in 1998 than in 1997, the difference was not statistically significant. However, weather data collected at a location near the study sites indicated 297 mm of precipitation in 1997 and 437 mm in 1998 (EPG Weather Bureau 2000).

At both sites, the greatest litterfall occurred in the traps north of the mesquite trunks, at the midpoint of the canopy radius, followed by those east of the trunk at the midpoint of the canopy radius. Weather records indicated an average annual wind direction from the SW, 217 ± 56 degrees in 1997 and 216 ± 21 degrees in 1998 (EPG Weather Bureau 2000). This confirms that litterfall deposition was not evenly distributed under the canopy, and that it was associated with prevailing wind conditions.

Significantly greater litterfall occurred at the midpoint of the canopy radius than at the edges of the tree canopies, regardless of direction, for all trees. This indicates that litter deposition remained localized under the canopies, agreeing with the results of Barth and Klemmedson (1982). Of the traps placed at the canopy edges, the northern trap consistently had the highest litterfall.

Mesquite litterfall resulted in an asymmetric deposition of inputs, consistent with prevailing wind conditions, in accord with the results of Welbourn et al. (1981). Our data indicates that most litterfall occurs to the north and east of the trunk. Tiedemann et al. (1977) found similar results; they suggested that warmer temperatures on the south side of trees may contribute to higher decomposition rates, and reduced litter accumulation on the south side. The comparison with inner versus outer ring litterfall trap data demonstrates that mesquite litterfall remains mainly under the canopy, supporting our hypothesis. Our data also indicated that most litterfall occurs during the winter, followed by a sharp reduction in the spring. Seasonal variation should therefore be considered when evaluating *P. velutina* litterfall inputs to grassland biogeochemical cycling.

Litterfall Chemical Analysis

Concentrations of litterfall C, N, and P displayed significant differences among seasons (Table 3). Inter-seasonal variation of N and P followed similar trends in 1997 and 1998. The highest concentrations of N and P in litterfall occurred during the summer months of both years, coincident with pollen, flower, and fruit formation, a major component of the litterfall that occurred during this period; minimum N and P concentrations occurred during the winter months. Conversely, maximum C concentrations occurred during the winter months, when litterfall was composed almost exclusively of leaves. The C:N ratios were lowest during the summer months for both years, and highest during the winter months. Litterfall C, N, and P concentrations did not differ significantly between Sites A and B.

Though we did not measure total N in green leaf tissue of *P. velutina*, Klemmedson (1974) determined that green leaves contained 2.6% N, identical to our overall mean value of

litterfall total N, but considerably less than the summer concentration of litterfall N. Killingbeck and Whitford (1996) compared green leaf with leaf litter tissue of *P. glandulosa*, finding 3.5% and 2.6%, respectively; this suggests a resorption rate of about 26%. In a comparison of arid land shrubs worldwide, they found that most litterfall contains less than 1.5% total N, after a 40–60% resorption rate.

Our results confirmed our hypothesis that there is significant seasonal variation in litterfall quantities and nutrient concentrations. Periods of maximum litterfall quantities were coincident with periods of maximum C concentration in litter, while N and P concentrations in litterfall were highest during the summer months, when litterfall inputs were significantly reduced.

Soil Nutrient Status

Site B contained significantly lower inorganic N concentrations throughout the sampling period than Site A (Table 4), associated with the smaller biomass of N-fixing plants which contributed lower litterfall inputs of fixed-atmospheric N. For each site, seasonal fluctuations did not follow a predictable pattern from season to season, or from year to year, within the measurement period.

Seasonal variation in N concentrations was more dramatic in the litterfall than in the soil, suggesting that concentrations of plant-available nutrients in the soil are temporally decoupled from concentrations of litterfall inputs due to immobilization and mineralization transformations. Although rates of mineralization were not evaluated in this study, the low C:N ratios of the summer litterfall suggest that rapid mineralization would take place during this period, slowing down considerably as the C:N ratios increase during the winter.

The variogram calculations indicated that variance was dependent on distance but not

direction (isotropic), and in most cases a linear model was representative, independent of season or site (Fig. 2). The range at which compared samples remained correlated was 30 m and 52 m on Site A and Site B, respectively. This model suggests that most sampling variation occurred over large distances (Warrick et al. 1986), and the probability of finding similar concentrations of soil inorganic N decreases linearly with distance.

The distribution of inorganic N was more heterogenous on Site A, both spatially and temporally (Fig. 2 through 6). Concentrations of plant-available soil N corresponded directly to mesquite distribution on this site. The location of high soil inorganic N concentrations on this site occurred where mesquite trees were in close proximity to each other, while low concentrations corresponded to open grassland patches between mesquites. The positioning of the high and low points on the contour maps remained consistent from season to season, but their elevation changed dramatically. Peaks were most sharply defined in the fall and winter of 1997.

Compared to Site A, the topography of inorganic N in Site B was more uniform, with little apparent correlation with mesquite locations (Fig. 5 and 6). Similarly, seasonal variation was more attenuated. From these results it is apparent that temporal and spatial changes in inorganic N concentrations are less affected by mesquite nutrient cycling in this more frequently burned landscape.

From the contour maps we estimated the mass of inorganic N found on each site, using the volume of the contours, the sample depth, site area, and bulk density data determined by Biggs (1997) at this location. Grouping all seasons, Site A contained 20.4 ± 3.7 kg/ha of inorganic N, while Site B contained 11.6 ± 2.1 kg/ha, to 10 cm depth.

Soil total N and TOC did not differ significantly between sites during the winter of 1997

(Table 5), although significantly higher concentrations were found under canopies than in the open on both sites (Fig. 7), within the 10 cm sampling depth. Furthermore, open areas in Site B had significantly higher concentrations of total N and total C than those of Site A, suggesting that greater *P. velutina* nutrient sequestration takes place at the less frequently burned location (Biggs 1997). Conversely, greater total N and TOC may be found in the intercanopy areas on Site B since less of these nutrients taken up by *P. velutina*. From these results, nutrient cycling by *P. velutina* plays a less important role in the more heavily disturbed landscape.

Compared to Site A, available P concentrations on Site B during the winter of 1997 were significantly higher (Table 5) and varied throughout the site, with zones of higher concentration not corresponding to *P. velutina* locations (Fig. 7). Concentrations ranged from 12.7 mg/kg to 2.3 mg/kg. Similar to total N and TOC, available P concentrations in Site A were significantly higher under or near *P. velutina* canopies than in open areas, ranging from 25 mg/kg under a canopy to 1.5 mg/kg in the open. The difference in available P between these sites may correspond to sequestration of this macronutrient by *P. velutina* on Site A; over time root uptake and subsequent litterfall could create higher concentrations under canopies, or P could be tied up within the standing biomass. Conversely, disturbance events such as fire could reverse this process, as *P. velutina* is either removed or reduced in stature.

Thirteen soil sampling locations in Site A and 7 locations in Site B were positioned under *P. velutina* canopies or within 1 m. Our experimental design did not explicitly assign these locations by proximity to mesquite canopies or litterfall trap locations, yet the samples that existed under *P. velutina* canopies contained significantly higher concentrations of inorganic N throughout the sampling period, and of available P, total N, and TOC during the winter of 1997

(Table 5). This demonstrates that the effects of *P. velutina* litterfall on soil nutrient concentrations remain localized, in accord with the results of previous studies (Biggs 1997, Tiedemann and Klemmedson 1986b, Virginia 1986, Virginia and Jarrell 1983), and reflects the role of *P. velutina* litterfall as a major source of soil N in this desert grassland. In addition, soil inorganic N under *P. velutina* canopies was significantly higher on Site A than similar locations at Site B, reflecting the difference of *P. velutina* litterfall inputs between the sites. Our results indicate that *P. velutina* sequester these soil nutrients over time; with disturbances such as fire, this sequestration process is reversed, and the soil nutrient topography becomes more homogenous.

The presence or absence of *P. velutina* is a main determinant of spatial and temporal availability of bio-available N and P, total N, and TOC in desert grasslands. In addition, the growth form of *P. velutina* can determine the degree of this availability. At our study sites the effects of previous fires on Site B was manifested by widely scattered and multiple-stemmed *P. velutina* which had a smaller canopy diameter and contributed less C, N, and P to the soil, even 8 years after the most recent fire. Both sites contained about the same number of trees, yet the nutrient topography of these landscapes differed considerably.

CONCLUSIONS

Fire not only alters the nutrient topography of the landscape in the short term through volatilization (Raison 1979), leaching (Smith 1970), or erosion (DeBell and Ralston 1970); it also plays an indirect role by reducing the ability of *P. velutina* to localize concentrations of macronutrients at frequently burned locations. *Prosopis* may often survive fires (Martin 1983, Wright et al. 1976), but basal resprouting of the surviving trees creates a different growth form of reduced stature (Ansley et al. 1996) and canopy diameter. Our results suggest that this

significantly reduces the impact of *P. velutina* upon soil macronutrients by reducing the quantity of litterfall inputs on this landscape. In addition, a reduction in *P. velutina* biomass as a result of fire would reduce the nutrient demands by these trees, resulting in a reduction in nutrient uptake.

LITERATURE CITED

- Analytical Software. 1998.** Statistix for windows. Analytical Software, Tallahassee, FL.
- Ansley, R.J., J.F. Cadenhead, and B.A. Kramp. 1996.** Mesquite savanna: A brush management option. *Cattleman*. 82: 10-12.
- Archer, S., C. Scifres, C.R. Bassham, and R. Maggio. 1988.** Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecol. Mon.* 52: 111-127.
- Bahre, C.J., and M.L. Shelton. 1993.** Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *J. Biogeo.* 20: 489-504.
- Bahre, C.J. 1985.** Wildfire in southeastern Arizona between 1850 and 1890. *Desert Plants* 74:190-194.
- Barth, R.C., and J.O. Klemmedson. 1982.** Amount and distribution of dry matter, nitrogen, and organic carbon in soil-plant systems of mesquite and palo verde. *J. Range Manage.* 35: 412-418.
- Biggs, T.H. 1997.** Fire frequency, nutrient concentrations and distributions, and ¹³C of soil organic matter and plants in southeastern Arizona grassland. Ph.D Thesis, Univ. Arizona, Tucson.
- Brown, D.E., and C.H. Lowe. 1980.** Biotic communities of the southwest. U.S. Department of Agriculture, Fort Collins, CO, RM-78.
- Cable, D.R., and S.C. Martin. 1971.** Invasion of semidesert grassland by velvet mesquite and associated vegetation changes. *J. Ariz. Aca. Sci.* 8:127-134.
- Cable, D.R. 1973.** Fire effects in southwestern semidesert grass-shrub communities. *Proc. Tall Timbers Fire Ecol. Conf.* 12:109-127.
- Cox, J.R., A. Alba-Avila, R.W. Rice, and J.N. Cox, 1993.** Biological and physical factors influencing *Acacia constricta* and *Prosopis velutina* establishment in the Sonoran Desert. *J. Range Manage.* 46: 43-48.

DeBell, D.S., and C.W. Ralston. 1970. Release of nitrogen by burning light forest fuels. *Soil Sci. Soc. Amer. Proc.* 34:936-938.

Englund, E., and A. Sparks. 1991. Geostatistical environmental assessment software. U.S. Environmental Protection Agency, Las Vegas, NV.

Glendening, G.E. 1952. Some quantitative data on the increase of mesquite and cactus on a desert Grassland range in southern Arizona. *Ecol.* 33: 319-328.

Gower, S.T., and Y Son. 1992. Differences in soil and leaf litterfall nitrogen dynamics for five forest plantations. *Soil Sci. Soc. Am. J.* 56:1959-1966.

Grover, H.D., and H.B. Musick. 1990. Shrubland encroachment in southern New Mexico, U.S.A.: An analysis of desertification processes in the American southwest. *Climatic Change.* 17: 305-330.

Hastings, J.R., and R.M. Turner. 1965. The changing mile: an ecological study of vegetation change with time in the lower mile of an arid and semi-arid region. Univ. Arizona Press, Tucson.

Heffner, R.A., M.J. Butler IV, and C. Keelan Reilly, 1996. Pseudoreplication revisited . *Ecol.* 77: 2558-2562.

Hendricks, D. 1985. Arizona soils. Univ. Arizona Press, Tucson, AZ.

Hughes, J.W., T.J. Fahey, and B. Browne. 1987. A better seed and litter trap. *Can. J. Forest Rest.* 17: 1623-1624.

Humphrey, R.R. 1958. The desert grasslands: a history of vegetational change and an analysis of causes. *Bot. Rev.* 24: 193-252.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Bull. Ecol. Soc. Am.* 67: 184-185.

Keckler, D. 1997. Surfer for windows. Golden Software, Inc, Golden, CO.

Keeney, D.R., and D.W. Nelsen. 1982. Nitrogen–inorganic forms. *in* Methods of Soil Analysis Part 2: Chemical and Microbiological Properties. Ed. by A.L Page, R.H. Miller, and D.R. Keeney. Am. Soc. of Agron. Series No. 9, Madison, WI.

Killingbeck, K.T. 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption efficiency. *Ecol.* 776:1716-1727.

- Killingbeck, K.T., and W.G. Whitford. 1996.** High foliar nitrogen in desert shrubs: An important ecosystem trait or defective desert doctrine? *Ecol.* 776: 1728-1737.
- Klemmedson, J. O. 1974.** Distribution and balance of biomass and nutrients in desert shrub ecosystems. US/IBP Desert biome research memorandum 74-6. International Biological Program, Logan, UT.
- Klemmedson, J.O., and A.R. Tiedemann. 1986.** Long-term effects of mesquite removal on soil characteristics: II. Nutrient availability. *Soil Sci. Soc. Am. J.* 50:476-480.
- Klemmedson, J.O., C.E. Meier, and R.E. Campbell. 1990.** Litter fall transfers of dry matter and nutrients in ponderosa pine stands. *Can. J. Forest. Res.* 20: 1105-1115.
- Martin, S.C. 1983.** Responses of semidesert grasses and shrubs to fall burning. *J. Range Manage.* 36: 604-610.
- Natural Resources Conservation Service. 1994.** Soil survey of U.S. Army Fort Huachuca, Cochise County, Arizona. Natural Resources Conservation Service, Tucson, AZ.
- Nelson, D.W., and L.E. Sommers. 1982.** Total carbon, organic carbon, and organic matter. *in* Methods of Soil Analysis Part 2: Chemical and Microbiological Properties. Ed. by A.L Page, R.H. Miller, and D.R. Keeney. Am. Soc. of Agron. Series No. 9, Madison, WI.
- Olsen, S.R., and L.E. Sommers. 1982.** Phosphorus. *in* Methods of Soil Analysis Part 2: Chemical and Microbiological Properties. Ed. by A.L Page, R.H. Miller, and D.R. Keeney. Am. Soc. of Agron. Series No. 9, Madison, WI.
- Raison, R.J. 1979.** Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. *Plant-Soil* 51:73-108.
- Reynolds, H.G., and G.E. Glendening. 1949.** Merriam kangaroo rat a factor in mesquite propagation on southern Arizona rangelands. *J. Range Manage.* 2: 193-197.
- Rundel, P.W., E.T. Nilsen, M.R. Sharifi, R.A. Virginia, W.M. Jarrell, K.H. Kohl, and G.B. Shearer. 1982.** Seasonal dynamics of nitrogen cycling for a *Prosopis* woodland in the Sonoran Desert. *Plant-Soil.* 67: 343-353.
- Schlesinger, W.H., J.F. Reynolds, G.L. Cunningham, L.F. Huenneke, W.M. Jarrell, R.A. Virginia, and W.E. Whitford. 1990.** Biological feedbacks in global desertification. *Sci.* 247:1043-1048.

- Sharifi, M.R., E.T. Nilsen, R.A. Virginia, P.W. Rundel, and W.M. Jarrell. 1983.** Phenological patterns of current season shoots of *Prosopis glandulosa* var. *torreyana* in the Sonoran desert of southern California. *Flora* 173:265-277.
- Smith, D.W. 1970.** Concentration of soil nutrients before and after fire. *Can. J. Soil Sci.* 50:17-29.
- Tiedemann, A.R., and J.O. Klemmedson. 1977.** Effect of mesquite trees on vegetation and soils of the desert grassland. *J. Range Manage.* 30: 361-367.
- Tiedemann, A.R., and J.O. Klemmedson. 1986.** Long-term effects of mesquite removal on soil characteristics: I. Nutrients and bulk density. *Soil Sci. Soc. Am. J.* 50:472-475.
- Virginia, R.A., and W.M. Jarrell, 1983.** Soil properties in a mesquite-dominated Sonoran desert ecosystem. *Soil Sci. Soc. Am. J.* 47: 138-144.
- Virginia, R.A. 1986.** Soil development under legume tree canopies. *Forest Ecol. Manage.* 16: 69-79.
- Warrick, A.W., D.E. Myers, and D.R. Nielsen. 1986.** Geostatistical methods applied to soil science. *in* Methods of Soil Analysis, Part I. Physical and mineralogical methods (2nd edition). Ed. by A. Klute. Am. Soc. of Agron. Series No. 9, Madison, WI.
- Warrick, A.W., and D.E. Myers. 1987.** Optimization of sampling locations for variogram calculations. *Water Resources Res.* 23: 496-500.
- Welbourn, M.L., E.L. Stone, and J.P. Lassoie. 1981.** Distribution of net litter inputs with respect to slope position and wind direction. *Forest Sci.* 27: 651-659.
- Wright, H.A., S.C. Bunting, and L.F. Neuenschwander. 1976.** Effect of fire on honey mesquite. *J. Range Manage.* 29: 461-471.



Figure 1. Aerial photo of an unburned (Site A) and frequently burned (Site B) desert grassland with mesquite trees at Fort Huachuca, southeastern Arizona. The distance between road intersections is 81 meters.

Figure 2. Sample variograms with a linear model fitted for soil inorganic N within an unburned (top) and frequently burned (bottom) location in a desert grassland in southeastern Arizona, U.S.A.

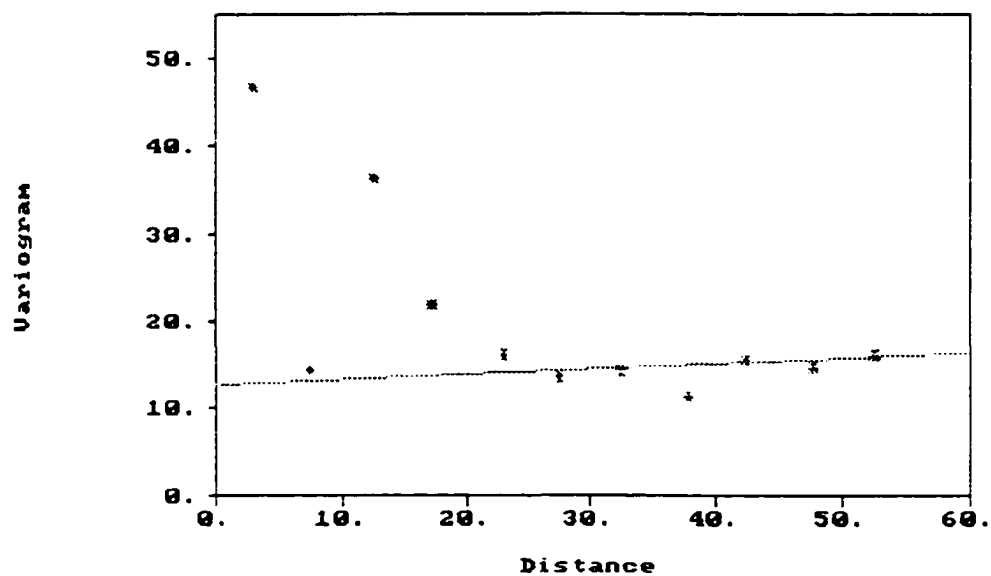
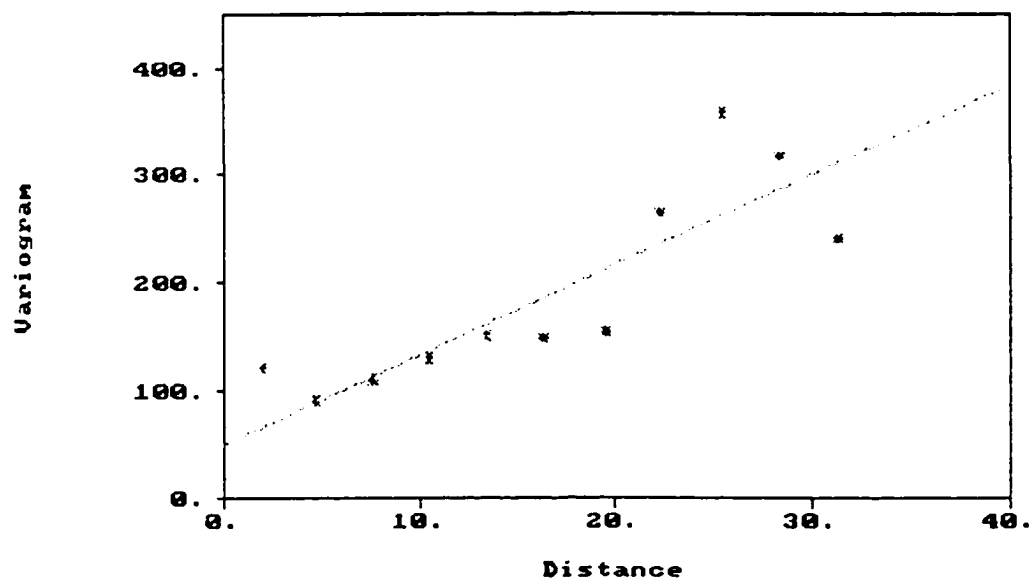


Figure 3. Comparison of the nutrient topography of inorganic N with mesquite locations at an infrequently burned site in a desert grassland in southeastern Arizona, 1997

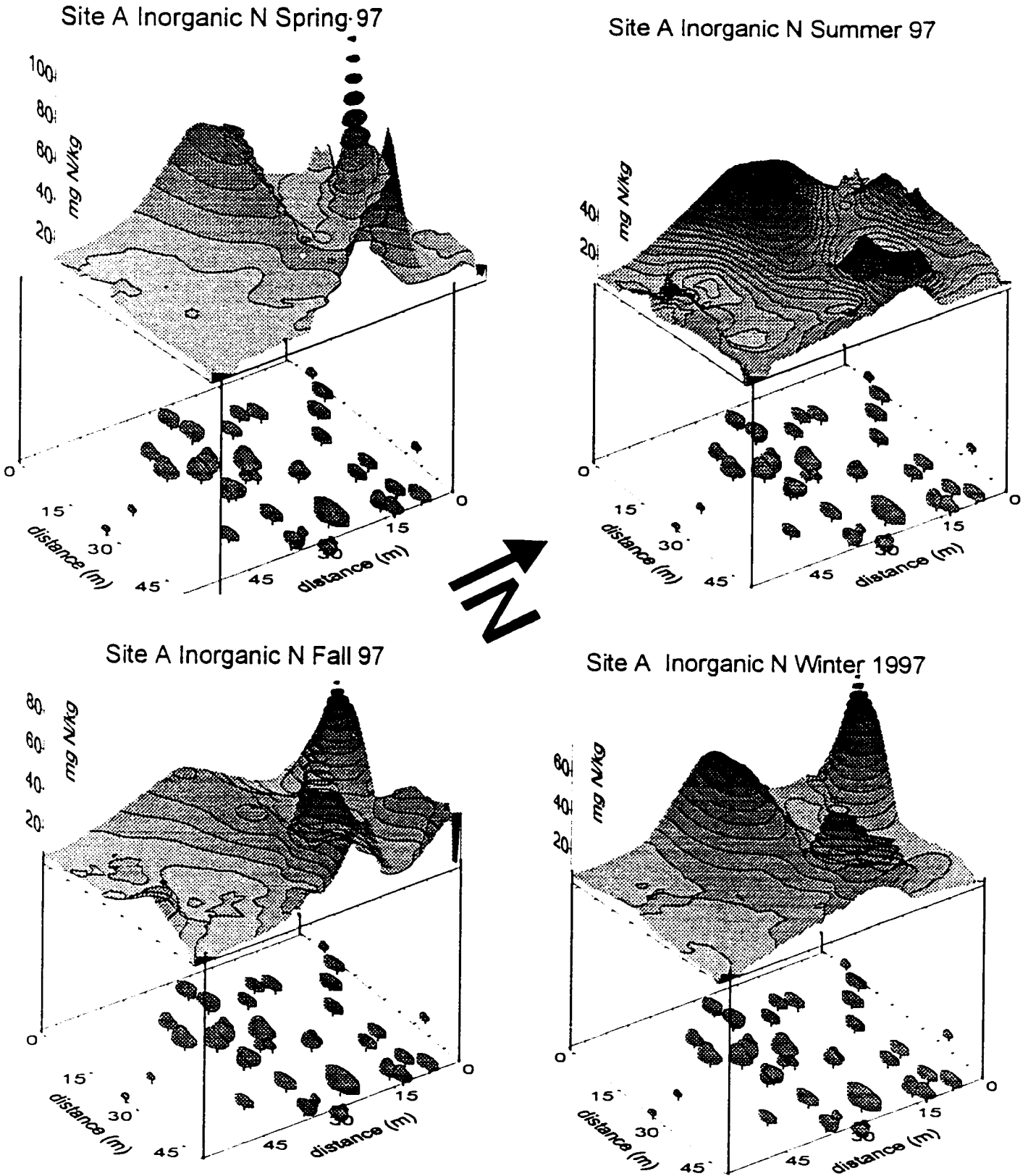
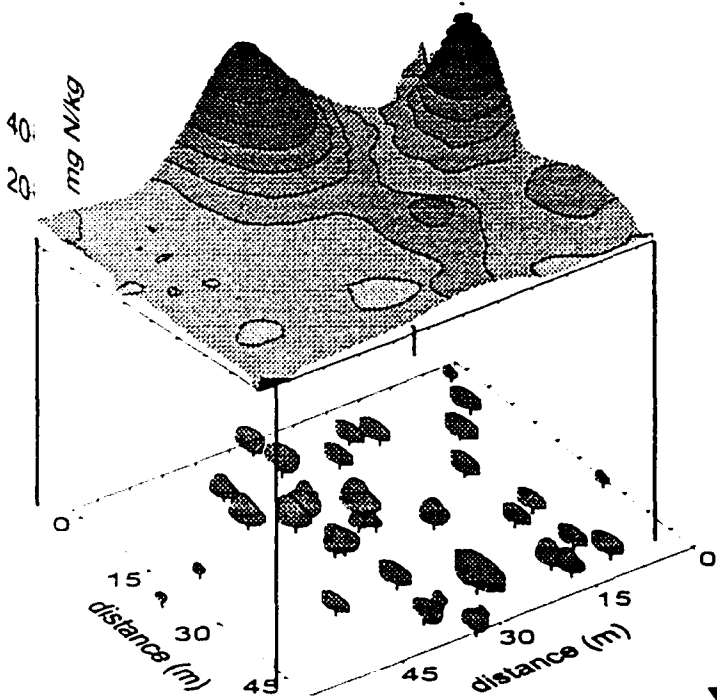
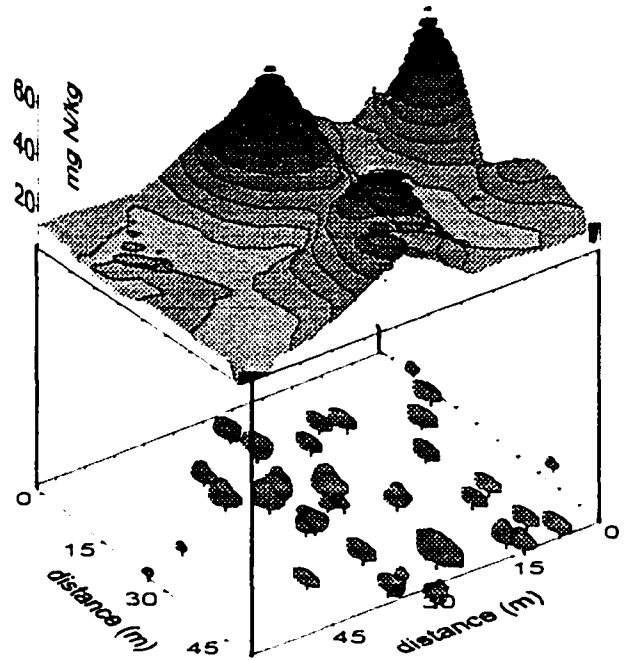


Figure 4. Comparison of the nutrient topography of inorganic N with mesquite locations at an infrequently burned site in a desert grassland in southeastern Arizona, 1998.

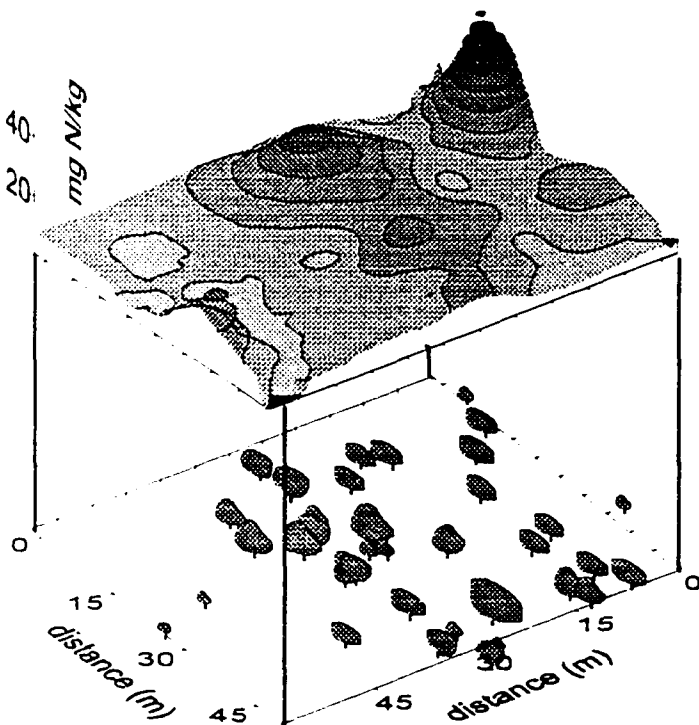
Site A Inorganic N Spring 98



Site A Inorganic N Summer 98



Site A Inorganic N Fall 98



Site A Inorganic N Winter 98

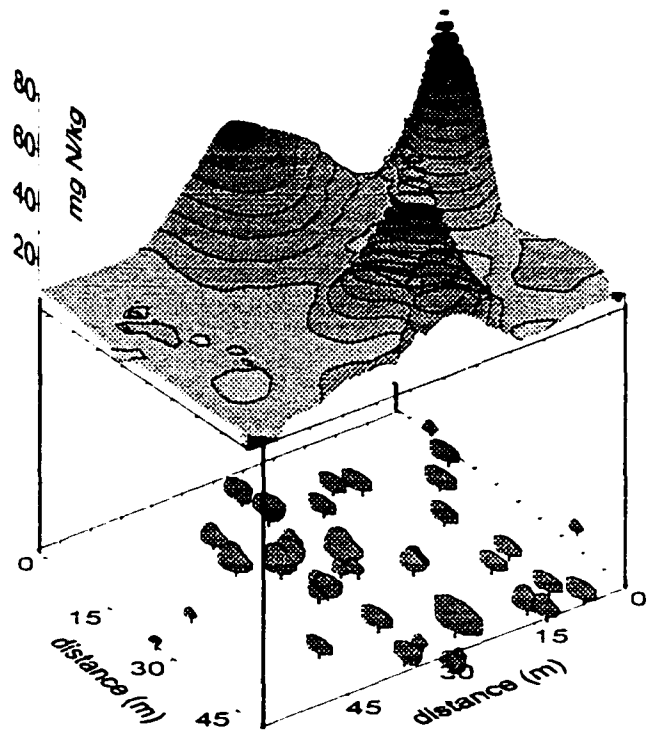
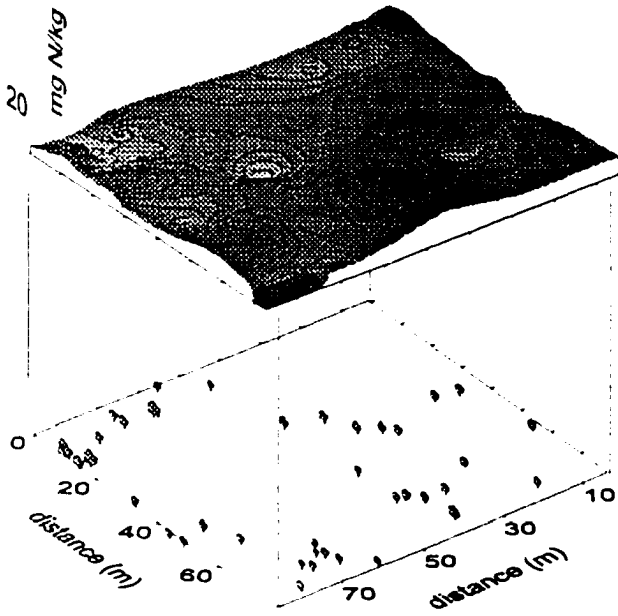
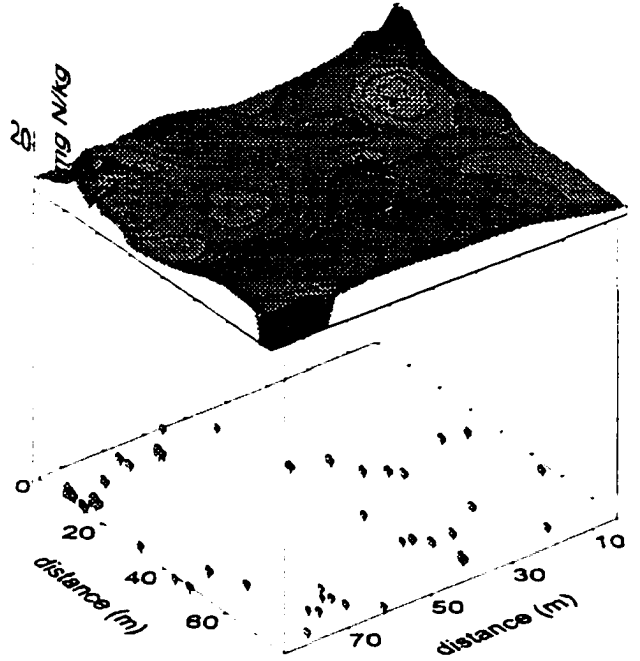


Figure 5. Comparison of the nutrient topography of inorganic N with mesquite locations at a frequently burned site in a desert grassland in southeastern Arizona, 1997.

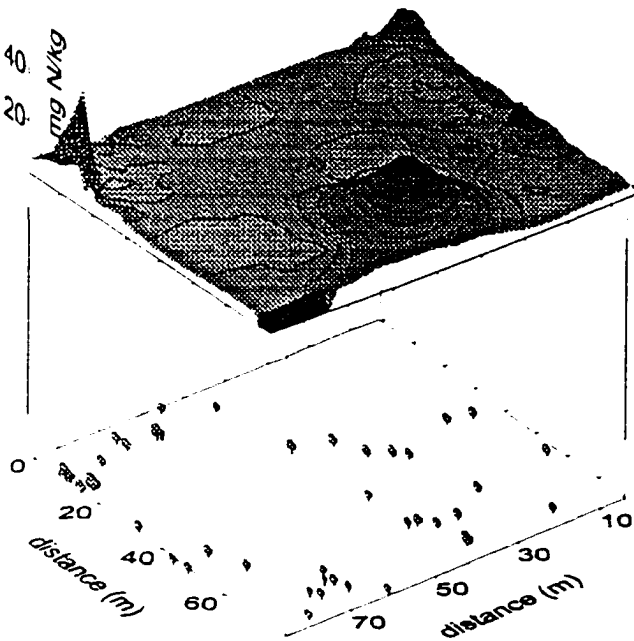
Site B Inorganic N Spring 97



Site B Inorganic N Summer 97



Site B Inorganic N Fall 97



Site B Inorganic N Winter 97

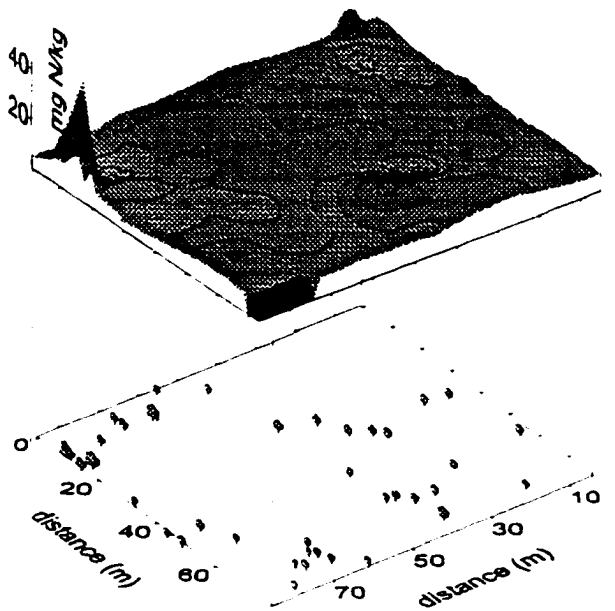
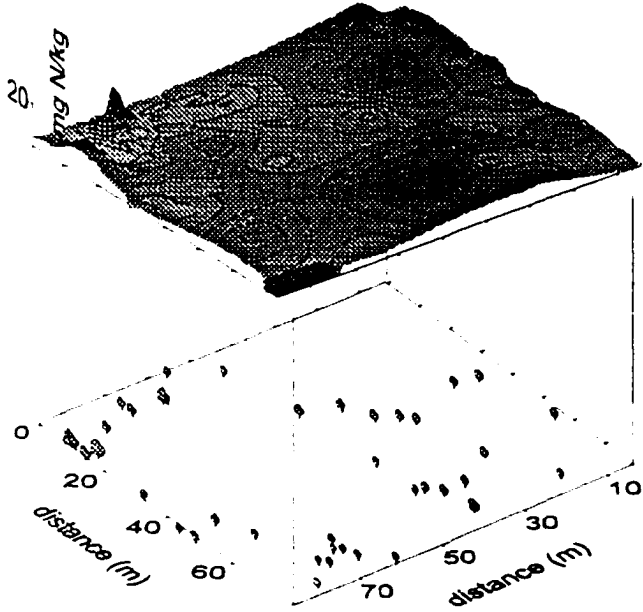
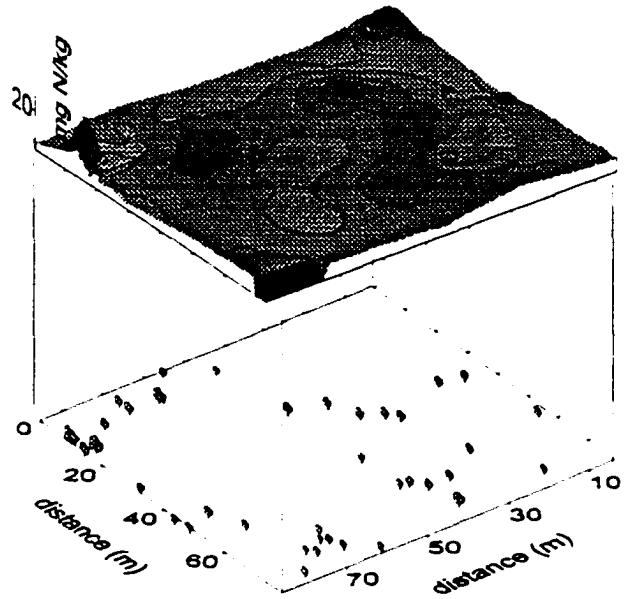


Figure 6. Comparison of the nutrient topography of inorganic N with mesquite locations at a frequently burned site in a desert grassland in southeastern Arizona, 1998.

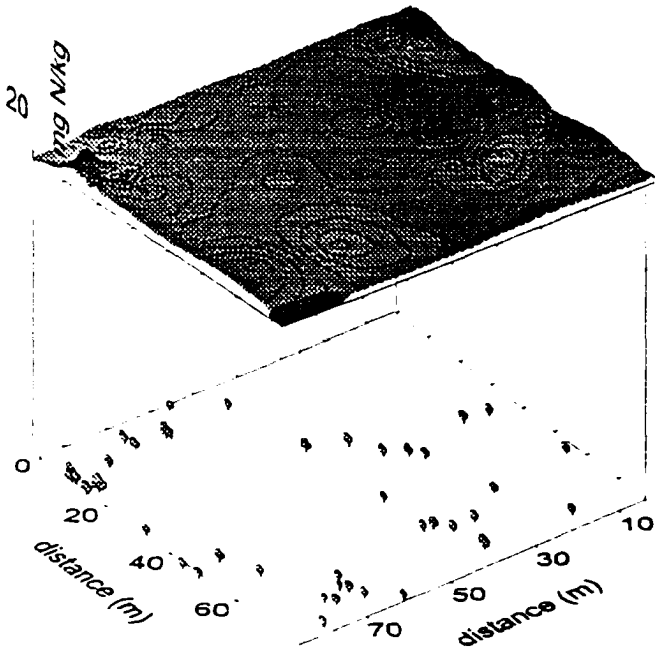
Site B Inorganic N Spring 98



Site B Inorganic N Summer 98



Site B Inorganic N Fall 98



Site B Inorganic N Winter 98

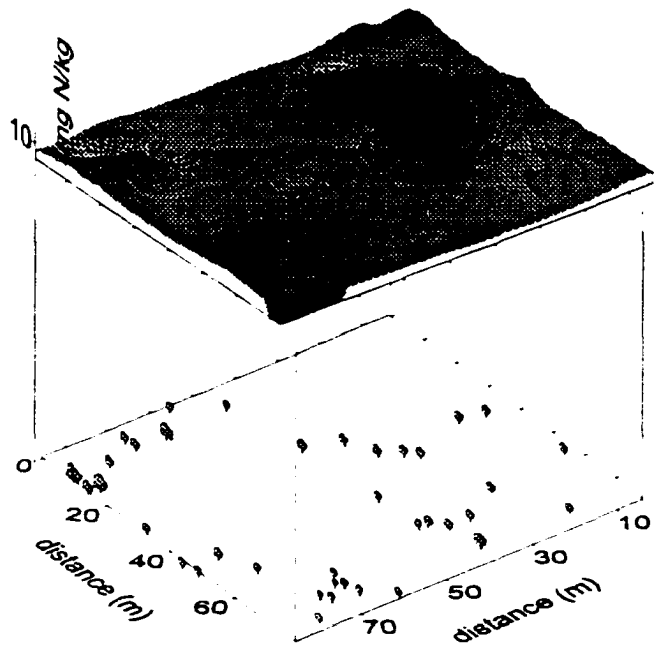
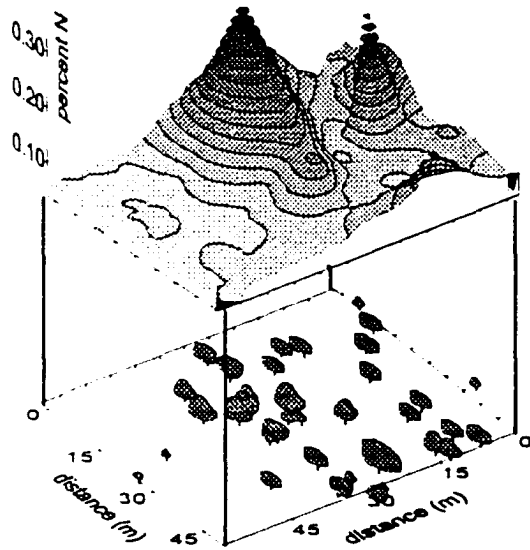
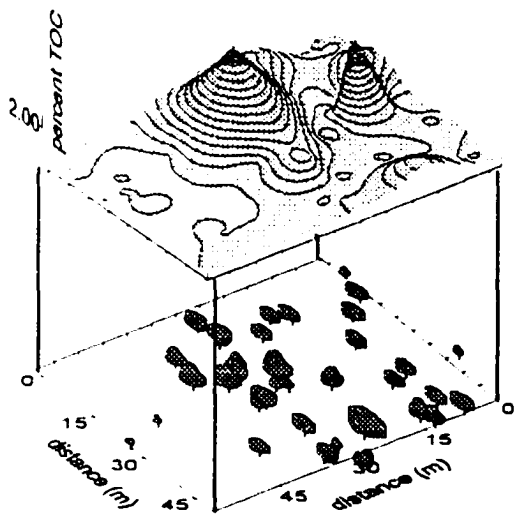
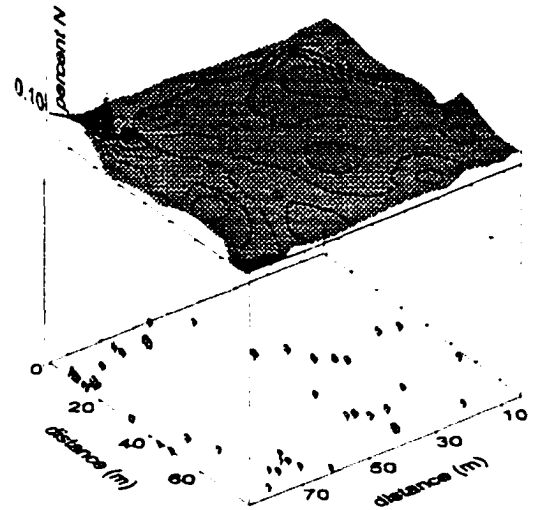


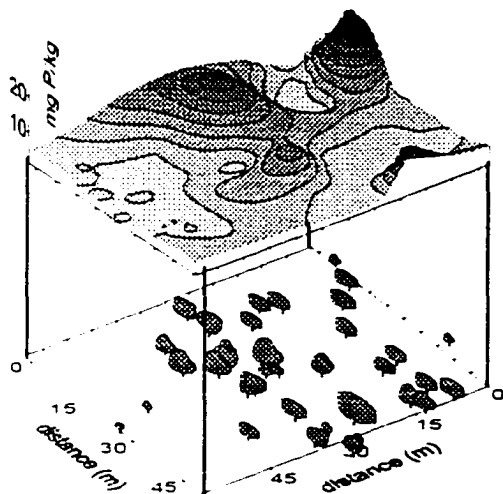
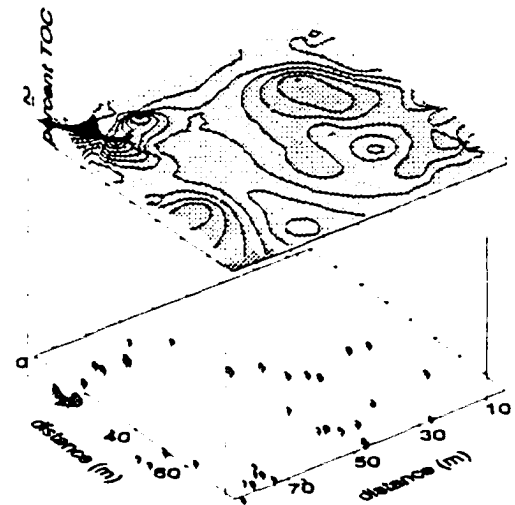
Figure 7. Comparison of the nutrient topography of total N (top pair), TOC (middle pair), and available P (bottom pair) with mesquite locations at an unburned location (at left), and frequently burned location (at right) in a desert grassland in southeastern Arizona, U.S.A., winter 1998.



total N



TOC



available P

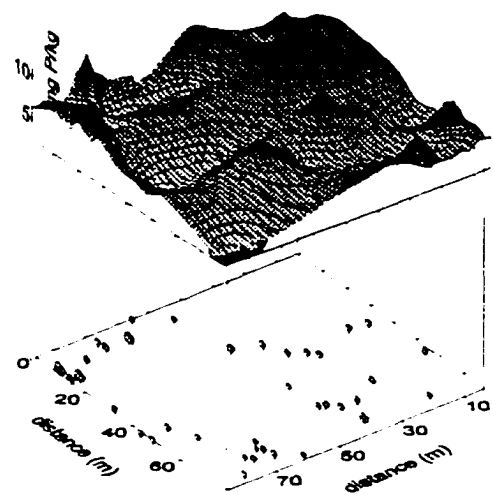


Table 1. Mesquite tree canopy size and litterfall dynamics on 2 sites of different fire history in a desert grassland in southeastern Arizona, U.S.A. Site A is an unburned location, and Site B is a frequently burned location.

| Site | Tree | Canopy Diameter | Litterfall | | Maximum Litterfall | | Minimum Litterfall | |
|------|-----------------|-----------------|----------------------------|-----------------|--------------------|--------------|------------------------------------|---------------------------|
| | | | 1997 | 1998 | 1997 | 1998 | 1997 | 1998 |
| | | (m) | (g) | (g) | (g/month) | | (g/month) | |
| A | 1 | 4.0 | 4.99± 7.85 ² | 10.97± 10.01 | 27.32 Dec | 27.35 Aug | 0 Apr | 0 Mar-May |
| A | 2 ¹ | 4.0 | 2.98± 4.62 | 3.55±4. 88 | 16.89 Nov | 13.77 Oct | 0 Apr, Jun, Aug | 0 Dec, Mar- May |
| A | 3 | 7.6 | 11.66± 17.74 | 17.31± 17.96 | 64.37 Dec | 51.20 Jun | 0 Feb, Apr | 0 Mar-May |
| A | 4 | 6.6 | 7.50± 6.62 | 21.27± 21.88 | 23.68 Mar | 74.34 Jan | 0 Apr | 0 Mar-May |
| A | 5 | 10.0 | 7.80± 8.56 | 19.19± 18.08 | 30.01 Dec | 61.74 Jan | 0 Apr | 0 Mar-May |
| B | 6 ¹ | 4.0 | 2.12± 3.09 | 5.52± 4.70 | 10.95 Dec | 13.19 Aug | 0 Apr, Jun | 0 Mar-May |
| B | 7 ¹ | 4.0 | 0.77± 1.29 | 3.24± 3.58 | 4.73 Dec | 11.48 Dec | 0 Apr, May, Aug, Oct | 0 Feb-May |
| B | 8 ¹ | 2.5 | 1.83± 2.92 | 3.63± 4.77 | 10.61 Dec | 16.89 Dec | 0 Apr, May, Oct | 0 Feb-May, Oct |
| B | 9 ¹ | 3.0 | 2.20± 3.84 | 10.39± 11.19 | 14.35 Dec | 32.77 Dec | 0 Feb, Apr, May, Aug, Oct | 0 Mar-May |
| B | 10 ¹ | 1.8 | 0.72± 1.23 | 1.06± 1.66 | 3.88 Nov | 4.9 Nov | 0 Apr-Jun, Aug, Oct | 0 Feb-May, Aug, Sep |

¹ Multiple stems at base

² Sample mean ± standard deviation

Table 2. Seasonal variation in mesquite litterfall throughout 1997 and 1998 on sites of different fire frequency at Fort Huachuca, southeastern Arizona.

| Season, year | Litterfall mass (g) | |
|----------------------------------|--------------------------|---------------|
| | Site A | Site B |
| Fire Frequency (burns/decade) | 0 | 4 |
| spring, 1997 | 0.32±1.36 c ¹ | 0.04±0.09 bc |
| summer, 1997 | 0.60±1.06 c | 0.05±0.14 c |
| fall, 1997 | 0.52±0.79 c | 0.06±0.21 c |
| winter, 1997 | 3.48±4.69 ab | 0.95±1.65 ab |
| spring, 1998 | 0.24±0.40 c | 0.06±0.14 c |
| summer98 | 1.45±1.90 bc | 0.41±0.78 bc |
| fall, 1998 | 1.41±1.99 bc | 0.55±1.62 abc |
| winter, 1998 | 2.69±3.28 a | 0.58±1.06 a |

Notes: The null hypothesis is that means and variances are equal, and we only report rejections of the null hypothesis at $p \leq 0.05$

¹Within any column, figures that lack one or more common letters are significantly different at the 0.05 level according to the Tukey's comparison of means test.

Table 3. Seasonal comparison of mesquite litterfall nutrient concentrations in 1997 and 1998 at Fort Huachuca, southeastern Arizona.

| Season, year | %Carbon | %Nitrogen | C:N | %Phosphorus |
|--------------|------------------------------|--------------|------|--------------|
| spring, 1997 | 45.46±1.13 ab ^{1,2} | 2.28±0.19 ab | 20:1 | 0.08±0.02 cd |
| summer, 1997 | 45.55 ±0.22 ab | 3.50±0.18 a | 13:1 | 0.18±0.03 b |
| fall, 1997 | 46.55±0.34 ab | 2.58±0.17 a | 18:1 | 0.09±0.02 cd |
| winter, 1997 | 46.62±0.83 a | 2.11±0.14 b | 22:1 | 0.06±0.01 d |
| spring, 1998 | 46.42±1.35 ab | 2.27±0.13 ab | 20:1 | 0.07±0.01 d |
| summer, 1998 | 43.87±1.15 b | 3.75±0.09 a | 12:1 | 0.27±0.05 a |
| fall, 1998 | 43.60±0.98 ab | 2.29±0.15 ab | 19:1 | 0.11±0.02 c |
| winter, 1998 | 45.93±0.62 ab | 2.08±0.18 b | 22:1 | 0.07±0.01 d |

¹ Sample mean ± standard deviation

² Within any column, figures that lack one or more common letters are significantly different at the 0.05 level according to the Tukey's comparison of means test.

Table 4. Seasonal comparison of soil inorganic N concentrations throughout 1997 and 1998 at Fort Huachuca, southeastern Arizona.

| Season, year | Inorganic N (mg/kg) | |
|--------------|------------------------------|--------------|
| | Site A | Site B |
| spring, 1997 | 14.85±20.38 a ^{1,2} | 7.18±2.92 b |
| summer, 1997 | 14.31±10.07 a | 10.72±5.56 a |
| fall, 1997 | 12.03±13.81 ab | 6.45±7.00 b |
| winter, 1997 | 13.40±13.14 ab | 8.34±6.81 b |
| spring, 1998 | 9.58±8.23 ab | 7.97±4.31 b |
| summer, 1998 | 14.40±12.82 a | 8.69±4.36 ab |
| fall, 1998 | 7.49±7.05 b | 6.45±1.96 b |
| winter, 1998 | 11.46±14.01 ab | 7.73±2.37 b |

¹ Sample mean ± standard deviation

² Within any column, figures that lack one or more common letters are significantly different at the 0.05 level according to the Tukey's comparison of means test.

Table 5. Mean concentrations of soil total C, total N, and plant-available P in 2 sites of different fire history at Fort Huachuca, southeastern Arizona

| Season, year | Total N (%) | Total C (%) | PO ₄ ⁻³ (ppm) |
|---------------|------------------------------|----------------|-------------------------------------|
| Site A | 0.08 ± 0.06 b ^{1,2} | 1.06 ± 0.61 b | 4.85 ± 4.01 c |
| Site A canopy | 0.16 ± 0.09 a | 1.89 ± 1.02 a | 9.60 ± 6.96 a |
| Site A open | 0.07 ± 0.02 b | 0.88 ± 0.22 b | 3.86 ± 1.82 c |
| Site B | 0.07 ± 0.02 b | 1.05 ± 0.27 b | 6.22 ± 2.33 b |
| Site B canopy | 0.10 ± 0.04 b | 1.35 ± 0.50 ab | 5.73 ± 1.49 bc |
| Site B open | 0.07 ± 0.02 b | 1.02 ± 0.20 b | 6.27 ± 2.27 b |

¹ Sample mean ± standard deviation

² Within any column, figures that lack one or more common letters are significantly different at the 0.05 level according to the Tukey's comparison of means test.

APPENDIX C

FIRE HISTORY AND SOIL NUTRIENT STATUS AT FORT HUACHUCA MILITARY RESERVATION, ARIZONA

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Abstract

Desert grassland fires may have important but poorly understood effects on soil-nutrient concentrations in the southwestern United States. These effects may either aid or hinder plant reestablishment, including that of non-native species such as the introduced *Eragrostis lehmanniana* (Lehmann lovegrass). The Fort Huachuca Military Reservation in southeastern Arizona has a well-documented fire history, possessing firing ranges with road-system controlled firebreaks. We evaluated effects of fire frequency on soil-nutrient status and above-ground biomass at adjacent areas with different fire histories. Objectives of this study were to determine the relations between fire frequency, aboveground plant biomass and composition, soil pH, plant-available P, total organic C, total N, and plant-available N. Nine plots on two upland surfaces were analyzed that had reasonably uniform soil physical characteristics but fire frequencies ranging from zero to five fires/decade. Overall, soil nutrient concentrations were not directly related to fire frequency, except for NH_4^+ , which significantly decreased with increased fire frequency on the Pleistocene surface, and plant-available P, which significantly decreased with increased fire frequency on the Holocene surface. Between the two surfaces, available P concentrations and pH were significantly different; however, aboveground biomass was similar. Soil nutrients were not related to biomass, which suggests that nutrients may not control plant distribution or recovery in desert grasslands. *E. lehmanniana* was negatively correlated with native grasses and forbs, and tended to increase with increasing fire frequency. Surface litter was positively correlated with *E. lehmanniana*, and is associated with fire frequency. These results suggest that this non-native species prefers frequently burned locations, an important consideration when implementing grassland fire management practices.

Keywords: fire frequency, desert grasslands, biogeochemical cycling, nitrogen, phosphorus, carbon

INTRODUCTION

In arid regions worldwide, soil nitrogen (N) may affect plant community structure and limit aboveground biomass. Previous studies have shown that fires may redistribute plant-available soil nutrients, including N (DeBell and Ralston 1970, Smith 1970, Raison 1979, Ojima et al. 1994). After a burn, soil N can be converted to NO_3^- and leach out of the root zone (Smith 1970), become volatilized as N_2 gas (Raison 1979), or be removed through soil erosion (DeBell and Ralston 1970). Some have interpreted this redistribution of soil nutrients as a release of plant-sequestered N, P, and S, creating a net increase in soil fertility (Vlaminis and Gowans 1961). However, DeBano and Conrad (1978) examined effects of burning on soil fertility in a manzanita-scrub oak community located on a 15% slope in California; they found that 11% of soil N was lost due to volatilization (146 kg/ha) and erosion (15 kg/ha).

Relatively few studies have focused on the long-term effects of repeated fires on soil N concentrations or availability. Sharrow et al. (1977) noted that burning a Texas grassland every 2 to 3 years resulted in a net loss of herbaceous biomass and a depletion of soil N; litter N took at least 5 years to attain pre-burn concentrations. For sustainable grazing, they recommended a fire frequency of no more than 2 fires/decade. However, Emmerich (1999) found that more than 98% of soil N was unaffected by repeated burn treatments in southeastern Arizona, and he suggested that fires would have to be repeated for many years before significant losses were detected.

Biomass and species composition may be affected by repeated fires. Prehistoric wildfires, whether aboriginal- or lightning-induced, have played a large role in the suppression of trees and shrubs in southeastern Arizona (Bahre 1991), leading to the association of wildfire with grasslands (Humphrey 1958, 1963, 1974, Humphrey and Mehrhoff 1958). Fire suppression, which began in

the early 1900s, has combined with livestock grazing to give shrubs and trees a competitive advantage over grasses (Griffiths 1910). In the latter 20th century, repeated burning has been commonly suggested as a management tool for the suppression of *Prosopis velutina* (velvet mesquite) and some other shrubs in the desert grassland (Humphrey 1949, Wright 1973, 1980, Cave and Patton 1984, Wilson et al. in press).

Using prescribed burning as a *Prosopis* management tool can create corollary effects. Fire-related changes in soil nutrient status and physical characteristics may confer an ecological advantage to certain plants, including non-native species. Both Ruyle et al. (1988) and Sumrall et al. (1991) found that seeds of *Eragrostis lehmanniana* (Lehmann lovegrass), a non-native grass introduced from South Africa, had significantly greater germination rates than native grasses in areas where cover was removed following fire. How repeated fires may affect germination and establishment of this species remains unclear. Furthermore, the degree to which fire and plant community structure are synergistically associated also remains poorly understood. For example, changes in species-dependent litter accumulation may determine the frequency and intensity of subsequent fires, particularly in ungrazed areas.

The effects of repeated burns in desert grasslands on soil nutrient concentrations, plant biomass, and plant species composition needs further elucidation. In field studies of the effects of fire management upon aboveground biomass and soil nutrient cycling, factors such as climate, soil type, and land-use history should be as uniform as possible. The Fort Huachuca Military Reservation, east of the Huachuca Mountains in southeastern Arizona, contains plots with different fire histories that exist in close proximity with a uniform soil type, topography, and land-use history (Robinett 1994, Biggs 1997). Our objectives in this study were to determine the relations

between fire frequency, plant biomass and composition (particularly the relative composition of native grasses versus *E. lehmanniana*), soil nutrients (total N, plant-available N, organic C (TOC), and plant-available phosphorus), and soil pH. We hypothesize that the availability and spatial distribution of soil total N, TOC, plant-available N, available P, and aboveground biomass will be reduced by increasing fire frequency, resulting in a reduction in grassland plant species composition and vegetative dynamics.

MATERIALS AND METHODS

Study Site

The study plots are located at the southern gunnery ranges at Fort Huachuca. No cattle grazing has occurred here since the late 1940s (Biggs 1997). The vegetation community is semidesert grassland (Brown 1994) consisting of native grasses (including the perennial species *Bouteloua curtipendula*, *B. gracilis*, and *Eragrostis intermedia*), *E. lehmanniana*, widely spaced shrubs (including *Mimosa aculeatacarpa*, *Calliandra eriopoda*, and *Eriogonum wrightii*), and mesquite (*Prosopis velutina*) growing to a maximum height of 6 m.

Nine 900 m² plots were located on Holocene- and Pleistocene-aged surfaces associated with an arroyo that exits Woodcutter's Canyon (Fig. 1). We selected plots on both surfaces to account for variability between locations that differed in soil age and origin. These surfaces are relatively flat and represent fluvial Holocene deposition to a depth of 0.5 m overlying a Pleistocene clay unit. By correlation with areas downslope, one surface is of Holocene age and the other is of late Pleistocene age (Demsey and Pearthree 1994). The location of each plot was determined from aerial photos, existing soils maps, historical fire maps (Cochrane 1993), the geological map (Hayes and Raup 1968), and proximity to the other plots. Each plot possessed a

different fire history, ranging from unburned within the past 30 years to 5 fires/decade.

The soil identified as a Holocene surface is formed in 0.5 to 1.0 m deep Holocene age alluvium, overlying a Pleistocene age buried soil. The surface A horizon ranges from 10 - 25 cm in thickness and is a very dark brown to very dark grayish-brown sandy loam. The subsurface horizon is a dark brown sandy clay loam, which abruptly changes to a buried argillic horizon which has a clay loam texture. This soil would be classified as a fine-loamy, mixed, thermic Ustollic Haplargid. The plots were located at 1,490 m elevation, on a uniform 4% slope, near a road junction which functioned as a firebreak (Fig. 2). Plots with three different fire frequencies, ranging from unburned to 5 fires/decade, were selected on this surface (Table 1).

The soil on the Pleistocene surface is formed in granitic-derived alluvium. The surface A horizon is a brown to dark brown sandy loam ranging from 5 to 25 cm in thickness. The subsurface horizon is a yellowish red heavy clay loam extending to a 0.5 m depth. The soil has a very well developed argillic horizon, and would be classified as a fine, mixed, thermic Typic Haplargid. Plots with six different fire frequencies, ranging from unburned to 5 fires/decade, were selected on this surface (Table 1). Most of the plots on this surface were located at 1,400 m elevation, on a uniform 3% slope, on either side of a road in the southern section of Fort Huachuca (Fig. 1). However, due to the spatial distribution of fires within this area in the past 30 years, the closest suitable location for the unburned plot was approximately 800 m north of the others on a southward-facing 6% slope; however, this plot possessed the same soil characteristics and plant species.

The effects of season for each burn was not evaluated in this study, since subsequent burns occurring during different seasons would have confounded these effects. Though we use

the nomenclature of fires/decade in this study to differentiate plots, we recognize that two plots with the same fire frequency/decade may be affected differently by fire due to the actual dates each fire occurred.

Sampling

Plots 30 x 30 m in size were delineated on each surface. Plots were selected that mainly excluded mesquite trees, because of their influence on soil nutrient concentrations (Rundel et al. 1982, Biggs 1997), and their limited response to burning (Wright et al. 1976, Wilson et al. University of Arizona, unpublished data). Using the means and standard deviations of soil nutrient data from 121 samples collected during a previous study at this site (Biggs 1997), and assuming they were population values, we calculated that we would require 25 samples to allow testing of differences in means (Petersen and Calvin 1986). Within each plot, 25 randomly located soil samples were collected in the spring of 1998 using a core sampler (Blake et al., 1986) with a sampling depth of 100 mm, a diameter of 30 mm, and a length of 70 mm (volume = 1.54×10^{-4} m³). Aboveground biomass was sampled during the subsequent fall from 15 random 1 m² plots within each plot. The biomass was subdivided by litter, forbs, shrubs, native grasses, and *E. lehmanniana*.

Analysis

Soil samples were dried for 24 hours at 105°C, then analyzed for particle-size distribution to compare the physical characteristics of the 2 surfaces. Soils were sieved with a 2 mm mesh to determine gravel %, and sand, silt, and clay % was determined using the hydrometer method (Gee and Bauder 1986). Soil pH was measured using a saturated paste extract (Rhoades 1982). Available P concentrations were determined using the Olsen extraction (Olsen and Sommers

1982), and colorimetric P analysis. Ammonium and NO_3^- were extracted with 2M KCl and analyzed using steam distillation (Keeney and Nelson 1982). Total N and TOC were analyzed using dry combustion (Nelson and Sommers 1982). Litterfall samples were dried for 48 hours at 65°C and weighed.

A Wilk-Shapiro/Rankit plot was used to determine if the data were normally distributed (Analytical Software 1998). Grouped data were analyzed using a 1-way ANOVA, and Tukey's Mean Separation Test was used to identify relationships between fire history, soil data, and aboveground plant biomass composition. Pearson's Correlation Coefficient (r) was used to identify associations between biomass categories among plots (Conover 1980), and regression analysis was used to identify associations between biomass categories and soil chemical properties. The null hypothesis of no differences was rejected if the significance level of $P < 0.05$ was verified. The analyses were performed using STATISTIX software (Analytical Software 1998).

RESULTS AND DISCUSSION

Aboveground Biomass

Across all plots, *Eragrostis lehmanniana* cover was negatively correlated with native grass cover ($r = -0.91$), and tended to increase with increasing fire frequency (Table 2), as observed previously in southeastern Arizona (Cable 1967, Robinett 1994). The greatest mean total aboveground biomass for sampling locations on both surfaces was at the 2 fires/decade plot (464 g/m^2), refuting our initial hypothesis. This biomass was composed mainly of *E. lehmanniana* (Table 2). At the adjacent 2 fires/decade plot the biomass totals were almost as high (371 g/m^2), yet they were composed mainly of native grasses. This plot also contained significantly more shrubs, including the legumes *Mimosa aculeatacarpa* and *Calliandra eriopoda*, which are

potentially capable of N-fixation. We did not identify a relation between increasing fire frequency and aboveground biomass composition, indicating that other factors also play a direct role in determining plant community structure on these plots.

On the Holocene surface, we did not identify significant differences among the plant species composition of aboveground biomass with increasing fire frequency. However, this surface tended to contain more litter and native grasses. No shrubs were found on the 5 fires/decade plot. Since shrubs collected at the lower fire frequency plots included species capable of N fixation, their absence may explain why soil NH_4^+ concentrations were more homogenous.

On both surfaces, forbs were negatively correlated with *E. lehmanniana* ($r = -0.65$) and positively correlated with native grasses ($r = 0.64$). Litter was not significantly correlated with *E. lehmanniana* in terms of percent total composition for each sampling location. However, they were in terms of unit mass on the Pleistocene surface ($r = 0.93$); each had a maximum mean value (125 g and 283 g, respectively) at the 4 fires/decade plot. This data supports the hypothesis presented by others (Cox et al. 1988, Anable et al. 1992) that *E. lehmanniana* establishment results in increased litter (fire fuel) accumulation, in turn increasing fire-frequency potential.

Our hypothesis that aboveground biomass is reduced with increasing fire frequency was not supported by our analysis. Our data suggests that increasing fire frequency reduces the biomass of native grasses while increasing the biomass of *E. lehmanniana*. Increasing fire frequency also reduces the diversity of plant species, favoring a monoculture of *E. lehmanniana* on these sites. For landscape management, altering fire frequencies to every seven to ten years (the historic levels suggested by McPherson and Weltzin (2000)) does not necessarily result in a re-establishment of plant community structure to historic dispositions, but favors the establishment of *E. lehmanniana*

(Ruyle et al. 1988, Sumrall et al. 1991).

Soil Properties

On the Holocene surface, the unburned plot contained significantly less gravel than the 2- and 4 fires/decade plots (Table 3). On the Pleistocene surface, the intermediate fire frequency plots contained significantly less gravel than the unburned, 1-, and 5 fires/decade plots (Table 3); overall, gravel % on the two surfaces was not significantly different (Table 3). Sand, silt, and clay content were not significantly different between surfaces; both have sandy loam soils. These results indicate that soil textural characteristics do not account for differences in soil chemical characteristics between the two surfaces.

On the Pleistocene surface, soil NH_4^+ concentrations were significantly higher ($P \leq 0.05$) in the plots with lower fire frequencies (unburned and 1 fire/decade), than for the plots with a higher fire frequency (Table 4). On the Holocene surface, NH_4^+ concentrations were significantly higher and more homogenous at the greatest fire frequency plot (5 fires/decade).

Soil NO_3^- concentrations were highest at the unburned plot on the Pleistocene surface; the soils at other plots on both surfaces held uniform concentrations (Table 4). On the Holocene surface at the unburned and 2 fires/decade plots, we found concentrations lower than those reported by Biggs (1997), who found an average of 4.85 mg/kg, and 3.71 mg/kg NO_3^- , respectively, for 121 measurements. However, Biggs (1997) found a lower mean concentration at the 5 fires/decade plot (2.12 mg/kg, verses our mean concentration of 3.25 mg/kg).

Our results do not support the hypothesis that there is a direct relation between soil inorganic N concentrations within our sampling depth and fire frequency. Long-term fire effects may be masked by seasonal variation. In a study evaluating seasonal variation of soil inorganic N

at the Holocene surface, soil inorganic N concentrations at the unburned plot varied from 14.9 mg/kg (spring, 1997) to 7.5 mg/kg (fall, 1998); at the 5 fires/decade plot they ranged from 10.7 mg/kg (summer, 1997) to 6.5 mg/kg (fall, 1998) (Wilson and Thompson, unpublished data). This variation indicates that results from single-season sampling of an area recovering from fire should be evaluated with caution.

On both surfaces, soil total N and organic C followed similar patterns with increasing fire frequency. For all plots, C:N ratios averaged 11:1. Concentrations of soil total N and total C increased with increasing fire frequency on the Holocene surface, and were significantly greater at the 5 fires/decade plot than at the unburned location (Table 4). The highest concentrations of soil total N and organic C on the Pleistocene surface were found at the 1 burn/decade plot; within 5 m of this plot, the 3 fires/decade plot had significantly lower concentrations (Table 4).

The 5 fires/decade plot on the Holocene surface contained the highest concentrations of soil total N, organic C, and NH_4^+ . This was not correlated with aboveground biomass, which was consistent among the 3 plots. However, these nutrient concentrations may be reduced by nearby *Prosopis* trees, which are larger and more numerous at the lower fire frequency plots (Fig. 2) and are capable of sequestering soil C and N through root uptake (Klemmedson and Tiedemann 1986, Biggs 1997, Wilson et al. University of Arizona, unpublished data). One result of the high fire frequency at the 5 fires/decade plot may be a redistribution of these soil nutrients from around *Prosopis* canopies into the intercanopy zones.

On the Pleistocene surface, the 3 fires/decade plot had the lowest concentrations of soil total N, organic C, and NO_3^- ; this may coincide with the low percentage of shrubs (including N-fixing plants) and relatively uniform representation by other plants and litter (Table 2). To more

rigorously define this relationship, more detailed work needs to be conducted to evaluate the role these shrubs play in contributing to N cycling within this plant community.

Concentrations of plant-available P did not differ significantly among plots on the Pleistocene surface, suggesting that available P is not directly affected by fire frequency. On the Holocene surface, available P concentrations significantly decreased with increasing fire frequency. Concentrations of available P at the less frequently burned plots may reflect the contribution of litterfall from adjacent mesquites, which occur in greater numbers at these locations (Wilson et al. University of Arizona, unpublished data). Their deep root systems allow access to available P that subsequently accumulates at shallow soil depths through degradation of litterfall, which contain up to 0.27% P (Wilson et al. University of Arizona, unpublished data). Although this has not yet been substantiated by direct evidence, Biggs (1997) found soil horizons below 1 m depth had reduced PO_4^{3-} in the vicinity of mature trees.

Soil pH decreased with increasing fire frequency on the Pleistocene surface (Table 2). The 4 fires/decade plot contained the most acidic soil (mean pH = 5.8), corresponding with the greatest mean aboveground litter biomass. The unburned and 5 fires/decade plots on the Holocene surface were not significantly different, but the 2 fires/decade plot was significantly more acidic. These results differ from those of Biggs (1997), who found that soil pH increased with increasing fire frequency within the same sampling depth.

Among all plots, soil nutrient concentrations were not reflected in the composition of aboveground biomass (e.g., pH verses biomass, $r^2 = 0.52$, $P \leq 0.05$; inorganic N verses biomass, $r^2 = 0.25$, $P \leq 0.05$). It is apparent that the effects of fire on soil nutrients are either too ephemeral to become cumulative through repeated burns, or fire frequency has little long-term effect on soil

nutrient pools (Emmerich 1999). Our results indicate that soil plant-available nutrient status is not a reliable indication of forage recovery following repeated fires.

Our experimental design did not quantify the effects of seasonal burning on soil nutrient status or plant biomass, yet the season in which a fire occurs may have a direct effect. For example, winter burns may have greater effects on production of winter-growing grasses, and warm-season burns may have greater effects on shrubs while they are growing (McPherson and Weltzin 2000). The season and amount of fuel present controls the intensity of fires, and fuel loading should be evaluated before prescribed burning if eradication of *Prosopis* or grassland restoration are the desired management objectives (Wilson et al. in press).

LITERATURE CITED

- Anable, M.E., M.P. McClaran, and G.B. Ruyle. 1992.** Spread of introduced Lehmann lovegrass (*Eragrostis lehmanniana* Nees.) in southern Arizona, U.S.A. *Biol. Conserv.* 61:181-188.
- Biggs, T.H. 1997.** Fire frequency, nutrient concentrations and distributions, and ¹³C of soil organic matter and plants in southeastern Arizona grassland. Ph.D Thesis, Univ. Arizona, Tucson.
- Blake, G.R., and K.H. Harge. 1986.** Bulk density. *In: Methods of Soil Analysis, Part 1. Physical and mineralogical methods (2nd edition).* Ed. by A. Klute. Am. Soc. of Agron. Series No. 9, Madison, WI.
- Cable, D.R. 1961.** Small velvet mesquite seedlings survive burning. *J. Range Manage.* 14:160-161.
- Cable, D.R. 1967.** Fire effects on semidesert grasses and shrubs. *J. Range Manage.* 20:170-176.
- Cable, D.R., and S.C. Martin. 1971.** Invasion of semidesert grassland by velvet mesquite and associated vegetation changes. *J. Ariz. Acad. Sci.* 8:127-134.
- Cable, D.R. 1973.** Fire Effects in southwestern semidesert grass-shrub communities. *Proc. Tall Timbers Fire Ecol. Conf.* 12:109-127.
- Conover, W.J. 1980.** Practical nonparametric statistics. New York: John Wiley.

- Debano, L.F., and C.E. Conrad. 1978.** The effect of fire on nutrients in a chaparral ecosystem. *Ecol.* 59:489-497.
- DeBell, D.S., and C.W. Ralston. 1970.** Release of nitrogen by burning light forest fuels. *Soil Sci. Soc. Amer. Proc.* 34:936-938.
- Demsey, K.A., and P.A. Pearthree. 1994.** Surficial and environmental geology of the Sierra Vista area, Cochise County, Arizona. Arizona Geological Survey Open-File Report 94-6.
- Emmerich, W.E.. 1999.** Nutrient dynamics of rangeland burns in southeastern Arizona. *J. Range Manage.* 52: 606-614.
- Gee, G.W., and J.W. Bauder. 1986.** Particle-size analysis. *In: Methods of Soil Analysis, Part 1. Physical and mineralogical methods (2nd edition).* Ed. by A. Klute. Am. Soc. of Agron. Series No. 9, Madison, WI.
- Hendricks, D. 1985.** Arizona Soils. Univ. Arizona Press, Tucson.
- Klemmedson, J.O., and A.R. Tiedemann. 1986.** Long-term effects of mesquite removal on soil characteristics: II. Nutrient availability. *Soil Sci. Soc. Am. J.* 50:476-480.
- McClaran, M.P., and T.R. Van Devender. 1995.** The desert grassland. Univ. Arizona Press, Tucson.
- Ojima, D.S., D.S. Schimel, W.J. Parton, and C.E. Owensby. 1994.** Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochem.* 24:67-84.
- Parker, K.W., and S.G. Martin. 1952.** The mesquite problem on southern Arizona range. USDA Circular 908. Washington D.C.
- Petersen, R.G., and L.D. Calvin. 1986.** Sampling. *In: Methods of Soil Analysis, Part 1. Physical and mineralogical methods (2nd edition).* Ed. by A. Klute. Am. Soc. of Agron. Series No. 9, Madison, WI.
- Raison, R.J. 1979.** Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. *Plant-Soil* 51:73-108.
- Robinett, D. 1994.** Fire effects on southeastern Arizona plains grasslands. *Rangelands* 16:143-148.
- Rundel, P.W.; Nilsen, E.T.; Sharifi, M.R.; Virginia, R.A.; Jarrell, W.M.; Kohl, K.H.; Shearer, G.B. 1982.** Seasonal dynamics of nitrogen cycling for a *Prosopis* woodland in the Sonoran Desert. *Plant-Soil.* 67:343-353.

- Ruyle, G.B., B.A. Roundy, and J.R. Cox. 1988.** Effects of burning on germinability of Lehmann lovegrass. *J. Range Manage.* 41:404-406.
- Schlesinger, W.H., J.F. Reynolds, G.L. Cunningham, L.F. Huenneke, W.M. Jarrell, R.A. Virginia, and W.E. Whitford. 1990.** Biological feedbacks in global desertification. *Sci.* 247:1043-1048.
- Smith, D.W. 1970.** Concentration of soil nutrients before and after fire. *Can. J. Soil Science* 50:17-29.
- Smith, S.J., and L.B. Young. 1975.** Distribution of nitrogen forms in virgin and cultivated soils. *Soil Science.* 120:354-360.
- Sumrall, L.B., B.A. Roundy, J.R. Cox, and V.K. Winkel. 1991.** Influence of canopy removal by burning or clipping on emergence of *Eragrostis lehmanniana* seedlings. *Int. J. of Wild. Fire.* 1:35-40.
- Vlams, J., and K.D. Gowans. 1961.** Availability of N, P, and S after brush burning. *J. Range Manage.* 14:38-40.
- Vohman, D. 1997.** The effects of agriculture on soil properties in a Sonoran desert ecosystem. M.S. Thesis, Univ. Arizona, Tucson.
- Woodmansee, R.G., and D.A. Duncan. 1980.** Nitrogen and phosphorus dynamics and budgets in annual grasslands. *Ecol.* 61:893-904.
- Wilson, T.B., R.H. Webb, T.L. Thompson. In Press.** Mechanisms of range expansion and removal of mesquite (*Prosopis spp.*) in desert grasslands of the southwestern United States. U.S.D.A. General Technical Report. Fort Collins, CO.
- Wilson, T.B., and T.L. Thompson. In Preparation.** Nutrient topographies of mesquite-dominated desert grasslands: changes in time and space.
- Wright, H.A., S.C. Bunting, and L.F. Neuenschwander. 1976.** Effect of fire on honey mesquite. *J. Range Manage.* 29:467-471.



Figure 1. Plots of different fire history on a Pleistocene surface in a desert grassland at Fort Huachuca Military Reservation, southeastern Arizona. Each number corresponds to a respective fire frequency (fires/decade), and sampling plot. The distance between the road at the center of the photo and the one to the left (west) is approximately 800 m, and the drainage in the upper left is Woodcutter's Canyon wash.

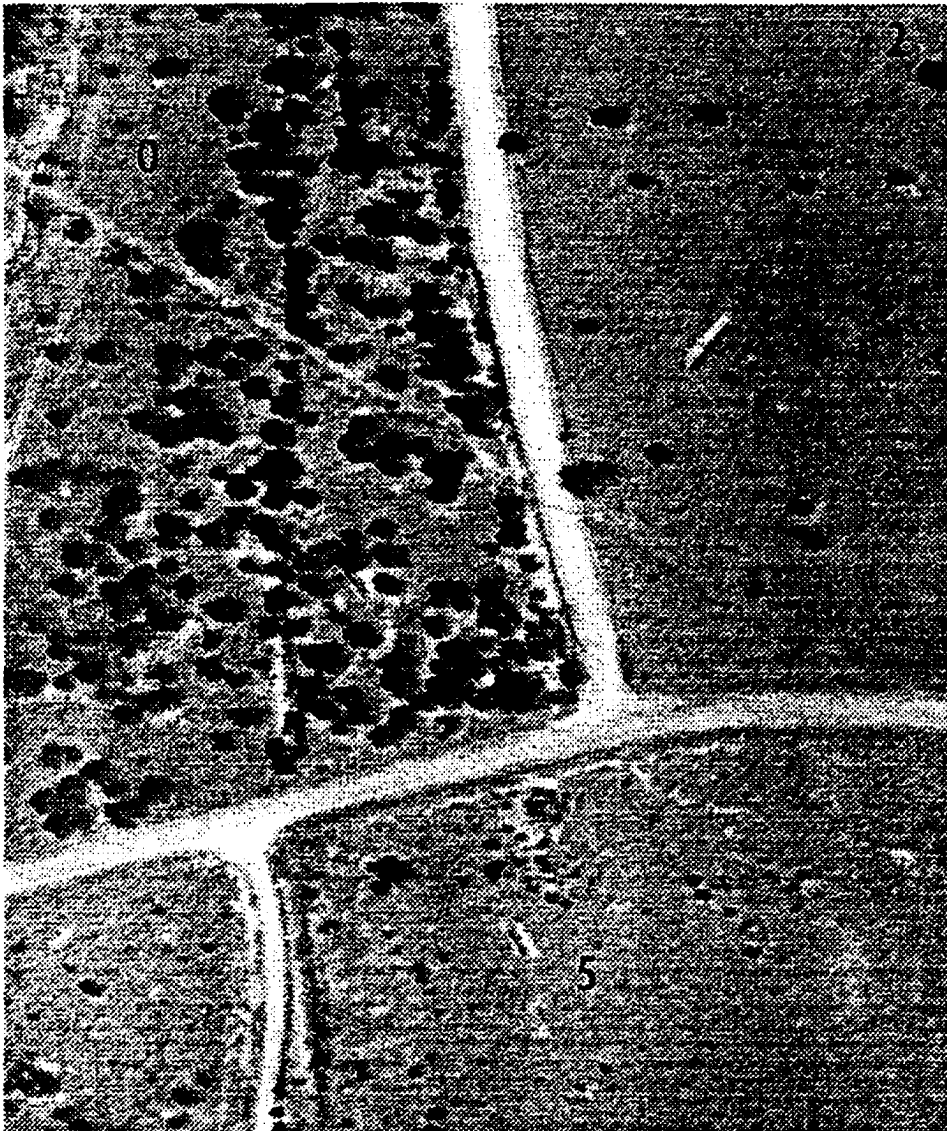


Figure 2. Plots of different fire history on a Holocene surface in a desert grassland at Fort Huachuca Military Reservation, southeastern Arizona. Each number corresponds to a respective fire frequency (fires/decade), and sampling plot. The trees in the upper left quadrant are mesquites (*Prosopis velutina*). The linear features on each site are trenches approximately 6 m long excavated during a previous study (Biggs, 1997). These plots are located approximately 1.2 km west of the plots shown in Fig. 1.

Table 1. Dates of fires in a southeastern Arizona grassland within the past 30 years.

| Upland surface (age) | Fire frequency (fires/decade) | Fire date (month/year) | Mean fire interval (years) |
|-------------------------|-------------------------------------|------------------------------|-------------------------------|
| Pleistocene | 0 | no fires within 30 years | -- |
| Pleistocene | 1 | 5/84 | -- |
| Pleistocene | 2 | 5/84, 1/91 | 7.7 |
| Pleistocene | 3 | 6/82, 6/83, 5/85 | 1.5 |
| Pleistocene | 4 | 6/82, 6/83, 5/85, 1/91 | 2.8 |
| Pleistocene | 5 | 6/82, 6/83, 5/85, 1/91, 6/91 | 2.2 |
| Holocene | 0 | no fires within 30 years | -- |
| Holocene | 2 | 7/83, 5/84, 1/91 | 3.6 |
| Holocene | 5 | 2/81, 7/83, 5/86, 2/88, 2/89 | 2 |

Table 2. Composition of aboveground biomass, expressed as the mean percentage of total biomass collected for each square meter sampled, from plots of different fire frequency in a southeastern Arizona grassland.

| Soil Surface(age) | Burns/decade | Litter (%) | Forbs (%) | Shrubs (%) | Native Grasses (%) | Eragrostis lehmanniana (%) | Mean Total Biomass (g) |
|-------------------|--------------|------------------------|-----------|------------|--------------------|----------------------------|------------------------|
| Pleistocene | 0 | 29.02 ab ²² | 16.00 a | 4.71 b | 35.88 ab | 12.77 c | 223.65 bc |
| Pleistocene | 1 | 37.68 ab | 14.67 a | 7.68 ab | 28.32 abc | 4.25 c | 181.84 c |
| Pleistocene | 2 | 19.12 b | 5.78 a | 18.76 a | 31.83 ab | 17.44 c | 370.56 abc |
| Pleistocene | 3 | 23.49 ab | 15.37 a | 3.17 b | 36.61 ab | 20.40 bc | 277.48 abc |
| Pleistocene | 4 | 26.72 ab | 4.40 a | 2.00 b | 6.90 c | 55.04 a | 464.26 a |
| Pleistocene | 5 | 29.37 ab | 3.76 a | 9.07 b | 17.10 bc | 38.74 ab | 312.38 abc |
| Holocene | 0 | 38.20 ab | 14.22 a | 0.86 b | 46.73 a | 0.00 c | 413.68 ab |
| Holocene | 2 | 43.67 a | 6.44 a | 0.00 b | 41.61 a | 8.28 c | 397.85 abc |
| Holocene | 5 | 28.14 ab | 14.02 a | 0.00 b | 40.42 ab | 14.42 c | 274.01 abc |

¹ Within any column, figures that lack one or more common letters are significantly different at the $P < 0.05$ level according to Tukey's comparison of means test.

² For all groups, $n = 15$.

Table 3. Soil particle-size distributions in plots of different fire frequency in a southeastern Arizona grassland.

| Soil Surface(age) | Burns/ decade | Gravel Content (%) | Sand (%) | Silt (%) | Clay (%) |
|-------------------|------------------|------------------------|-------------|-------------|-------------|
| Pleistocene | 0 | 29.2 ab ^{1,2} | 72.8 | 10.9 | 16.3 |
| Pleistocene | 1 | 30.2 a | 80.9 | 8.5 | 10.6 |
| Pleistocene | 2 | 17.6 c | 78.3 | 6.1 | 15.6 |
| Pleistocene | 3 | 16.4 c | 62.6 | 20.5 | 16.9 |
| Pleistocene | 4 | 16.5 c | 72.8 | 13.5 | 13.7 |
| Pleistocene | 5 | 29.6 ab | 71.1 | 15.1 | 13.7 |
| Holocene | 0 | 18.6 c | 77.9 | 13.4 | 8.7 |
| Holocene | 2 | 24.2 b | 77.9 | 10.9 | 11.2 |
| Holocene | 5 | 24.6 b | 73.1 | 12.5 | 14.4 |

¹ Within any column, figures that lack one or more common letters are significantly different at the $P < 0.05$ level according to Tukey's Mean Separation Test.

² For all groups, $n = 25$.

Table 4. Mean soil chemical properties in plots of different fire frequency in a southeastern Arizona grassland.

| Soil Surface(age) | Burns/decade | Total N (%) | Total C (%) | NH ₄ ⁺ (mg/kg) | NO ₃ ⁻ (mg/kg) | PO ₄ ⁻³ (mg/kg) | pH |
|-------------------|--------------|-----------------------|-------------|--------------------------------------|--------------------------------------|---------------------------------------|---------|
| Pleistocene | 0 | 0.09 b ^{1,2} | 1.01 e | 1.66 a | 4.71 a | 4.75 c | 6.02 d |
| Pleistocene | 1 | 0.10 a | 1.10 a | 1.37 a | 2.16 b | 5.08 c | 7.02 a |
| Pleistocene | 2 | 0.07 cde | 0.80 de | 0.55 bc | 1.32 b | 5.40 c | 6.0 de |
| Pleistocene | 3 | 0.06 e | 0.66 e | 0.31 c | 1.05 b | 5.39 c | 6.18 cd |
| Pleistocene | 4 | 0.07 de | 0.82 de | 0.25 c | 1.77 b | 5.00 c | 5.79 f |
| Pleistocene | 5 | 0.08 bcd | 0.91 bcd | 0.25 c | 2.39 b | 3.41 c | 5.82 ef |
| Holocene | 0 | 0.07 de | 0.83 cde | 0.38 c | 1.57 b | 24.26 a | 6.52 b |
| Holocene | 2 | 0.07 bcd | 0.92 abcd | 0.21 c | 1.14 b | 17.57 b | 6.29 c |
| Holocene | 5 | 0.09 bc | 1.07 ab | 1.08 ab | 3.25 b | 5.40 c | 6.48 b |

¹ Within any column, figures that lack one or more common letters are significantly different at the P<0.05 level according to Tukey's Mean Separation Test.

² For all groups, n = 25.

APPENDIX D:

Raw data set from nutrient topographies of mesquite-dominated desert grasslands: changes in time and space manuscript

Table 1. Raw data from 1997-1998 soil nutrient study of Site A.

| LOCATION | X (m) | Y (m) | INORGANIC N (mg/kg) | | | | | | | | | | | | | | Total N Jan98 (%) | TOC Jan98 (%) | PO ₄ ⁻³ Jan98 (mg/kg) | | |
|----------|-------|-------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|--|-------|-------|
| | | | Mar97 | | Jul97 | | Oct97 | | Jan98 | | Mar98 | | Jul98 | | Oct98 | | | | | Jan99 | |
| | | | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | | | |
| 1 | 8 10 | 4 57 | 3.1 | 5.31 | 8.21 | 4.89 | 2.07 | 7.95 | 2.59 | 4.20 | 4.02 | 14.89 | 2.78 | 8.06 | 5.84 | 2.46 | 2.28 | 13.02 | 0.11 | 1.22 | 5.28 |
| 2 | 8 10 | 13 72 | 8.2 | 32.61 | 10.52 | 20.07 | 16.91 | 48.70 | 21.22 | 60.61 | 10.41 | 42.54 | 17.70 | 47.82 | 15.72 | 33.96 | 23.52 | 60.00 | 0.19 | 2.06 | 25.32 |
| 3 | 8 10 | 22 86 | 3.0 | 1.98 | 26.39 | 8.86 | 5.00 | 11.27 | 5.87 | 5.41 | 2.30 | 9.20 | 4.20 | 11.84 | 3.12 | 7.32 | 5.16 | 8.18 | 0.07 | 0.78 | 6.65 |
| 4 | 8 10 | 32 00 | 5.8 | 7.78 | 8.21 | 11.44 | 3.97 | 25.42 | 2.78 | 5.75 | 10.06 | 68.88 | 7.44 | 19.02 | 7.08 | 8.40 | 8.06 | 5.82 | 0.11 | 1.28 | 4.72 |
| 5 | 8 10 | 41 15 | 4.9 | 3.58 | 5.00 | 4.54 | 12.94 | 16.96 | 2.59 | 4.03 | 2.99 | 2.47 | 7.08 | 4.80 | 3.12 | 2.10 | 2.82 | 6.00 | 0.06 | 0.74 | 4.88 |
| 6 | 18 29 | 4 57 | 7.2 | 9.51 | 18.11 | 15.58 | 2.78 | 8.81 | 2.93 | 11.96 | 3.16 | 12.48 | 8.16 | 14.52 | 5.46 | 3.54 | 9.48 | 18.06 | 0.17 | 2 | 8.73 |
| 7 | 18 29 | 13 72 | 4.4 | 0.00 | 10.87 | 8.96 | 1.72 | 13.17 | 3.97 | 4.03 | 5.40 | 3.51 | 5.28 | 7.32 | 3.12 | 11.84 | 7.68 | 3.12 | 0.1 | 1.22 | 2.09 |
| 8 | 18 29 | 22 86 | 4.2 | 3.21 | 5.35 | 4.72 | 2.42 | 4.89 | 3.45 | 7.30 | 2.99 | 4.37 | 3.12 | 4.98 | 4.56 | 3.18 | 3.00 | 4.38 | 0.04 | 0.54 | 7.81 |
| 9 | 18 29 | 32 00 | 4.7 | 27.01 | 5.89 | 8.27 | 1.21 | 18.45 | 5.87 | 7.48 | 4.02 | 8.16 | 2.40 | 4.82 | 5.84 | 7.88 | 1.92 | 6.90 | 0.06 | 0.81 | 2.84 |
| 10 | 18 29 | 41 15 | 8.2 | 4.78 | 31.05 | 43.18 | 8.21 | 12.85 | 22.25 | 15.41 | 4.37 | 2.82 | 4.56 | 8.04 | 3.12 | 1.74 | 8.42 | 5.10 | 0.12 | 1.53 | 5.12 |
| 11 | 30 48 | 4 57 | 22.1 | 35.58 | 13.28 | 29.04 | 22.00 | 115.46 | 20.53 | 27.49 | 10.92 | 39.90 | 11.40 | 17.04 | 3.30 | 8.96 | 5.70 | 41.10 | 0.16 | 1.8 | 12.47 |
| 12 | 30 48 | 13 72 | 36.9 | 30.33 | 13.80 | 32.14 | 4.49 | 18.17 | 12.77 | 54.74 | 25 | 2.82 | 22.38 | 42.42 | 22.56 | 8.40 | 20.82 | 52.44 | 0.35 | 3.96 | 19.83 |
| 13 | 30 48 | 22 86 | 11.0 | 20.36 | 10.52 | 10.93 | 3.82 | 28.35 | 5.87 | 20.07 | 2.99 | 5.75 | 8.16 | 16.14 | 7.90 | 5.70 | 4.80 | 29.04 | 0.18 | 2.05 | 8.37 |
| 14 | 30 48 | 32 00 | 11.7 | 21.93 | 10.52 | 9.20 | 4.31 | 5.58 | 10.70 | 13.89 | 3.16 | 4.37 | 30.30 | 12.72 | 11.22 | 8.58 | 22.44 | 15.54 | 0.16 | 1.89 | 12.96 |
| 15 | 30 48 | 41 15 | 5.8 | 8.28 | 9.14 | 8.86 | 1.90 | 4.54 | 15.35 | 7.82 | 6.78 | 5.75 | 18.82 | 10.38 | 9.78 | 5.52 | 20.28 | 12.30 | 0.09 | 1.04 | 2.44 |
| 16 | 42 87 | 4 57 | 4.4 | 14.58 | 9.32 | 13.51 | 10.01 | 46.12 | 4.83 | 4.72 | 3.88 | 2.64 | 5.84 | 5.52 | 3.12 | 5.70 | 4.98 | 3.86 | 0.07 | 0.93 | 10.84 |
| 17 | 42 87 | 13 72 | 5.1 | 4.26 | 0.00 | 4.72 | 3.45 | 3.68 | 6.04 | 6.81 | 2.64 | 5.40 | 3.12 | 4.82 | 5.84 | 3.00 | 2.82 | 7.82 | 0.05 | 0.78 | 4.07 |
| 18 | 42 87 | 22 86 | 5.8 | 2.86 | 5.18 | 2.82 | 1.90 | 0.00 | 4.31 | 7.13 | 4.71 | 3.33 | 2.78 | 5.70 | 2.94 | 2.82 | 2.64 | 4.74 | 0.06 | 0.86 | 4.06 |
| 19 | 42 87 | 32 00 | 7.0 | 2.88 | 6.38 | 2.99 | 1.04 | 4.54 | 4.14 | 5.75 | 3.16 | 4.54 | 5.82 | 6.78 | 3.84 | 5.52 | 3.54 | 3.86 | 0.05 | 0.71 | 7.54 |
| 20 | 42 87 | 41 15 | 5.8 | 2.51 | 7.42 | 5.06 | 1.55 | 2.99 | 4.31 | 6.96 | 2.64 | 2.82 | 6.36 | 6.06 | 5.84 | 2.82 | 6.24 | 5.84 | 0.07 | 0.88 | 4.68 |
| 21 | 54 86 | 4 57 | 2.5 | 8.38 | 4.43 | 3.85 | 1.44 | 4.54 | 1.04 | 5.12 | 2.64 | 7.99 | 4.82 | 9.36 | 5.70 | 1.80 | 4.26 | 4.36 | 0.06 | 0.92 | 5.44 |
| 22 | 54 86 | 13 72 | 3.0 | 1.73 | 4.95 | 4.89 | 0.58 | 37.49 | 2.24 | 4.77 | 2.47 | 5.75 | 4.08 | 4.86 | 4.80 | 2.16 | 4.08 | 2.78 | 0.05 | 0.81 | 8.08 |
| 23 | 54 86 | 22 86 | 3.4 | 1.90 | 7.02 | 3.34 | 1.78 | 3.16 | 1.38 | 2.19 | 2.30 | 3.85 | 3.90 | 6.30 | 3.90 | 1.26 | 3.54 | 6.18 | 0.07 | 1.04 | 6.98 |
| 24 | 54 86 | 32 00 | 3.4 | 1.73 | 6.33 | 7.13 | 2.65 | 25.59 | 1.38 | 3.74 | 3.16 | 2.30 | 6.80 | 3.96 | 21.54 | 2.70 | 2.64 | 3.84 | 0.05 | 0.67 | 4.20 |
| 25 | 54 86 | 41 15 | 4.3 | 1.73 | 7.02 | 4.20 | 1.27 | 2.65 | 2.24 | 2.19 | 2.99 | 2.99 | 6.42 | 2.70 | 3.72 | 0.54 | 3.90 | 2.76 | 0.06 | 0.82 | 5.38 |
| 26 | 2 44 | 20 97 | 3.2 | 4.18 | 3.74 | 8.34 | 0.92 | 2.99 | 2.42 | 5.46 | 5.06 | 6.27 | 5.52 | 8.82 | 4.44 | 1.08 | 7.50 | 7.08 | 0.08 | 1.05 | 3.43 |
| 27 | 8 34 | 5 36 | 4.8 | 4.70 | 8.15 | 5.06 | 1.44 | 2.47 | 3.79 | 6.87 | 3.88 | 4.71 | 5.88 | 8.64 | 3.18 | 1.44 | 10.92 | 7.08 | 0.08 | 1.03 | 6.32 |
| 28 | 8 83 | 3 90 | 3.4 | 0.50 | 5.63 | 7.82 | 1.61 | 4.89 | 3.45 | 8.22 | 3.33 | 9.03 | 5.16 | 4.68 | 4.26 | 1.96 | 3.90 | 6.72 | 0.12 | 1.81 | 4.05 |
| 29 | 8 83 | 39 99 | 2.9 | 1.73 | 6.33 | 6.10 | 1.27 | 4.03 | 4.14 | 5.81 | 6.78 | 3.51 | 4.98 | 17.10 | 3.90 | 0.00 | 3.36 | 3.48 | 0.08 | 1.1 | 2.01 |
| 30 | 7 90 | 2 93 | 82.1 | 18.78 | 19.43 | 45.08 | 30.76 | 15.76 | 9.32 | 10.98 | 5.23 | 3.68 | 5.16 | 7.74 | 3.54 | 1.26 | 5.34 | 8.34 | 0.06 | 0.91 | 2.63 |
| 31 | 8 29 | 4 39 | 111.7 | 21.50 | 5.12 | 4.20 | 1.61 | 2.47 | 3.28 | 5.63 | 4.54 | 11.10 | 4.26 | 8.64 | 4.44 | 1.26 | 3.72 | 2.78 | 0.09 | 1.18 | 2.65 |
| 32 | 8 78 | 3 90 | 4.3 | 3.13 | 5.81 | 13.51 | 1.27 | 13.86 | 1.55 | 5.81 | 3.16 | 7.13 | 4.98 | 6.30 | 5.16 | 1.26 | 6.60 | 4.02 | 0.07 | 1.04 | 1.71 |
| 33 | 11 22 | 24 87 | 3.4 | 3.83 | 5.46 | 8.17 | 1.27 | 4.54 | 5.89 | 7.38 | 5.75 | 3.51 | 3.90 | 4.32 | 7.32 | 1.80 | 5.16 | 7.26 | 0.11 | 1.54 | 4.77 |
| 34 | 11 22 | 37 06 | 5.5 | 33.58 | 4.60 | 5.41 | 1.61 | 16.45 | 9.32 | 11.50 | 6.44 | 4.37 | 5.88 | 7.02 | 6.96 | 4.14 | 5.34 | 3.48 | 0.07 | 0.93 | 2.21 |
| 35 | 11 70 | 11 22 | 5.8 | 5.58 | 5.12 | 5.92 | 1.44 | 4.03 | 5.35 | 8.22 | 4.02 | 7.47 | 2.82 | 7.38 | 4.08 | 1.80 | 5.52 | 9.24 | 0.09 | 1.2 | 3.98 |
| 36 | 12 88 | 20 97 | 7.9 | 18.18 | 9.09 | 34.58 | 29.04 | 60.00 | 8.58 | 58.77 | 8.27 | 8.51 | 25.68 | 20.34 | 6.42 | 6.66 | 20.28 | 55.86 | 0.34 | 4.1 | 8.04 |
| 37 | 14 14 | 19 02 | 16.3 | 12.23 | 9.26 | 12.48 | 2.30 | 4.54 | 3.28 | 9.43 | 3.85 | 15.41 | 8.78 | 13.32 | 9.86 | 2.70 | 6.24 | 9.24 | 0.07 | 1 | 2.94 |
| 38 | 16 09 | 34 83 | 5.0 | 2.25 | 5.83 | 8.10 | 2.65 | 15.07 | 5.18 | 8.05 | 5.40 | 5.58 | 4.08 | 4.32 | 3.18 | 1.44 | 5.34 | 2.22 | 0.08 | 1.08 | 2.08 |
| 39 | 16 09 | 34 83 | 4.4 | 1.90 | 3.56 | 5.41 | 1.96 | 3.16 | 5.00 | 7.71 | 3.33 | 5.40 | 3.72 | 3.96 | 3.54 | 1.98 | 4.26 | 3.30 | 0.05 | 0.76 | 3.48 |
| 40 | 17 56 | 43 40 | 5.8 | 14.50 | 25.47 | 23.86 | 11.10 | 17.14 | 6.04 | 0.98 | 3.85 | 3.16 | 30.18 | 25.02 | 7.50 | 4.88 | 10.38 | 20.04 | 0.17 | 1.84 | 15.01 |
| 41 | 22 92 | 30 24 | 1.9 | 2.63 | 3.45 | 2.93 | 1.09 | 2.42 | 2.59 | 6.44 | 2.19 | 1.38 | 1.80 | 7.92 | 5.58 | 1.80 | 3.06 | 10.26 | 0.08 | 0.96 | 3.36 |
| 42 | 22 92 | 45 35 | 4.6 | 2.63 | 6.45 | 9.49 | 1.78 | 14.49 | 8.45 | 11.10 | 2.88 | 4.31 | 12.42 | 11.88 | 3.78 | 1.80 | 8.28 | 6.86 | 0.11 | 1.16 | 3.29 |
| 43 | 25 35 | 34 14 | 1.9 | 2.10 | 17.08 | 5.87 | 2.30 | 4.14 | 7.59 | 6.78 | 2.53 | 2.59 | 3.24 | 4.14 | 0.90 | 1.80 | 1.62 | 5.40 | 0.06 | 0.73 | 4.25 |
| 44 | 31 21 | 38 53 | 3.7 | 2.10 | 5.87 | 4.31 | 1.78 | 4.83 | 6.04 | 5.06 | 2.01 | 1.72 | 1.80 | 8.10 | 1.80 | 1.98 | 0.36 | 3.96 | 0.07 | 0.71 | 3.93 |
| 45 | 33 16 | 39 99 | 3.7 | 2.28 | 6.21 | 3.97 | 1.96 | 4.49 | 2.42 | 3.33 | 3.57 | 2.93 | 2.34 | 9.00 | 0.90 | 2.16 | 0.18 | 4.50 | 0.07 | 0.8 | 4.08 |
| 46 | 35 11 | 24 87 | 3.9 | 3.68 | 6.04 | 7.94 | 2.47 | 12.94 | 6.56 | 6.61 | 2.01 | 2.93 | 14.40 | 26.64 | 1.82 | 3.42 | 1.98 | 5.76 | 0.07 | 0.82 | 2.49 |
| 47 | 49 74 | 20 97 | 2.1 | 5.25 | 5.00 | 2.59 | 0.58 | 3.45 | 4.83 | 4.37 | 1.50 | 2.24 | 6.84 | 7.74 | 1.26 | 1.80 | 1.80 | 0.72 | 0.06 | 0.74 | 3.57 |

| LOCATION | | INORGANIC N (mg/kg) | | | | | | | | | | | | | | | | Total N | TOC | PO ₄ ³⁻ | |
|----------|-------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|---------|-------|-------------------------------|------|
| X (m) | Y (m) | Mar97 | | Jul97 | | Oct97 | | Jan98 | | Mar98 | | Jul98 | | Oct98 | | Jan99 | | Jan98 | Jan98 | Jan98 | |
| | | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | (%) | (%) | (mg/kg) | |
| 48 | 49.74 | 22.43 | 4.8 | 3.50 | 2.93 | 2.07 | 1.27 | 5.00 | 4.31 | 3.35 | 4.43 | 2.41 | 0.72 | 8.82 | 0.38 | 1.26 | 0.90 | 0.90 | 0.08 | 0.78 | 3.71 |
| 49 | 50.23 | 21.95 | 3.3 | 2.98 | 7.59 | 30.88 | 1.27 | 3.79 | 2.07 | 18.34 | 2.38 | 5.17 | 0.18 | 5.40 | 0.90 | 3.24 | 0.18 | 3.42 | 0.08 | 0.79 | 3.99 |
| 50 | 50.23 | 36.58 | 4.6 | 8.83 | 5.18 | 8.38 | 2.65 | 4.49 | 2.93 | 5.75 | 2.53 | 4.33 | 2.34 | 7.92 | 1.98 | 0.72 | 1.80 | 3.42 | 0.08 | 0.79 | 2.35 |
| 51 | 51.21 | 12.58 | 2.3 | 4.90 | 8.04 | 3.11 | 4.54 | 3.82 | 4.88 | 8.81 | 4.08 | 2.78 | 9.54 | 2.34 | 0.00 | 3.24 | 1.80 | 1.98 | 0.05 | 0.7 | 3.88 |
| 52 | 51.89 | 33.65 | 4.2 | 15.93 | 8.45 | 9.48 | 1.81 | 4.83 | 5.00 | 5.58 | 4.77 | 4.83 | 2.18 | 8.12 | 4.50 | 1.80 | 0.38 | 5.58 | 0.07 | 0.92 | 1.52 |
| 53 | 52.18 | 30.24 | 3.7 | 8.83 | 3.11 | 1.73 | 1.81 | 3.97 | 3.97 | 2.82 | 4.77 | 3.79 | 2.18 | 4.50 | 1.82 | 3.98 | 1.82 | 3.24 | 0.05 | 0.89 | 1.34 |
| 54 | 52.18 | 33.18 | 4.4 | 1.75 | 3.82 | 3.45 | 1.78 | 3.45 | 3.28 | 3.51 | 1.87 | 3.11 | 3.08 | 2.18 | 3.42 | 0.38 | 1.82 | 2.70 | 0.08 | 0.89 | 2.18 |
| 55 | 53.16 | 14.83 | 6.7 | 4.20 | 2.78 | 2.59 | 1.27 | 2.78 | 2.78 | 3.51 | 2.38 | 2.93 | 2.34 | 8.30 | 1.82 | 1.90 | 3.60 | 4.14 | 0.07 | 0.92 | 2.82 |
| 56 | 53.18 | 32.19 | 4.4 | 17.33 | 4.83 | 3.80 | 3.51 | 10.01 | 2.07 | 5.23 | 3.91 | 1.21 | 2.18 | 3.42 | 1.80 | 1.80 | 0.90 | 1.98 | 0.04 | 0.83 | 2.53 |
| 57 | 53.84 | 18.04 | 5.1 | 0.00 | 8.58 | 3.28 | 1.81 | 3.11 | 3.97 | 5.23 | 3.22 | 2.24 | 2.18 | 3.42 | 3.60 | 0.90 | 2.52 | 3.08 | 0.08 | 0.77 | 3.19 |
| 58 | 53.84 | 20.97 | 5.4 | 2.80 | 3.82 | 2.59 | 0.92 | 2.24 | 2.78 | 3.33 | 0.81 | 2.07 | 3.08 | 3.08 | 1.82 | 2.70 | 1.44 | 0.00 | 0.08 | 0.78 | 2.58 |
| 59 | 54.13 | 13.86 | 0.7 | 2.28 | 3.11 | 2.24 | 1.44 | 2.59 | 2.42 | 3.16 | 2.19 | 1.90 | 2.34 | 4.88 | 1.82 | 0.00 | 0.18 | 1.82 | 0.05 | 0.72 | 1.81 |
| 60 | 54.13 | 14.83 | 1.4 | 1.40 | 5.00 | 1.55 | 1.27 | 3.11 | 1.04 | 2.30 | 2.38 | 2.07 | 5.40 | 4.50 | 2.52 | 3.60 | 1.98 | 1.98 | 0.04 | 0.82 | 3.85 |
| 61 | 54.13 | 18.04 | 7.70 | 1.89 | 8.90 | 2.59 | 1.44 | 3.45 | 2.41 | 4.43 | 1.21 | 1.95 | 1.44 | 5.58 | 1.82 | 0.00 | 1.82 | 1.08 | 0.07 | 0.99 | 2.74 |
| 62 | 54.82 | 15.12 | 8.30 | 2.22 | 7.59 | 1.90 | 2.47 | 3.82 | 5.88 | 5.81 | 1.90 | 2.30 | 5.22 | 3.24 | 1.82 | 1.80 | 0.38 | 0.90 | 0.05 | 0.73 | 3.03 |
| 63 | 54.82 | 18.58 | 3.50 | 2.04 | 3.28 | 3.97 | 3.18 | 5.35 | 3.97 | 7.71 | 3.11 | 4.54 | 4.32 | 5.04 | 0.38 | 1.98 | 3.08 | 1.90 | 0.05 | 0.86 | 2.89 |
| 64 | 55.11 | 18.04 | 4.90 | 2.39 | 3.97 | 2.93 | 1.09 | 13.28 | 3.11 | 5.48 | 3.28 | 4.02 | 3.42 | 3.24 | 1.80 | 0.90 | 4.14 | 2.34 | 0.07 | 0.91 | 2.57 |
| 65 | 55.11 | 19.99 | 8.00 | 2.22 | 4.88 | 3.28 | 2.82 | 2.42 | 1.38 | 4.08 | 2.78 | 1.95 | 1.80 | 2.52 | 2.52 | 0.00 | 1.80 | 3.42 | 0.08 | 0.88 | 2.25 |
| 66 | 55.80 | 19.02 | 3.00 | 2.39 | 5.52 | 3.11 | 1.98 | 4.83 | 1.90 | 3.05 | 1.38 | 3.16 | 4.32 | 3.24 | 0.72 | 0.38 | 2.18 | 1.90 | 0.04 | 0.84 | 3.52 |
| 67 | 55.80 | 19.99 | 5.00 | 3.82 | 5.87 | 3.97 | 2.65 | 2.93 | 2.41 | 3.74 | 2.24 | 2.30 | 1.98 | 1.98 | 1.44 | 0.54 | 1.26 | 1.80 | 0.05 | 0.77 | 3.18 |
| 68 | 55.80 | 22.43 | 5.00 | 5.88 | 3.28 | 3.28 | 1.81 | 7.59 | 3.97 | 3.74 | 3.79 | 4.88 | 4.88 | 7.92 | 2.88 | 2.34 | 2.34 | 2.18 | 0.05 | 0.81 | 3.44 |
| 69 | 56.08 | 18.53 | 5.00 | 7.82 | 5.52 | 8.97 | 2.85 | 8.11 | 2.59 | 8.87 | 4.88 | 5.58 | 1.98 | 3.24 | 1.26 | 0.72 | 2.52 | 4.88 | 0.05 | 0.73 | 4.03 |
| 70 | 56.08 | 24.28 | 3.00 | 3.09 | 5.52 | 3.80 | 0.92 | 2.59 | 3.79 | 3.74 | 2.42 | 4.02 | 3.42 | 2.70 | 1.80 | 1.80 | 2.18 | 1.80 | 0.08 | 0.81 | 1.70 |
| 71 | 57.08 | 19.51 | 3.00 | 8.07 | 4.14 | 2.07 | 2.47 | 4.49 | 2.07 | 5.84 | 2.78 | 2.30 | 3.78 | 4.50 | 1.08 | 1.08 | 1.44 | 1.26 | 0.05 | 0.71 | 8.57 |
| 72 | 57.08 | 23.90 | 3.00 | 7.82 | 4.14 | 3.45 | 0.40 | 4.31 | 2.58 | 3.91 | 2.78 | 1.44 | 1.98 | 3.60 | 1.98 | 1.80 | 0.38 | 4.14 | 0.05 | 0.79 | 1.88 |
| 73 | 58.03 | 21.48 | 3.00 | 11.84 | 5.18 | 2.93 | 2.47 | 3.82 | 2.59 | 4.08 | 2.42 | 2.82 | 1.80 | 4.88 | 1.82 | 1.80 | 0.90 | 2.70 | 0.05 | 0.78 | 2.74 |
| 74 | 59.01 | 17.07 | 3.00 | 3.97 | 2.78 | 2.78 | 2.47 | 6.38 | 2.78 | 4.08 | 3.82 | 14.72 | 8.48 | 4.32 | 10.44 | 1.98 | 4.14 | 0.90 | 0.04 | 0.71 | 2.43 |
| 75 | 59.01 | 17.58 | 3.00 | 5.88 | 3.28 | 9.48 | 0.75 | 2.42 | 8.80 | 7.88 | 2.59 | 3.51 | 2.18 | 3.78 | 1.80 | 1.80 | 3.60 | 1.90 | 0.08 | 0.84 | 3.84 |

Table 2. Raw data from 1997-1998 soil nutrient study of Site B.

| LOCATION | X (m) Y (m) | | INORGANIC N (mg/kg) | | | | | | | | | | | | | | | | | | Total N Jan98 (%) | TOC Jan98 (%) | PO ₄ ⁻³ Jan98 (mg/kg) |
|----------|-------------|-------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|----------------------|------------------|--|
| | | | Mar97 | | Jul97 | | Oct97 | | Jan98 | | Mar98 | | Jul98 | | Oct98 | | Jan99 | | | | | | |
| | | | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | | | |
| 1 | 8 99 | 8 10 | 4.8 | 2.07 | 4.31 | 2.93 | 2.42 | 1.84 | 1.81 | 3.39 | 7.02 | 3.22 | 0.30 | 7.56 | 1.74 | 2.10 | 3.90 | 2.94 | 0.08 | 1.07 | 8.53 | | |
| 2 | 8 99 | 24 29 | 5.1 | 2.94 | 4.14 | 2.93 | 0.52 | 0.81 | 1.78 | 3.57 | 2.19 | 2.36 | 3.54 | 3.42 | 3.00 | 2.10 | 5.70 | 0.24 | 0.05 | 0.86 | 7.93 | | |
| 3 | 8 99 | 40 49 | 5.8 | 2.80 | 4.88 | 3.28 | 0.69 | 1.32 | 2.30 | 4.08 | 4.08 | 5.29 | 2.84 | 8.84 | 2.10 | 4.62 | 4.28 | 2.22 | 0.08 | 1.17 | 7.22 | | |
| 4 | 8 99 | 56 88 | 5.8 | 4.00 | 2.59 | 5.00 | 2.42 | 1.32 | 3.33 | 5.84 | 5.29 | 3.39 | 3.00 | 8.12 | 5.52 | 3.54 | 5.34 | 2.40 | 0.08 | 1.23 | 3.05 | | |
| 5 | 8 99 | 72 97 | 6.0 | 3.99 | 3.28 | 2.78 | 1.72 | 2.36 | 2.99 | 4.28 | 1.50 | 2.36 | 3.00 | 8.66 | 3.00 | 2.28 | 4.44 | 3.48 | 0.07 | 1.05 | 8.92 | | |
| 6 | 26 97 | 8 10 | 3.5 | 0.00 | 3.97 | 5.00 | 2.42 | 2.53 | 3.51 | 3.05 | 2.88 | 4.28 | 2.48 | 3.96 | 3.54 | 3.36 | 2.10 | 2.04 | 0.08 | 0.92 | 8.87 | | |
| 7 | 26 97 | 24 29 | 4.4 | 4.52 | 4.49 | 3.79 | 1.72 | 3.05 | 2.99 | 8.50 | 5.81 | 9.28 | 3.90 | 7.74 | 4.08 | 4.44 | 8.78 | 5.82 | 0.1 | 1.42 | 11.10 | | |
| 8 | 26 97 | 40 49 | 6.8 | 4.70 | 5.00 | 6.21 | 2.24 | 2.70 | 2.64 | 8.15 | 3.74 | 3.22 | 8.06 | 5.58 | 5.88 | 3.00 | 3.36 | 9.24 | 0.09 | 1.37 | 8.44 | | |
| 9 | 26 97 | 56 88 | 3.5 | 3.65 | 5.18 | 6.04 | 2.42 | 2.19 | 3.51 | 5.81 | 1.84 | 3.39 | 2.64 | 5.58 | 3.36 | 1.92 | 2.84 | 3.12 | 0.08 | 0.84 | 4.58 | | |
| 10 | 26 97 | 72 97 | 3.7 | 5.92 | 5.00 | 7.76 | 0.86 | 2.01 | 6.09 | 8.15 | 5.64 | 23.40 | 5.34 | 7.56 | 4.80 | 2.82 | 2.64 | 3.30 | 0.05 | 1.19 | 4.73 | | |
| 11 | 44 96 | 8 10 | 2.8 | 3.47 | 3.62 | 5.35 | 1.38 | 2.36 | 3.68 | 3.57 | 2.36 | 3.39 | 2.28 | 4.50 | 4.28 | 2.64 | 2.64 | 4.02 | 0.07 | 0.89 | 3.45 | | |
| 12 | 44 96 | 24 29 | 4.2 | 4.17 | 5.87 | 4.66 | 2.24 | 2.19 | 4.02 | 3.91 | 4.95 | 2.36 | 2.46 | 5.76 | 5.16 | 1.74 | 5.52 | 2.22 | 0.08 | 1.07 | 8.97 | | |
| 13 | 44 96 | 40 49 | 4.2 | 5.05 | 11.04 | 5.00 | 1.04 | 2.88 | 2.99 | 3.91 | 1.87 | 5.46 | 0.30 | 7.20 | 4.44 | 2.82 | 3.90 | 2.94 | 0.08 | 1.11 | 5.43 | | |
| 14 | 44 96 | 56 88 | 5.8 | 8.20 | 8.38 | 11.39 | 2.24 | 26.68 | 2.99 | 12.71 | 5.81 | 5.64 | 2.84 | 9.90 | 2.10 | 4.44 | 3.00 | 4.56 | 0.09 | 1.19 | 3.85 | | |
| 15 | 44 96 | 72 87 | 8.1 | 8.55 | 3.97 | 9.14 | 2.42 | 33.75 | 3.16 | 4.95 | 3.39 | 5.81 | 1.92 | 5.76 | 1.38 | 4.82 | 4.08 | 2.76 | 0.07 | 0.99 | 5.81 | | |
| 16 | 82 94 | 8 10 | 4.9 | 2.07 | 13.46 | 4.14 | 1.21 | 2.88 | 2.82 | 4.08 | 2.88 | 2.36 | 2.64 | 4.50 | 4.28 | 1.74 | 3.18 | 2.76 | 0.08 | 0.85 | 3.81 | | |
| 17 | 82 94 | 24 29 | 4.2 | 4.00 | 5.00 | 2.76 | 2.78 | 2.88 | 2.64 | 2.88 | 4.80 | 4.08 | 4.62 | 7.92 | 5.70 | 1.02 | 5.52 | 2.94 | 0.07 | 0.98 | 8.24 | | |
| 18 | 82 94 | 40 49 | 4.9 | 5.22 | 6.21 | 2.42 | 2.24 | 2.19 | 2.64 | 2.53 | 3.39 | 4.90 | 4.62 | 3.90 | 3.36 | 3.00 | 3.00 | 3.66 | 0.07 | 0.91 | 2.89 | | |
| 19 | 82 94 | 56 88 | 3.7 | 3.12 | 7.76 | 8.90 | 0.69 | 2.53 | 1.81 | 4.43 | 3.57 | 3.91 | 2.64 | 3.96 | 2.64 | 1.56 | 5.52 | 3.12 | 0.08 | 0.86 | 4.86 | | |
| 20 | 82 94 | 72 87 | 4.2 | 4.17 | 9.49 | 5.18 | 7.76 | 2.88 | 4.37 | 5.12 | 1.87 | 4.28 | 1.74 | 7.92 | 4.28 | 1.56 | 4.28 | 3.66 | 0.05 | 0.74 | 5.02 | | |
| 21 | 80 92 | 8 10 | 4.9 | 4.24 | 6.21 | 3.11 | 1.38 | 1.78 | 2.13 | 3.79 | 1.81 | 2.36 | 2.76 | 3.06 | 4.82 | 1.20 | 4.28 | 1.50 | 0.07 | 0.98 | 7.70 | | |
| 22 | 80 92 | 24 29 | 6.8 | 4.76 | 8.73 | 4.14 | 2.07 | 2.30 | 2.47 | 5.00 | 2.13 | 8.15 | 4.02 | 5.94 | 4.62 | 3.72 | 3.54 | 3.48 | 0.14 | 2 | 8.83 | | |
| 23 | 80 92 | 40 49 | 3.8 | 1.79 | 3.97 | 2.93 | 1.21 | 1.09 | 2.99 | 2.93 | 2.13 | 3.74 | 3.66 | 5.04 | 4.82 | 1.38 | 3.18 | 3.66 | 0.08 | 1.05 | 2.25 | | |
| 24 | 80 92 | 56 88 | 5.7 | 8.61 | 7.42 | 10.35 | 0.89 | 4.03 | 3.33 | 7.07 | 5.08 | 5.46 | 4.02 | 5.94 | 5.52 | 3.18 | 3.72 | 7.44 | 0.1 | 1.41 | 5.91 | | |
| 25 | 80 92 | 72 87 | 5.7 | 0.04 | 8.11 | 3.11 | 1.38 | 3.85 | 1.95 | 5.52 | 2.47 | 4.77 | 5.82 | 5.04 | 3.90 | 2.84 | 8.42 | 2.04 | 0.08 | 1.14 | 2.93 | | |
| 26 | 4 39 | 47 90 | 3.8 | 0.00 | 4.49 | 2.76 | 0.86 | 3.18 | 2.82 | 2.59 | 2.30 | 3.91 | 3.84 | 4.14 | 3.36 | 1.38 | 4.28 | 2.04 | 0.05 | 0.83 | 4.33 | | |
| 27 | 4 39 | 55 75 | 2.4 | 10.01 | 17.77 | 16.22 | 11.04 | 10.08 | 2.64 | 6.38 | 5.75 | 2.36 | 5.46 | 8.10 | 4.98 | 4.44 | 3.36 | 7.44 | 0.11 | 1.28 | 4.97 | | |
| 28 | 5 36 | 89 88 | 2.1 | 0.39 | 4.86 | 2.93 | 1.04 | 1.78 | 3.33 | 3.11 | 2.47 | 2.36 | 2.94 | 5.04 | 3.54 | 2.82 | 2.82 | 3.12 | 0.07 | 0.9 | 5.98 | | |
| 29 | 6 83 | 84 38 | 2.1 | 4.76 | 13.83 | 8.56 | 2.42 | 2.30 | 7.82 | 14.15 | 4.71 | 4.77 | 2.40 | 8.48 | 3.54 | 3.72 | 2.46 | 2.58 | 0.08 | 1.06 | 4.74 | | |
| 30 | 8 29 | 10 21 | 2.4 | 3.01 | 5.00 | 3.28 | 0.86 | 2.13 | 2.64 | 2.24 | 4.37 | 1.87 | 4.74 | 2.70 | 2.84 | 1.74 | 3.54 | 1.86 | 0.08 | 0.87 | 8.38 | | |
| 31 | 8 78 | 0 79 | 5.7 | 3.71 | 4.49 | 3.97 | 0.86 | 3.16 | 4.37 | 4.49 | 2.64 | 7.02 | 4.74 | 8.84 | 3.36 | 1.56 | 4.98 | 2.76 | 0.08 | 0.96 | 4.05 | | |
| 32 | 9 27 | 70 66 | 4.0 | 3.54 | 4.83 | 3.82 | 0.86 | 5.92 | 3.51 | 2.24 | 1.26 | 5.81 | 1.86 | 4.88 | 2.64 | 1.38 | 5.52 | 2.22 | 0.08 | 0.84 | 9.76 | | |
| 33 | 11 70 | 3 14 | 5.7 | 3.54 | 5.00 | 5.89 | 2.42 | 10.58 | 4.71 | 5.87 | 2.47 | 8.15 | 2.78 | 3.78 | 4.98 | 1.02 | 3.72 | 3.12 | 0.07 | 1.01 | 4.03 | | |
| 34 | 11 70 | 6 28 | 5.4 | 2.84 | 5.69 | 4.83 | 1.55 | 7.30 | 3.51 | 4.49 | 3.51 | 5.12 | 4.74 | 3.24 | 8.40 | 0.86 | 4.08 | 2.58 | 0.05 | 0.81 | 8.51 | | |
| 35 | 11 70 | 89 88 | 4.5 | 2.14 | 8.58 | 3.82 | 2.07 | 1.09 | 3.33 | 8.04 | 2.47 | 2.01 | 3.48 | 4.32 | 4.08 | 1.38 | 2.82 | 3.30 | 0.09 | 1.34 | 9.56 | | |
| 36 | 11 70 | 72 24 | 4.2 | 1.79 | 5.87 | 2.76 | 2.59 | 3.34 | 4.20 | 4.31 | 4.37 | 5.84 | 1.86 | 2.16 | 4.98 | 1.20 | 2.92 | 1.86 | 0.06 | 1 | 4.74 | | |
| 37 | 13 66 | 3 93 | 5.0 | 1.81 | 8.90 | 3.97 | 0.86 | 2.82 | 4.20 | 3.82 | 3.51 | 5.46 | 3.66 | 2.38 | 5.52 | 1.92 | 5.70 | 2.22 | 0.08 | 0.92 | 8.98 | | |
| 38 | 14 63 | 2 36 | 3.3 | 2.31 | 8.04 | 8.58 | 2.93 | 4.03 | 5.23 | 3.82 | 4.20 | 5.84 | 2.22 | 3.42 | 4.82 | 1.20 | 4.08 | 3.12 | 0.05 | 0.98 | 5.56 | | |
| 39 | 14 63 | 6 28 | 2.6 | 3.54 | 5.52 | 5.18 | 0.86 | 2.47 | 5.40 | 3.82 | 9.37 | 4.26 | 4.20 | 2.88 | 4.44 | 2.84 | 6.78 | 2.58 | 0.08 | 0.9 | 9.08 | | |
| 40 | 20 97 | 79 30 | 4.7 | 4.08 | 5.35 | 6.56 | 2.78 | 2.82 | 3.85 | 3.45 | 1.78 | 1.32 | 2.76 | 2.34 | 5.70 | 2.28 | 6.24 | 3.66 | 0.08 | 0.91 | 5.78 | | |
| 41 | 22 43 | 76 95 | 4.4 | 0.87 | 4.86 | 18.63 | 1.09 | 2.85 | 2.53 | 2.36 | 1.61 | 2.47 | 1.92 | 4.82 | 3.18 | 1.56 | 2.46 | 1.56 | 0.07 | 0.9 | 4.08 | | |
| 42 | 22 92 | 10 99 | 2.3 | 0.35 | 3.79 | 3.45 | 2.30 | 3.51 | 4.08 | 3.22 | 2.13 | 3.16 | 2.70 | 4.44 | 2.84 | 3.00 | 2.82 | 2.46 | 0.08 | 0.96 | 8.13 | | |
| 43 | 23 41 | 79 30 | 2.1 | 0.87 | 3.45 | 2.07 | 1.78 | 2.13 | 3.39 | 3.05 | 1.44 | 2.64 | 2.34 | 4.26 | 2.10 | 1.92 | 4.08 | 1.74 | 0.07 | 0.93 | 7.87 | | |
| 44 | 28 29 | 79 30 | 2.6 | 3.33 | 3.45 | 2.42 | 1.78 | 1.81 | 3.39 | 4.95 | 3.33 | 4.37 | 2.34 | 4.44 | 4.98 | 2.10 | 4.28 | 1.20 | 0.06 | 0.96 | 9.63 | | |
| 45 | 30 24 | 76 95 | 4.4 | 2.98 | 5.00 | 4.14 | 1.78 | 3.85 | 3.91 | 4.77 | 2.64 | 1.78 | 0.18 | 5.38 | 3.54 | 1.56 | 3.90 | 2.28 | 0.07 | 1.01 | 8.73 | | |
| 46 | 32 19 | 43 97 | 4.2 | 3.68 | 3.79 | 2.93 | 1.27 | 8.68 | 4.60 | 4.77 | 2.82 | 2.82 | 3.06 | 3.72 | 2.48 | 3.18 | 3.72 | 4.26 | 0.07 | 0.99 | 4.93 | | |
| 47 | 32 67 | 45 54 | 5.3 | 2.98 | 4.49 | 1.90 | 0.75 | 4.03 | 4.95 | 4.08 | 2.47 | 4.54 | 2.88 | 4.26 | 4.26 | 1.74 | 4.80 | 1.02 | 0.07 | 1.12 | 9.93 | | |

| LOCATION | X (m) Y (m) | | INORGANIC N (mg/kg) | | | | | | | | | | | | | | | | Total N Jan98 | TOC Jan98 | PO ₄ ⁻³ Jan98 | | |
|----------|-------------|-------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|--|-----|---------|
| | | | Mar97 | | Jul97 | | Oct97 | | Jan98 | | Mar98 | | Jul98 | | Oct98 | | Jan99 | | | | | | |
| | | | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | NH ₄ ⁺ | NO ₃ ⁻ | (%) | (%) | (mg/kg) |
| 48 | 40.97 | 4.71 | 2.8 | 3.33 | 3.79 | 5.89 | 2.82 | 15.41 | 3.57 | 5.84 | 5.75 | 2.47 | 2.34 | 15.24 | 3.54 | 2.28 | 3.54 | 4.82 | 0.08 | 0.87 | 10.28 | | |
| 49 | 58.52 | 54.18 | 3.0 | 3.50 | 3.11 | 2.07 | 4.03 | 1.96 | 3.22 | 2.88 | 4.54 | 1.78 | 1.98 | 7.68 | 4.28 | 3.00 | 3.54 | 3.54 | 0.06 | 0.93 | 8.50 | | |
| 50 | 57.30 | 15.70 | 4.0 | 1.93 | 4.49 | 3.97 | 2.30 | 2.13 | 2.70 | 5.98 | 4.02 | 3.51 | 2.34 | 8.96 | 3.38 | 2.84 | 3.18 | 3.18 | 0.11 | 1.5 | 5.70 | | |
| 51 | 69.25 | 24.34 | 4.4 | 2.28 | 1.90 | 2.59 | 0.92 | 2.30 | 2.38 | 3.39 | 1.78 | 2.64 | 2.34 | 5.34 | 2.10 | 3.54 | 4.82 | 1.74 | 0.06 | 1 | 8.03 | | |
| 52 | 70.23 | 5.50 | 3.0 | 3.15 | 7.42 | 5.89 | 1.44 | 2.85 | 2.70 | 3.74 | 3.51 | 3.33 | 3.24 | 7.86 | 4.08 | 2.10 | 4.28 | 5.52 | 0.07 | 0.98 | 3.68 | | |
| 53 | 70.23 | 7.85 | 3.7 | 1.58 | 8.21 | 2.93 | 2.30 | 1.44 | 2.88 | 3.22 | 3.51 | 3.51 | 2.34 | 8.08 | 4.28 | 2.84 | 3.72 | 1.92 | 0.06 | 0.83 | 3.99 | | |
| 54 | 71.20 | 7.07 | 2.8 | 2.98 | 5.35 | 4.31 | 0.40 | 3.18 | 4.08 | 8.67 | 4.71 | 4.89 | 3.80 | 3.90 | 3.00 | 2.28 | 3.72 | 1.92 | 0.05 | 0.8 | 8.73 | | |
| 55 | 71.20 | 10.21 | 4.4 | 2.28 | 4.83 | 5.89 | 1.81 | 3.34 | 5.98 | 4.95 | 8.44 | 4.54 | 3.42 | 3.72 | 2.84 | 1.92 | 5.18 | 2.82 | 0.05 | 0.79 | 4.78 | | |
| 56 | 72.18 | 3.93 | 4.9 | 1.75 | 8.73 | 3.97 | 1.27 | 2.13 | 7.02 | 3.91 | 5.92 | 8.90 | 2.52 | 4.80 | 5.70 | 2.10 | 7.86 | 3.18 | 0.06 | 0.89 | 12.89 | | |
| 57 | 73.15 | 8.28 | 3.0 | 1.93 | 8.21 | 2.24 | 1.98 | 5.75 | 3.39 | 4.08 | 13.51 | 21.91 | 3.24 | 3.54 | 2.82 | 2.48 | 3.54 | 3.18 | 0.07 | 0.97 | 8.87 | | |
| 58 | 73.84 | 4.71 | 2.8 | 1.05 | 4.83 | 2.93 | 2.30 | 12.31 | 3.91 | 3.05 | 4.37 | 7.25 | 2.18 | 2.84 | 4.82 | 1.74 | 4.28 | 2.48 | 0.06 | 0.89 | 5.89 | | |
| 59 | 74.13 | 9.42 | 2.8 | 0.00 | 4.66 | 4.48 | 12.85 | 3.51 | 5.81 | 2.53 | 2.99 | 11.21 | 5.04 | 2.84 | 3.54 | 2.84 | 4.44 | 3.18 | 0.06 | 0.83 | 5.35 | | |
| 60 | 78.52 | 4.71 | 1.8 | 0.87 | 5.35 | 1.90 | 4.20 | 2.85 | 2.53 | 2.01 | 1.28 | 7.42 | 1.44 | 3.54 | 2.28 | 3.00 | 4.28 | 0.30 | 0.06 | 0.83 | 2.81 | | |
| 61 | 78.52 | 13.35 | 2.1 | 1.40 | 5.52 | 2.07 | 0.75 | 1.27 | 1.73 | 3.82 | 1.28 | 1.84 | 1.74 | 3.12 | 3.38 | 1.58 | 4.80 | 0.48 | 0.07 | 0.99 | 3.10 | | |
| 62 | 78.52 | 18.49 | 1.9 | 2.10 | 8.73 | 4.83 | 1.44 | 2.85 | 0.89 | 3.11 | 2.13 | 5.84 | 2.48 | 2.04 | 3.90 | 2.84 | 3.38 | 2.82 | 0.07 | 1.12 | 4.84 | | |
| 63 | 79.49 | 18.08 | 2.8 | 2.45 | 2.24 | 2.42 | 2.13 | 2.82 | 1.04 | 2.59 | 2.30 | 1.50 | 2.48 | 3.84 | 3.72 | 3.72 | 4.08 | 4.82 | 0.08 | 1.28 | 7.11 | | |
| 64 | 79.98 | 11.78 | 2.3 | 2.28 | 8.04 | 2.59 | 1.09 | 2.13 | 1.55 | 4.31 | 2.30 | 1.50 | 3.72 | 2.22 | 4.28 | 1.74 | 8.08 | 3.00 | 0.06 | 0.81 | 4.22 | | |
| 65 | 80.47 | 15.70 | 2.8 | 2.45 | 8.80 | 5.52 | 2.82 | 1.44 | 2.07 | 2.93 | 3.18 | 1.15 | 4.44 | 1.50 | 3.54 | 1.58 | 7.86 | 8.78 | 0.18 | 2.38 | 8.15 | | |
| 66 | 80.95 | 25.91 | 4.4 | 5.08 | 8.04 | 3.79 | 0.40 | 2.13 | 1.04 | 2.24 | 4.02 | 5.84 | 5.70 | 5.84 | 4.28 | 0.84 | 8.04 | 5.18 | 0.09 | 1.38 | 8.37 | | |
| 67 | 81.44 | 20.41 | 1.9 | 2.10 | 8.45 | 2.42 | 0.58 | 3.51 | 1.21 | 2.78 | 1.95 | 1.84 | 1.38 | 3.12 | 8.08 | 1.58 | 5.88 | 2.82 | 0.09 | 1.35 | 8.41 | | |
| 68 | 82.42 | 20.41 | 1.8 | 2.98 | 7.25 | 4.14 | 2.99 | 4.03 | 2.59 | 2.24 | 2.13 | 2.70 | 2.48 | 3.48 | 3.54 | 2.84 | 8.98 | 1.92 | 0.07 | 1.01 | 11.29 | | |
| 69 | 82.91 | 19.83 | 4.4 | 8.48 | 8.11 | 5.18 | 2.82 | 4.89 | -0.34 | 3.28 | 3.09 | 2.88 | 3.90 | 4.56 | 3.54 | 2.82 | 5.70 | 3.38 | 0.07 | 1.04 | 9.16 | | |
| 70 | 83.88 | 22.77 | 3.7 | 1.75 | 4.48 | 3.11 | 1.81 | 1.78 | 1.04 | 3.82 | 1.78 | 3.74 | 4.44 | 7.98 | 5.70 | 1.58 | 5.34 | 4.82 | 0.07 | 1.1 | 9.43 | | |
| 71 | 83.98 | 25.91 | 4.4 | 1.23 | 3.79 | 3.28 | 1.27 | 8.17 | 1.21 | 8.58 | 1.28 | 12.88 | 2.28 | 8.18 | 2.84 | 1.92 | 8.24 | 2.84 | 0.06 | 1 | 8.25 | | |
| 72 | 84.37 | 11.78 | 5.1 | 11.90 | 18.39 | 21.56 | 4.03 | 49.05 | 1.73 | 59.89 | 3.18 | 12.54 | 15.60 | 22.02 | 7.14 | 12.18 | 7.32 | 8.24 | 0.12 | 1.88 | 8.41 | | |
| 73 | 85.34 | 43.97 | 5.3 | 2.83 | 4.49 | 3.82 | 1.98 | 2.47 | 1.73 | 3.11 | 4.37 | 3.74 | 4.08 | 5.84 | 4.98 | 2.82 | 8.78 | 4.44 | 0.07 | 1.13 | 8.32 | | |
| 74 | 85.83 | 44.75 | 3.9 | 5.08 | 7.94 | 8.97 | 2.13 | 2.47 | 3.45 | 8.80 | 2.13 | 3.39 | 8.08 | 13.74 | 4.28 | 1.20 | 7.86 | 5.18 | 0.06 | 0.91 | 3.43 | | |
| 75 | 87.29 | 47.11 | 3.5 | 1.75 | 4.31 | 2.42 | 1.44 | 2.85 | 8.80 | 3.45 | 3.51 | 4.28 | 1.92 | 4.74 | 5.18 | 0.84 | 3.72 | 3.38 | 0.07 | 1.14 | 8.41 | | |

Table 3. Raw data from mesquite leaf nutrient study.

| TREE | TOC (%) | | | | | | | | | | | | Total N (%) | | | | | | | | | | | | Total P (%) | | | | | | | | | | | |
|------|---------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------------|--|--|--|--|--|--|--|--|--|--|--|
| | Mar97 | Jul97 | Oct97 | Jan98 | Mar98 | Jul98 | Oct98 | Jan99 | Mar97 | Jul97 | Oct97 | Jan98 | Mar98 | Jul98 | Oct98 | Jan99 | Mar97 | Jul97 | Oct97 | Jan98 | Mar98 | Jul98 | Oct98 | Jan99 | | | | | | | | | | | | |
| 1 | 46.77 | 45.55 | 44.94 | 45.93 | 48.82 | 44.72 | 42.3 | 45.21 | 2.38 | 3.83 | 2.55 | 1.98 | 2.58 | 4.09 | 2.02 | 2.04 | 0.07 | 0.27 | 0.11 | 0.08 | 0.08 | 0.21 | 0.13 | 0.08 | | | | | | | | | | | | |
| 2 | 45.12 | 42.51 | 43.38 | 45.93 | 38.07 | 45.04 | 45.93 | 48.14 | 2.45 | 3.44 | 1.96 | 1.78 | 1.8 | 3.21 | 1.81 | 2.04 | 0.07 | 0.15 | 0.08 | 0.04 | 0.05 | 0.2 | 0.05 | 0.06 | | | | | | | | | | | | |
| 3 | 45.51 | 46.19 | 46.5 | 44.09 | 45.15 | 42.81 | 43.73 | 43.92 | 2.43 | 3.44 | 2.59 | 1.89 | 1.99 | 4.2 | 2.81 | 1.93 | 0.08 | 0.17 | 0.09 | 0.05 | 0.07 | 0.27 | 0.12 | 0.08 | | | | | | | | | | | | |
| 4 | 46.43 | 46.87 | 48.07 | 46.22 | 47.3 | 46.07 | 46.99 | 46.73 | 2.38 | 3.18 | 2.39 | 2.38 | 2.35 | 3.81 | 2.25 | 2.12 | 0.10 | 0.16 | 0.07 | 0.07 | 0.06 | 0.21 | 0.07 | 0.08 | | | | | | | | | | | | |
| 5 | 47.98 | 45.94 | 48.06 | 47 | 47.11 | 43.44 | 44.4 | 46.75 | 2.45 | 2.85 | 2.41 | 2.05 | 1.9 | 3.08 | 2.1 | 2.09 | 0.14 | 0.16 | 0.09 | 0.08 | 0.07 | 0.18 | 0.1 | 0.07 | | | | | | | | | | | | |
| 6 | 46.05 | 45.1 | 48.55 | 48.29 | 48.02 | 43.42 | 41.89 | 47.9 | 2.38 | 3.81 | 2.78 | 2.14 | 2.18 | 3.51 | 2.04 | 2.05 | 0.07 | 0.17 | 0.08 | 0.08 | 0.06 | 0.29 | 0.14 | 0.08 | | | | | | | | | | | | |
| 7 | 43.29 | 45.98 | 40.87 | 45.81 | | 42.74 | 40.75 | 42.5 | 1.55 | 3.88 | 2.82 | 2.07 | | 4.05 | 2.07 | 1.84 | 0.05 | 0.18 | 0.14 | 0.08 | | 0.31 | 0.13 | 0.09 | | | | | | | | | | | | |
| 8 | 48.33 | 44.89 | 47.49 | 48.78 | | 43.99 | 45.04 | 48.7 | 2.27 | 3.88 | 2.81 | 2 | | 4.15 | 2.64 | 1.9 | 0.05 | 0.24 | 0.1 | 0.05 | | 0.33 | 0.1 | 0.05 | | | | | | | | | | | | |
| 9 | 45.43 | 48.52 | 50.21 | 47.11 | 46.87 | 42.87 | 43.35 | 43.99 | 1.94 | 3.87 | 3.01 | 2.3 | 2.52 | 4.08 | 2.57 | 1.93 | 0.05 | 0.17 | 0.08 | 0.08 | 0.06 | 0.31 | 0.15 | 0.07 | | | | | | | | | | | | |
| 10 | 45.58 | 46.52 | 46.17 | 47.43 | | 39.76 | | 45.08 | 2.19 | 2.37 | 1.98 | 2.08 | | 3.44 | | 1.86 | 0.05 | 0 | 0 | 0.06 | | 0.27 | | 0.05 | | | | | | | | | | | | |

Table 6. Raw data from 1998 mesquite litterfall study for Site A.

| SAMPLE ID | LITTERFALL MASS (g) | | | | | | | | | | | |
|-----------|---------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| | Jan97 | Feb97 | Mar97 | Apr97 | May97 | Jun97 | Jul97 | Aug97 | Sep97 | Oct97 | Nov97 | Dec97 |
| 1N1 | 8.03 | 0.36 | 0 | 0 | 0 | 5.62 | 2.32 | 8.82 | 0.68 | 2.52 | 4.35 | 8.42 |
| 1N2 | 0.99 | 0 | 0 | 0 | 0 | 2.03 | 0.37 | 0 | 0 | 0 | 3.76 | 0 |
| 1E1 | 5.31 | 0.23 | 0 | 0 | 0 | 5.59 | 3.56 | 2.28 | 0.28 | 1.74 | 4.41 | 8.13 |
| 1E2 | 0.43 | 0.21 | 0 | 0 | 0 | 1.32 | 0.28 | 0 | 0 | 0 | 0 | 0 |
| 1S1 | 1.53 | 0 | 0 | 0 | 0 | 3.4 | 2.08 | 10.33 | 2.28 | 1.74 | 3.28 | 3.6 |
| 1S2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.63 | 0 | 0 |
| 1W1 | 3.27 | 0 | 0 | 0 | 0 | 2.57 | 0.54 | 5.92 | 1.89 | 0 | 0 | 5.36 |
| 1W2 | 0.47 | 0 | 0 | 0 | 0 | 0.71 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2N1 | 0.22 | 0.12 | 0 | 0 | 0 | 0.57 | 0.1 | 0 | 0.38 | 1.4 | 2.87 | 0 |
| 2N2 | 0.06 | 0 | 0 | 0 | 0 | 0.27 | 0.36 | 0 | 0 | 1.33 | 0 | 0 |
| 2E1 | 0.23 | 0 | 0 | 0 | 0 | 0.27 | 0.16 | 0 | 0.01 | 1.16 | 1.93 | 0 |
| 2E2 | 0.09 | 0 | 0 | 0 | 0 | 0.47 | 0 | 0 | 0.01 | 0 | 0 | 0 |
| 2S1 | 0.21 | 0.21 | 0 | 0 | 0 | 0.48 | 0.56 | 0.31 | 3.48 | 6.09 | 4.83 | 0 |
| 2S2 | 0.17 | 0 | 0 | 0 | 0 | 0.39 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2W1 | 0.29 | 0.05 | 0 | 0 | 0 | 0.62 | 0.38 | 0.28 | 2.37 | 3.79 | 0 | 0 |
| 2W2 | 0.29 | 0.7 | 0 | 0 | 0 | 1 | 0.07 | 0 | 0 | 0 | 3.97 | 0 |
| 3N1 | 7.8 | 0.85 | 0 | 0 | 0 | 23.03 | 0 | 1.18 | 1.04 | 4.06 | 22.59 | 17.3 |
| 3N2 | 0.9 | 0.24 | 0 | 0 | 0 | 2.21 | 0.22 | 0 | 0 | 0 | 0.46 | 0 |
| 3E1 | 5.81 | 2.26 | 0 | 0 | 0 | 13.19 | 3.31 | 0.76 | 4.95 | 2.55 | 9.82 | 10.61 |
| 3E2 | 1.91 | 0.26 | 0 | 0 | 0 | 2 | 0.17 | 0 | 0 | 0.01 | 2.39 | 1.78 |
| 3S1 | 5.29 | 0 | 0 | 0 | 0 | 4.14 | 3 | 6.37 | 2.32 | 0.87 | 2.7 | 0 |
| 3S2 | 1.05 | 0.29 | 0 | 0 | 0 | 0.5 | 0.33 | 0 | 0 | 0 | 0.35 | 0 |
| 3W1 | 8.58 | 0.41 | 0 | 0 | 0 | 5.27 | 1.23 | 0.59 | 0.75 | 2.71 | 5.73 | 7.01 |
| 3W2 | 1.27 | 0.49 | 0 | 0 | 0 | 0.86 | 0.53 | 0 | 0 | 0 | 1.42 | 0 |
| 4N1 | 20.94 | 3.23 | 0 | 0 | 0 | 0.4 | 3.21 | 1.86 | 1.54 | 3.4 | 5.42 | 8.61 |
| 4N2 | 9.77 | 2.86 | 0 | 0 | 0 | 1.78 | 1.23 | 1.18 | 0.5 | 2.18 | 0 | 5.7 |
| 4E1 | 14 | 0.07 | 0 | 0 | 0 | 9.28 | 5.17 | 2.6 | 2.28 | 4.34 | 7.73 | 16.6 |
| 4E2 | 1.28 | 1.18 | 0 | 0 | 0 | 1 | 0.63 | 0 | 0 | 0 | 0.88 | 0 |
| 4S1 | 0 | 0 | 0 | 0 | 0 | 3.85 | 2.59 | 3 | 4.18 | 2.98 | 3.29 | 4.32 |
| 4S2 | 0 | 0 | 0 | 0 | 0 | 1.64 | 0.48 | 0 | 0.64 | 0.59 | 2.15 | 1.29 |
| 4W1 | 21.71 | 2.49 | 0 | 0 | 0 | 5 | 3.49 | 1.54 | 2.48 | 2.34 | 14.89 | 10.55 |
| 4W2 | 6.64 | 0.01 | 0 | 0 | 0 | 0 | 0.67 | 0 | 0.82 | 1.64 | 5.62 | 3.5 |
| 5N1 | 6.76 | 1.54 | 0 | 0 | 0 | 5.32 | 4.59 | 3.71 | 0.85 | 2.88 | 6.53 | 5.92 |
| 5N2 | 10.54 | 2.5 | 0 | 0 | 0 | 0.06 | 1.41 | 2.16 | 6.33 | 2.43 | 5.87 | 6.92 |
| 5E1 | 16.7 | 5.51 | 0 | 0 | 0 | 8.49 | 2.05 | 2.09 | 2.01 | 10.17 | 11.53 | 14.33 |
| 5E2 | 0 | 0.23 | 0 | 0 | 0 | 0.36 | 0.51 | 0 | 0 | 0.05 | 0.67 | 2.49 |
| 5S1 | 15.1 | 2.31 | 0 | 0 | 0 | 4.5 | 0.92 | 0 | 0.65 | 0.14 | 3.93 | 6.66 |
| 5S2 | 0.85 | 0.3 | 0 | 0 | 0 | 0 | 0.48 | 2.73 | 0 | 0 | 0 | 0 |
| 5W1 | 8.37 | 0.48 | 0 | 0 | 0 | 6.15 | 0.85 | 2.71 | 0.36 | 1.5 | 4.87 | 3.19 |
| 5W2 | 3.42 | 0 | 0 | 0 | 0 | 1.85 | 0.44 | 0 | 0.38 | 0.39 | 1.29 | 1.92 |

Figure 1. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site A, March, 1997.

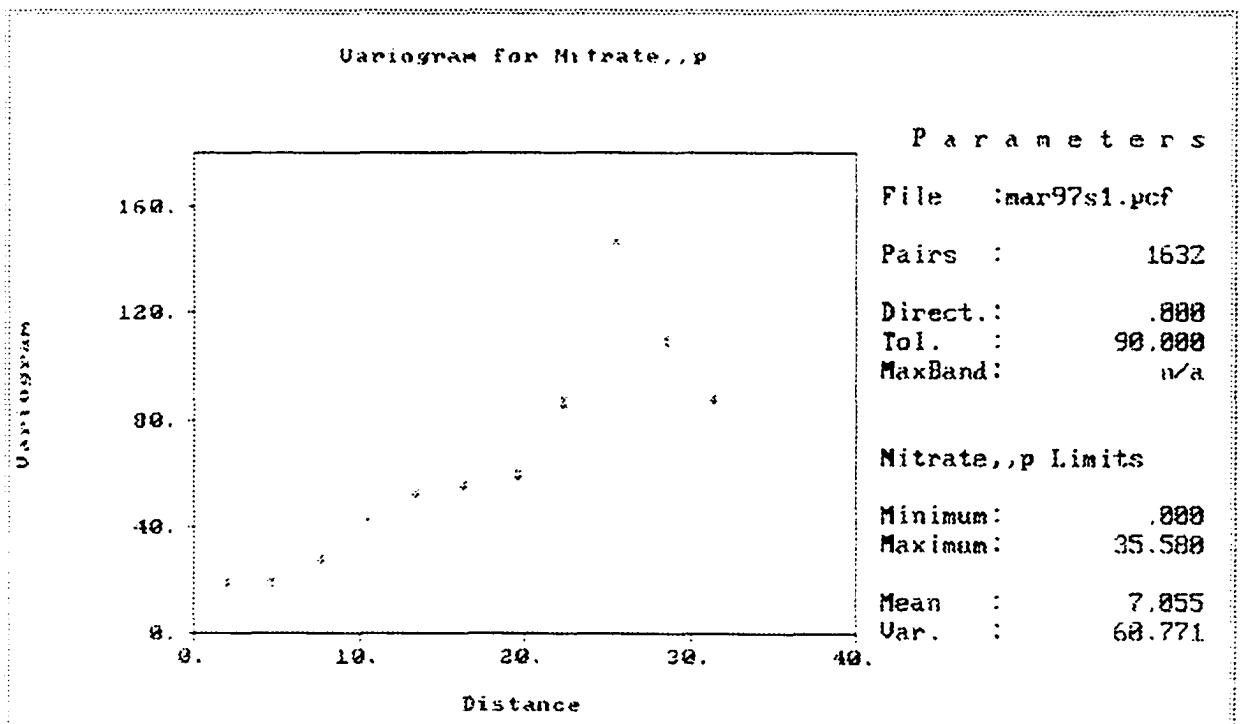
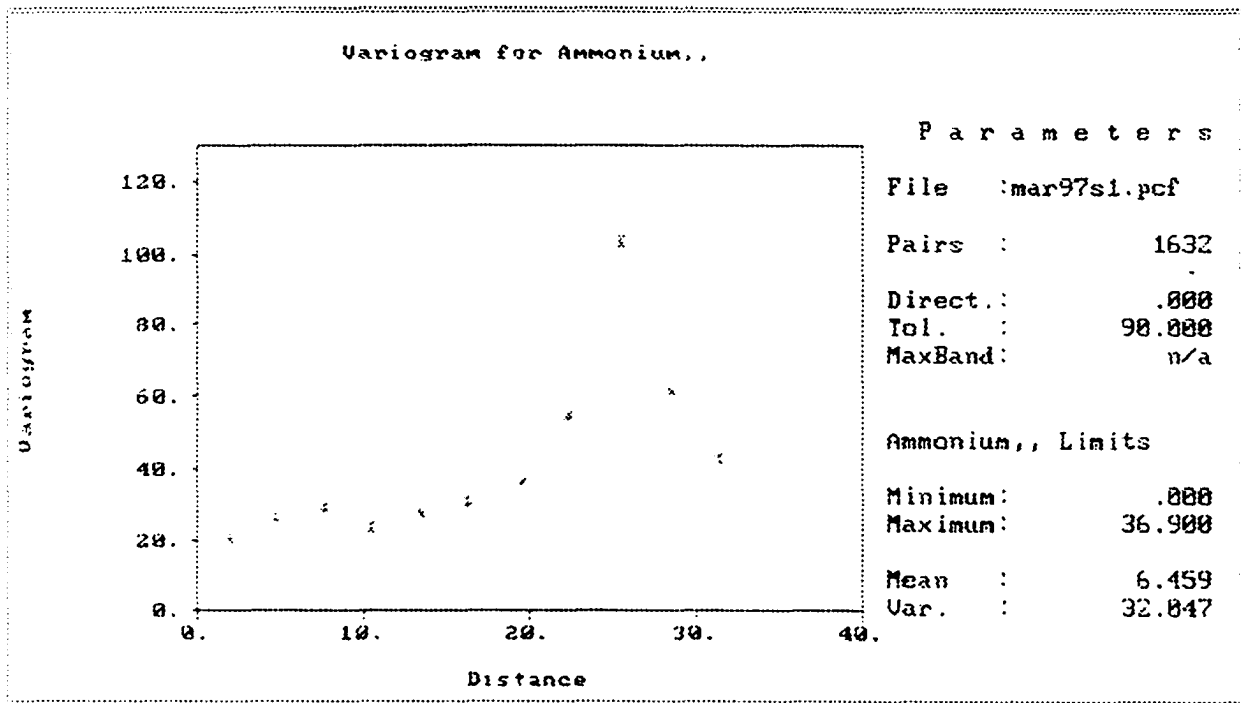


Figure 2. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site B, March, 1997.

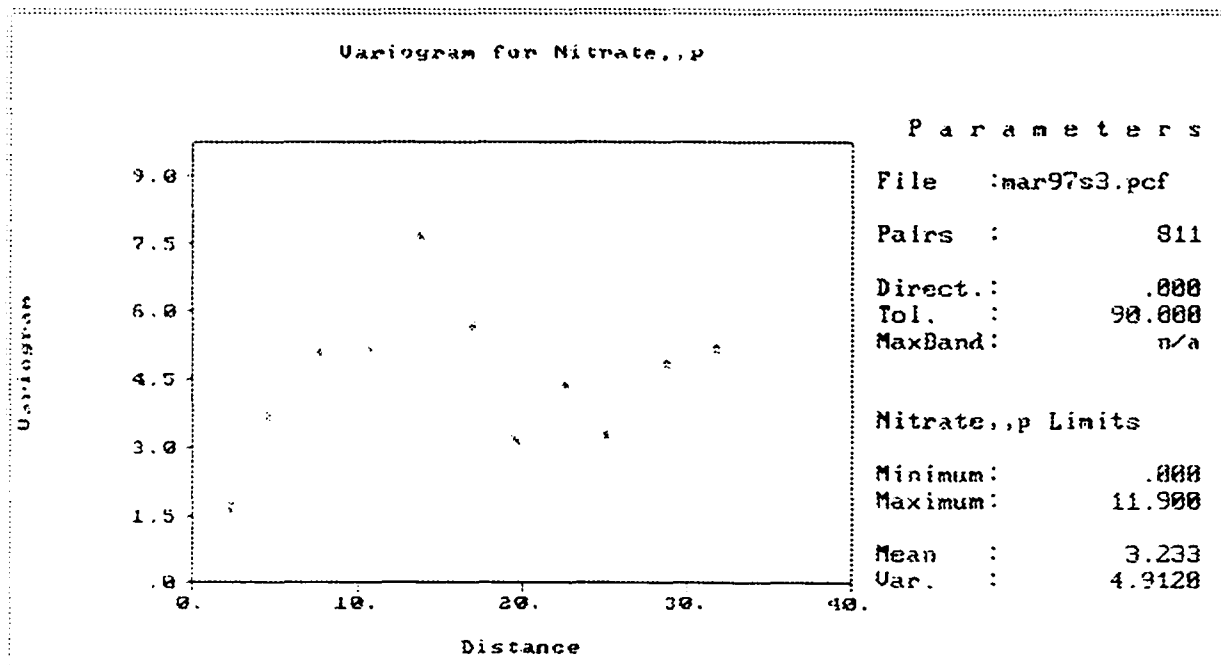
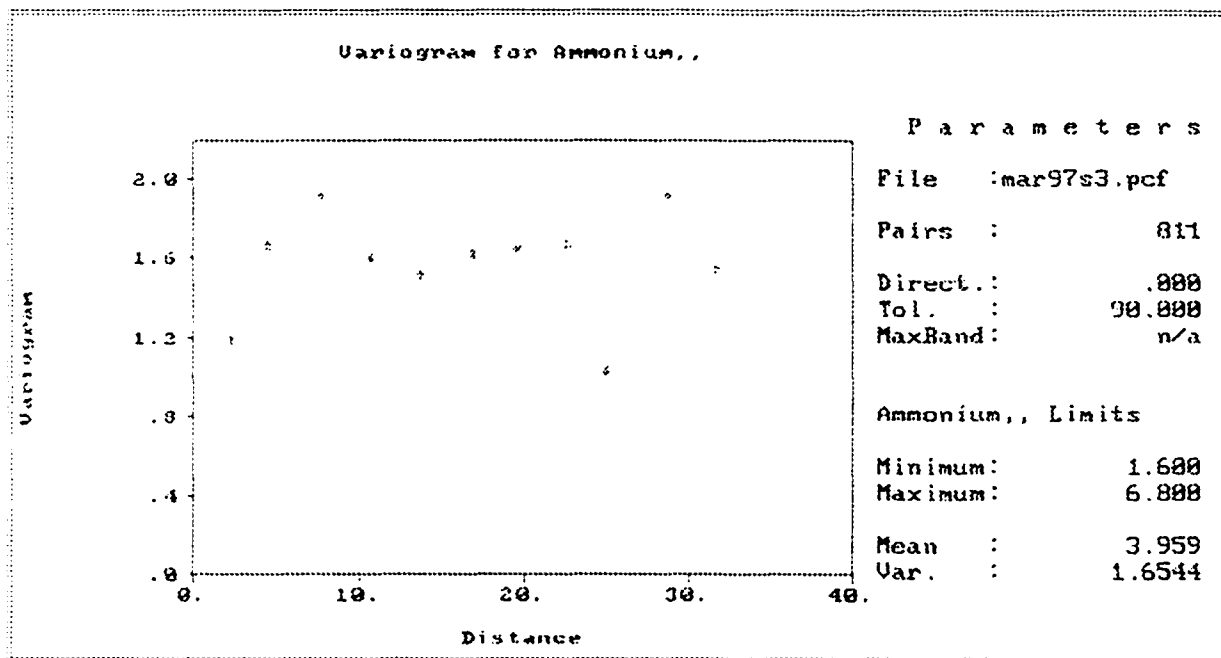


Figure 3. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site A, July, 1997.

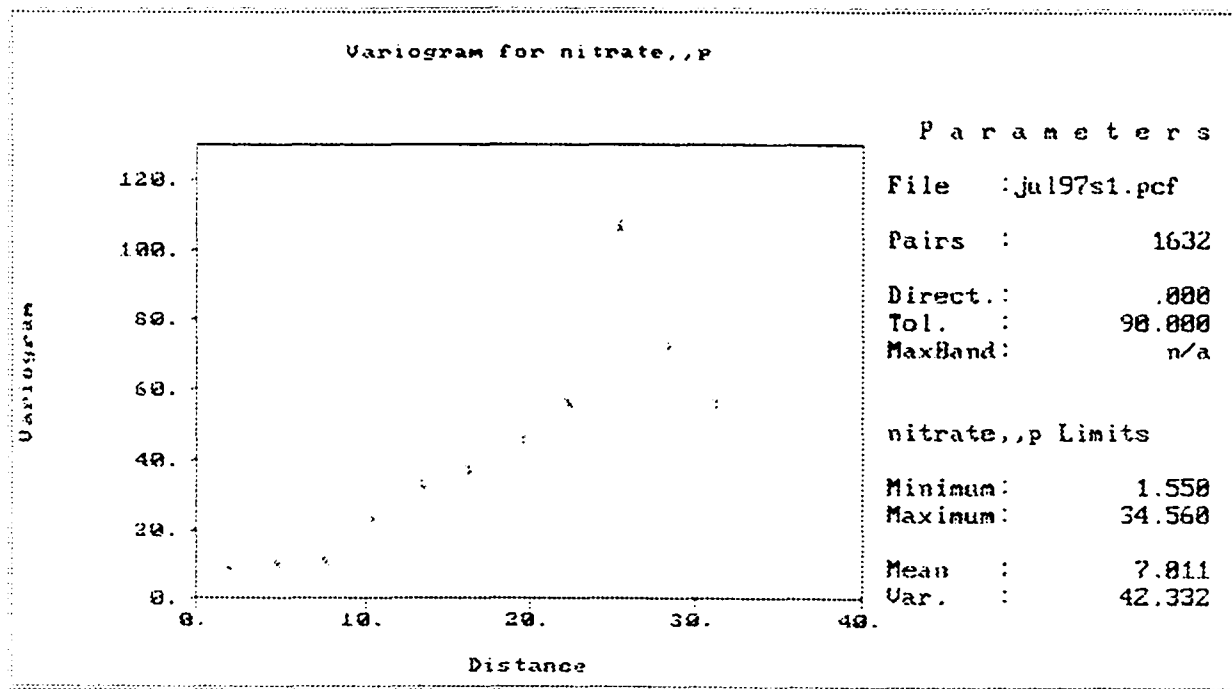
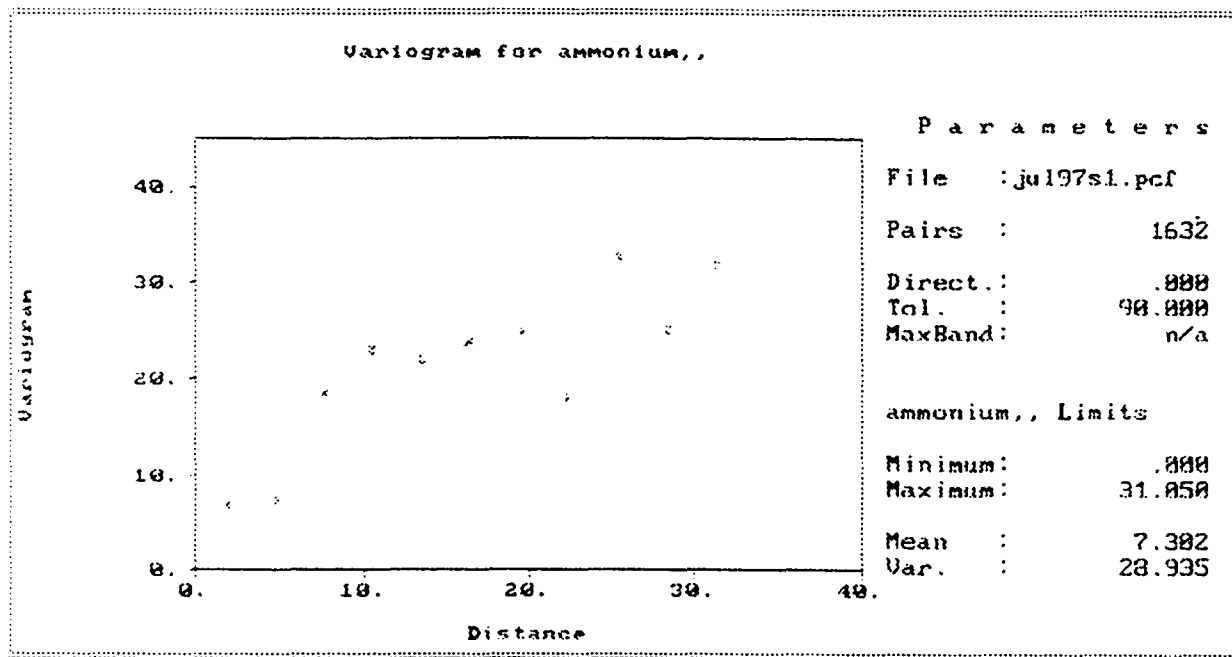


Figure 4. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site B, July, 1997.

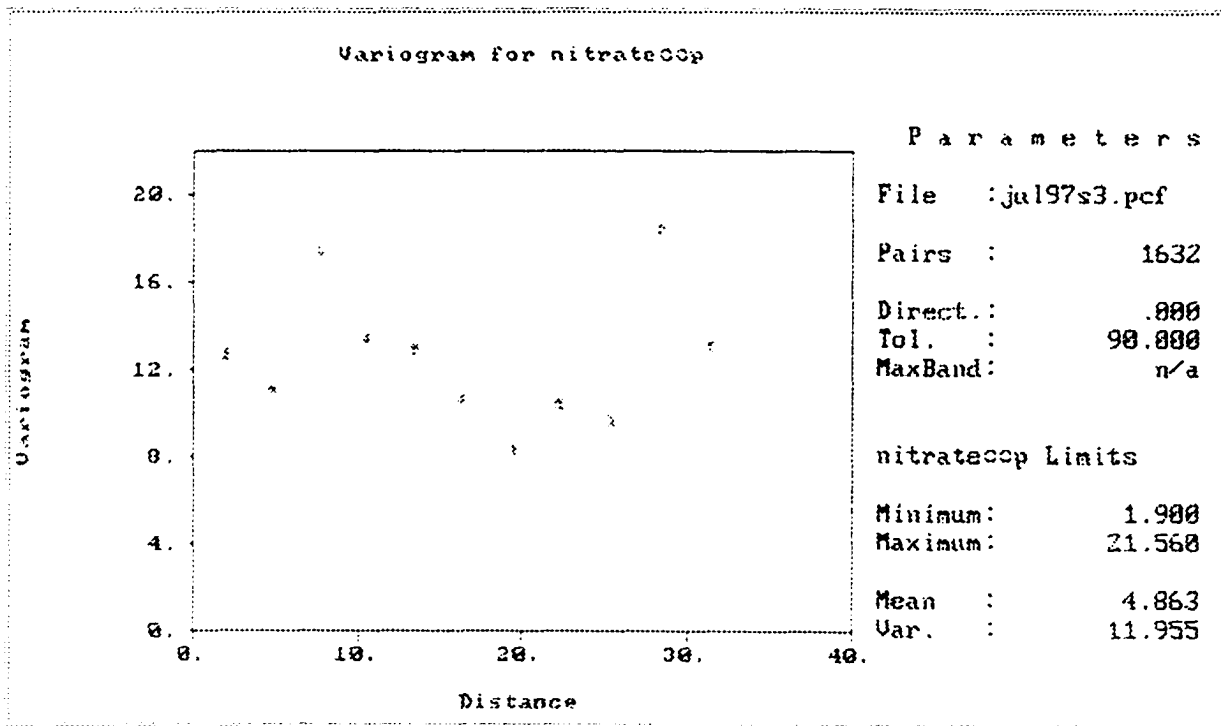
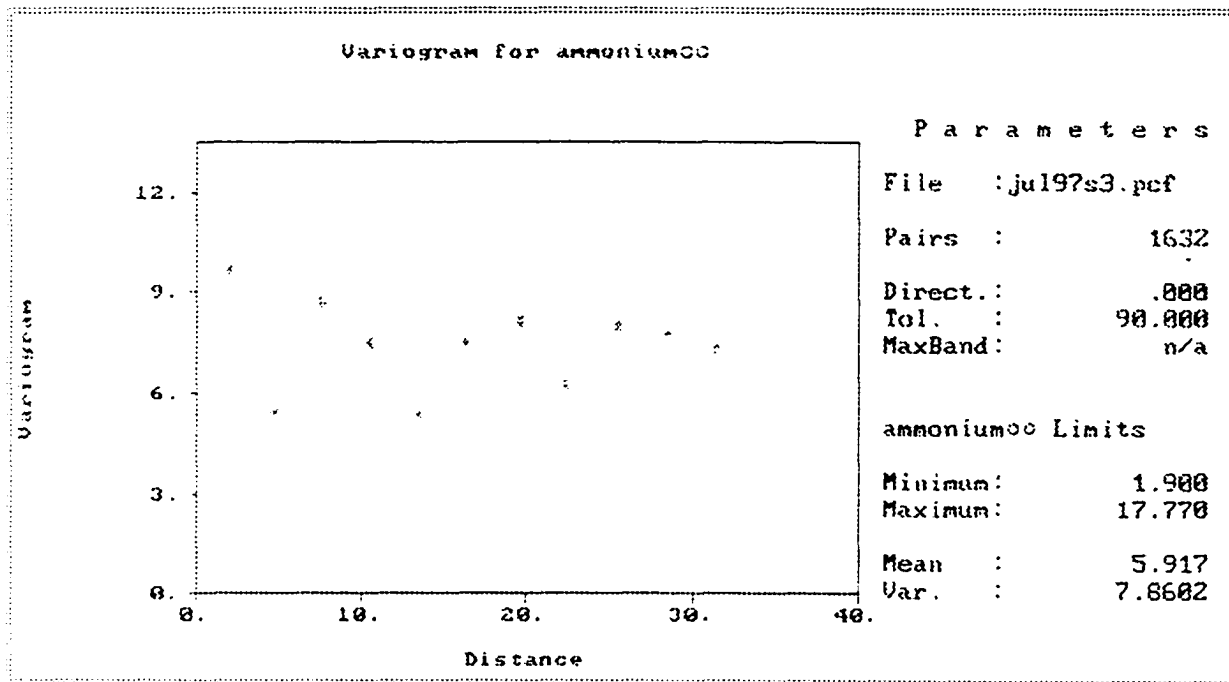


Figure 5. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site A, October, 1997.

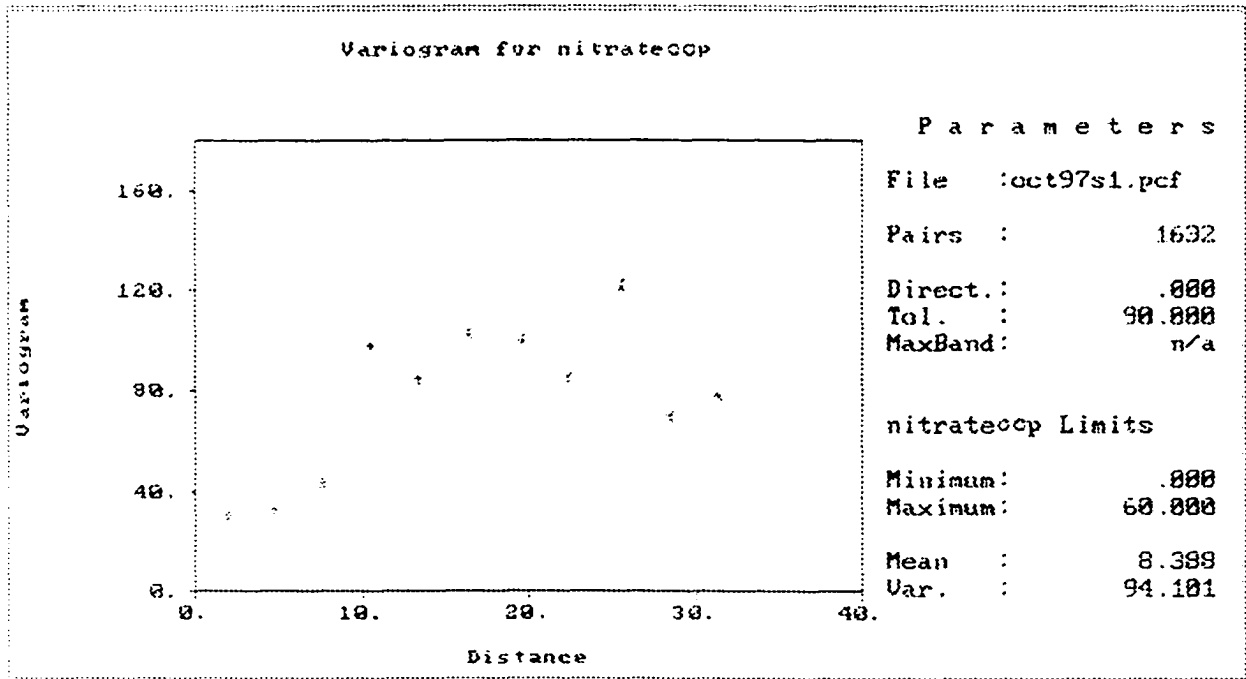
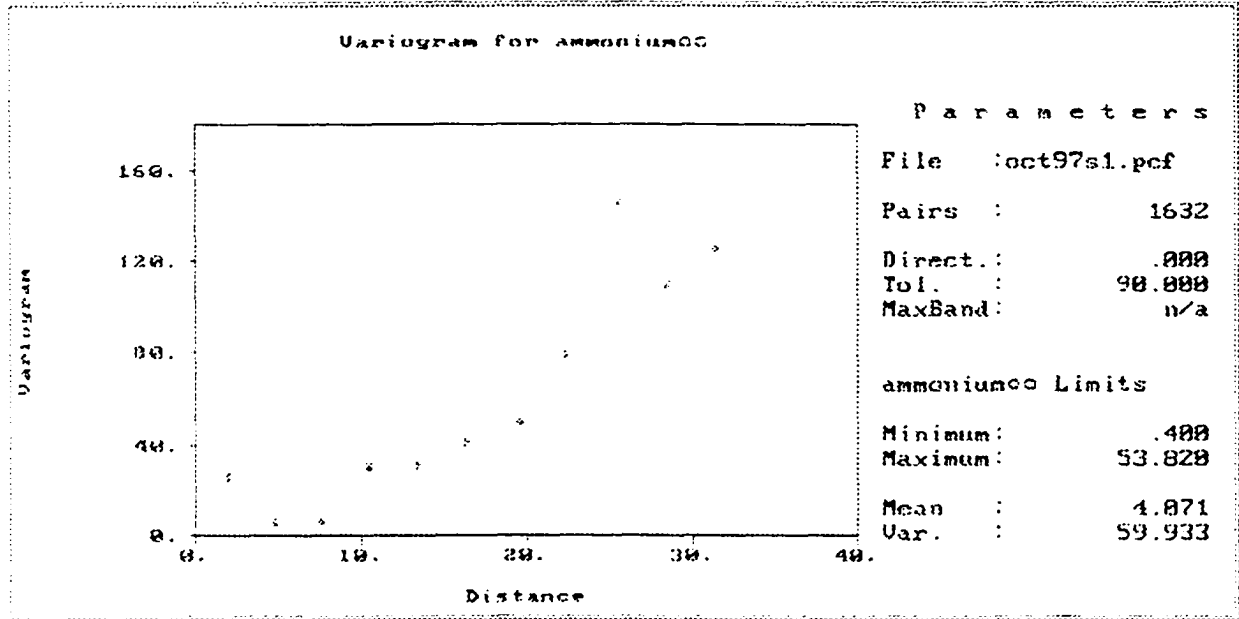


Figure 6. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site B, October, 1997.

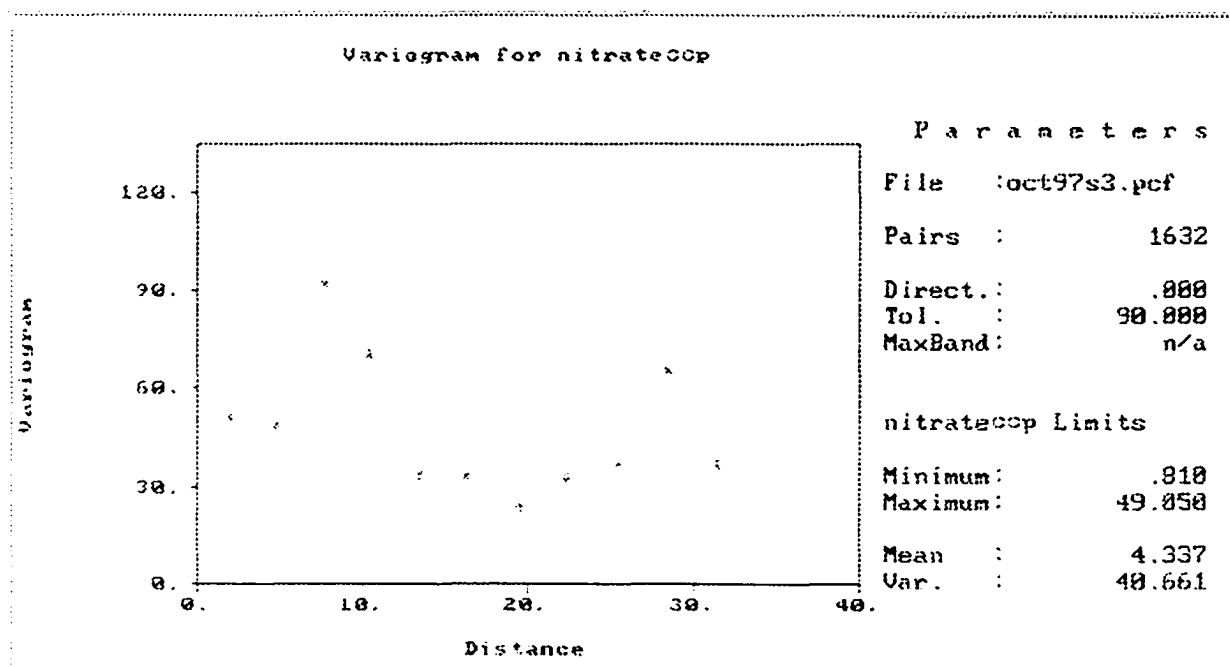
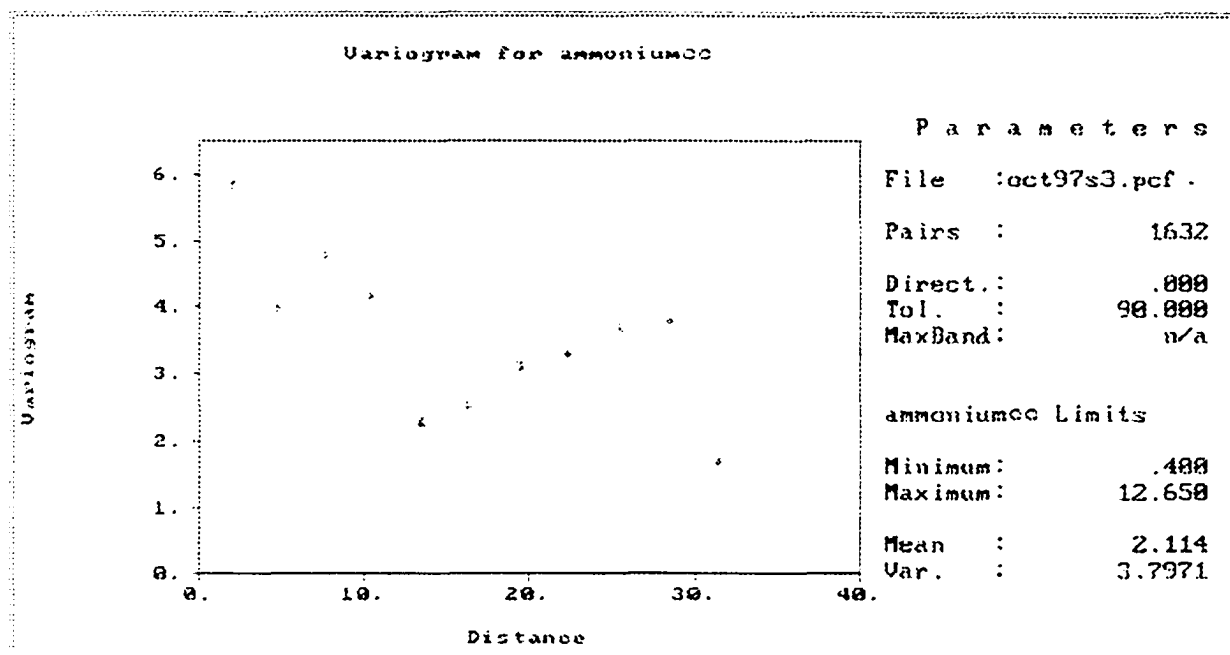


Figure 7. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site A, January, 1998.

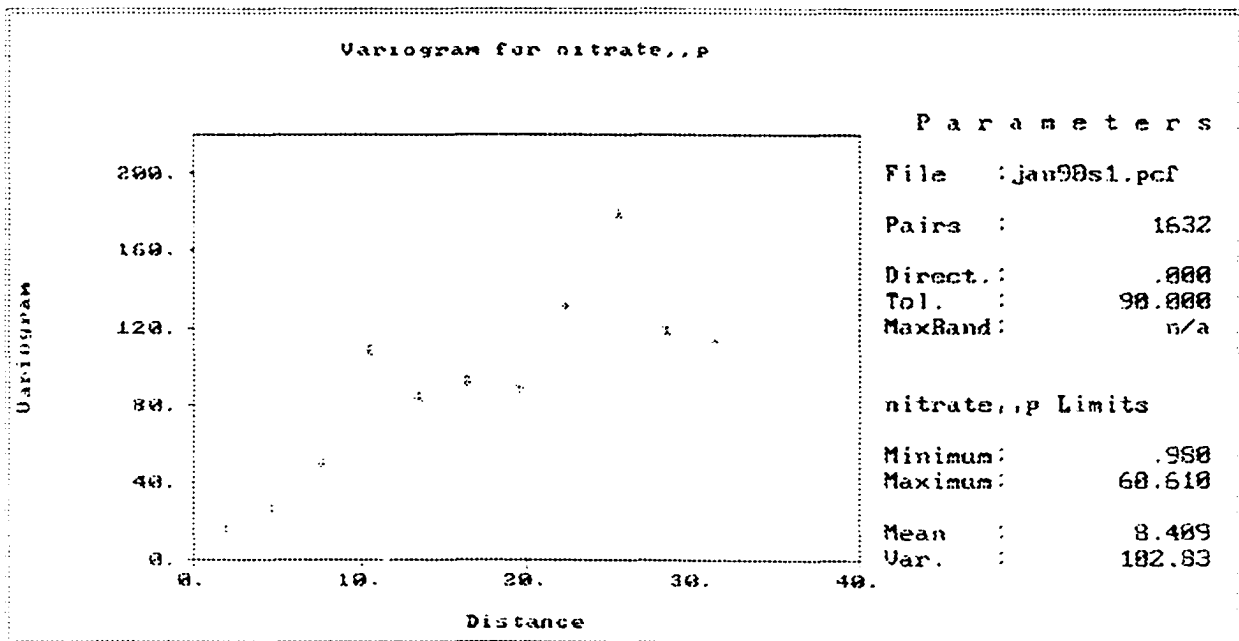
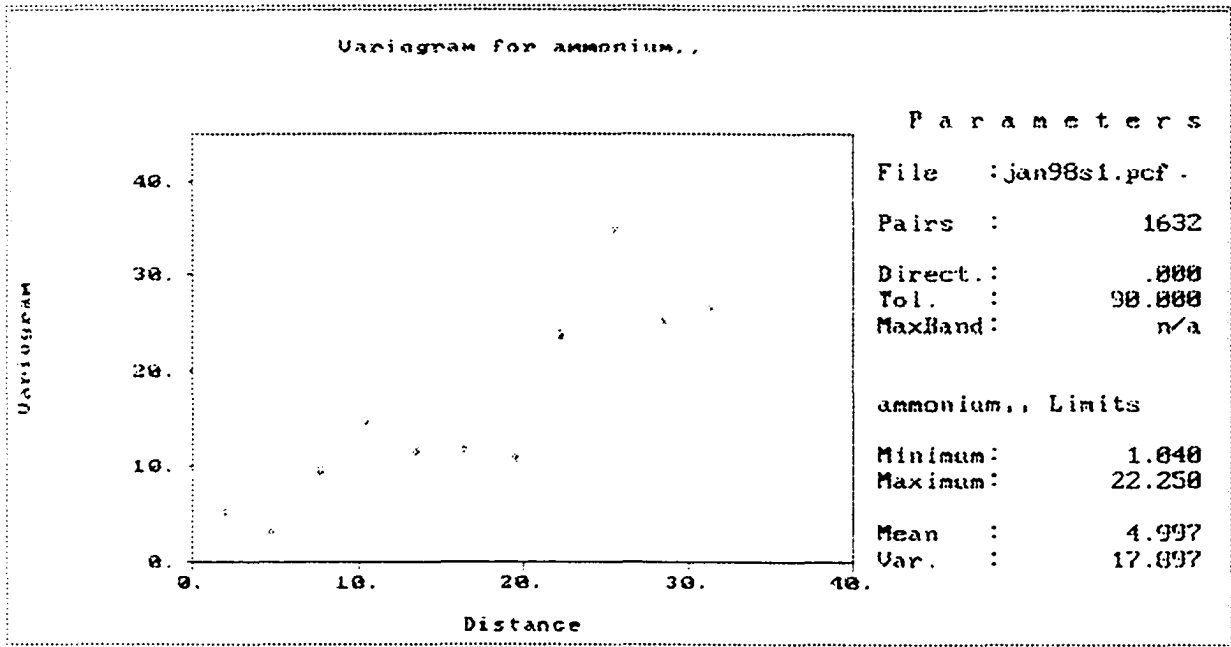


Figure 8. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site B, January, 1998.

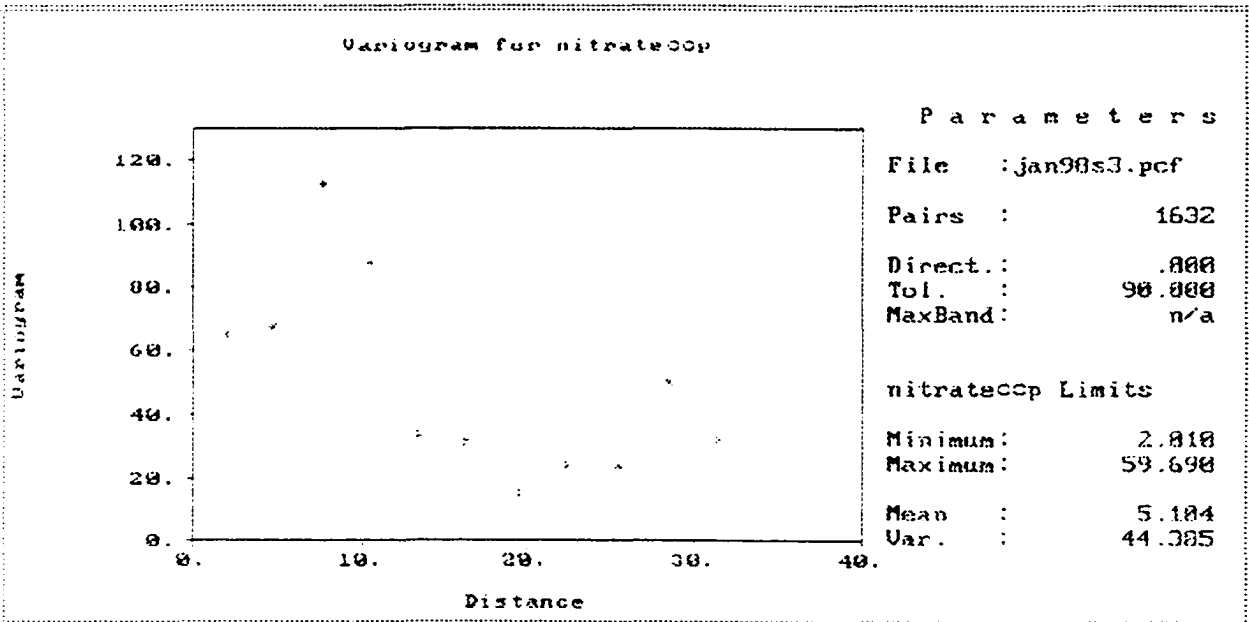
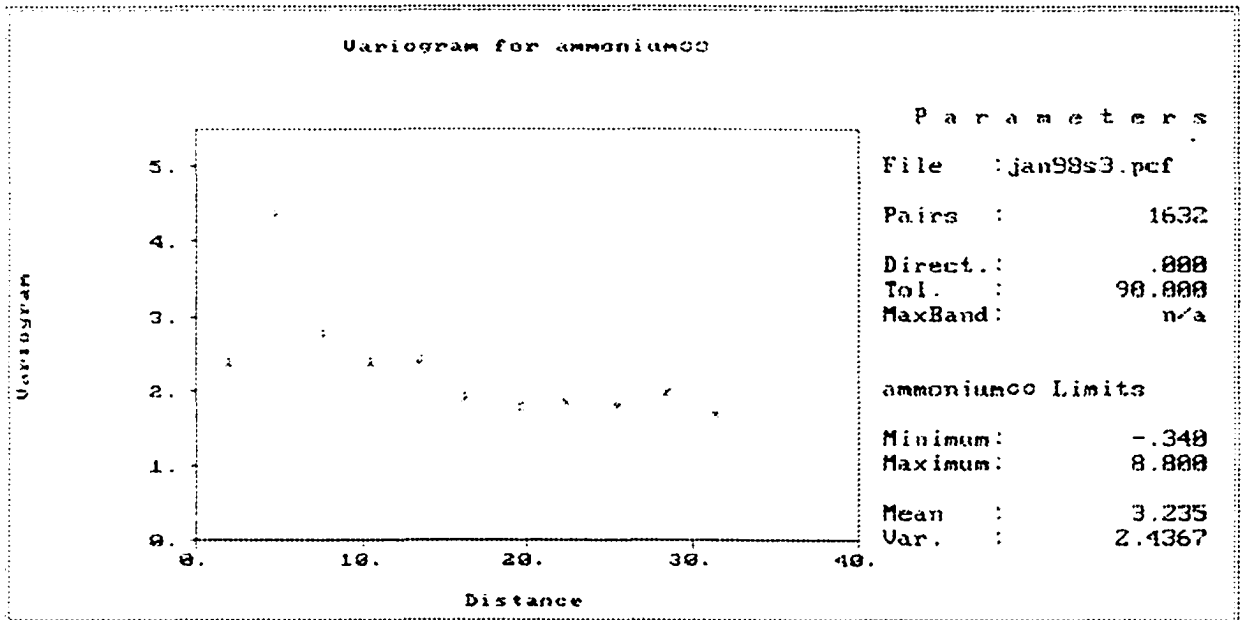


Figure 9. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site A, March, 1998.

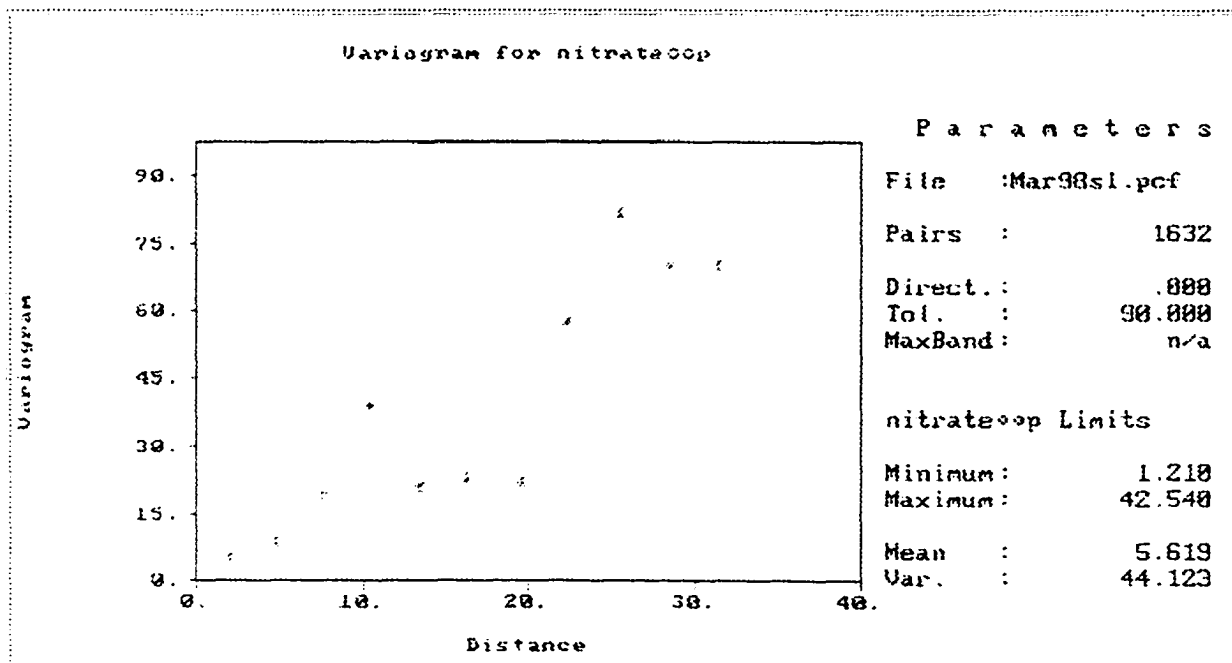
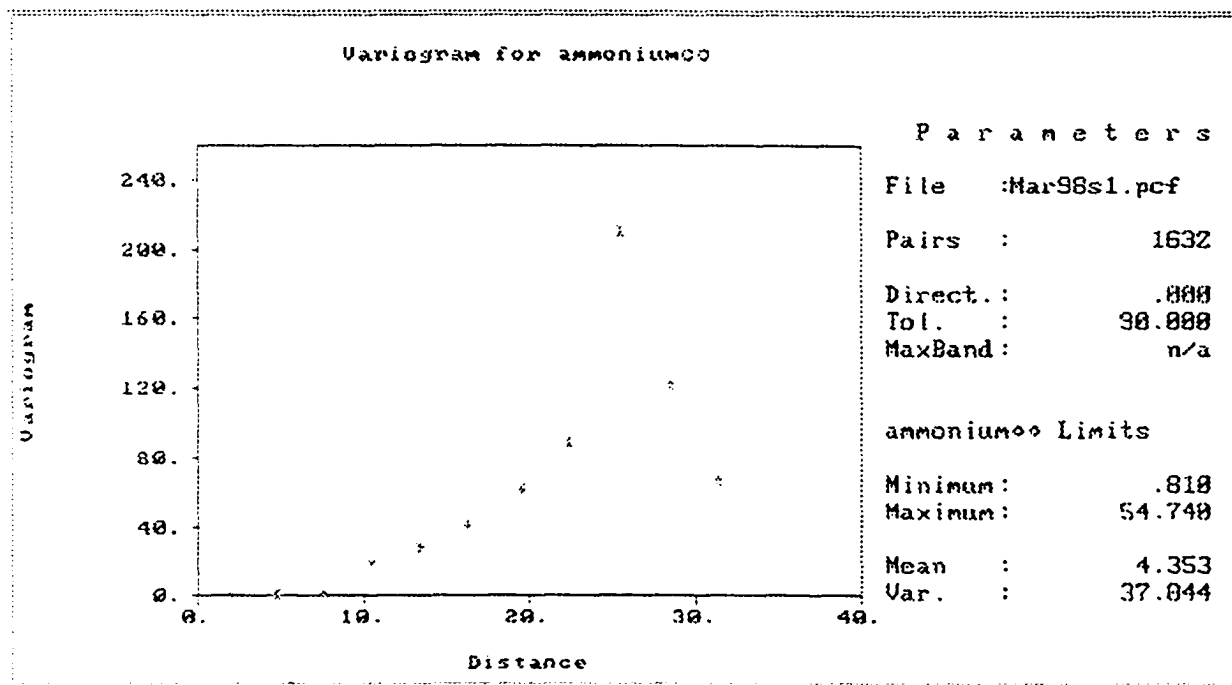


Figure 10. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site B, March, 1998.

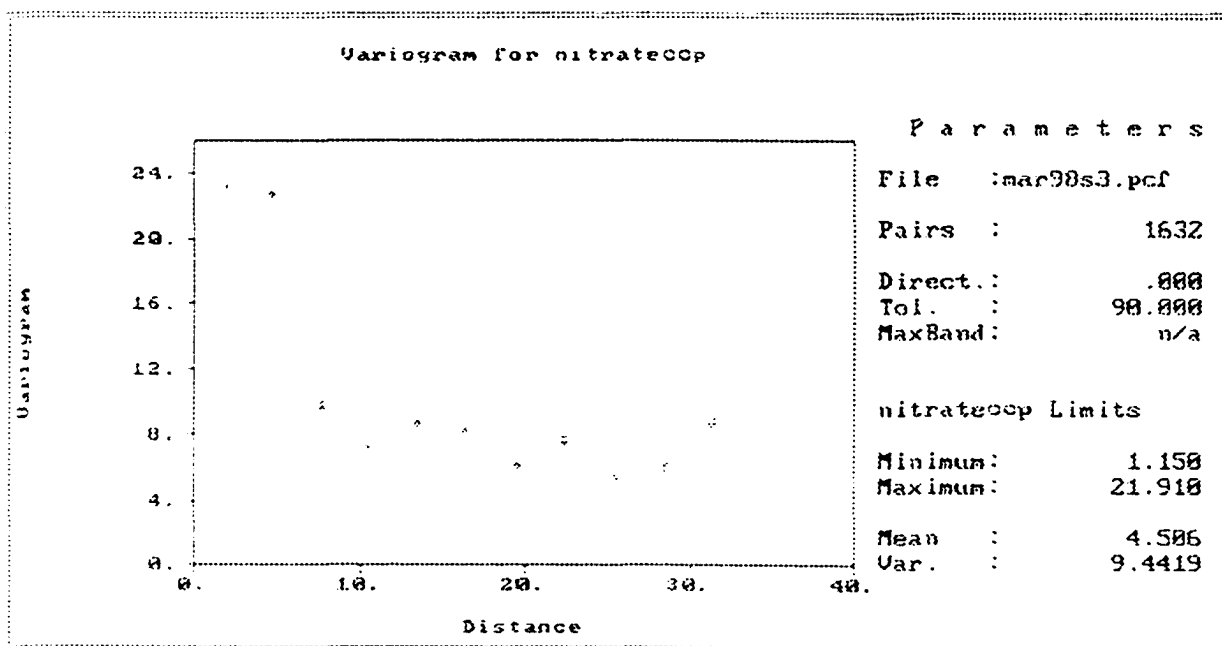
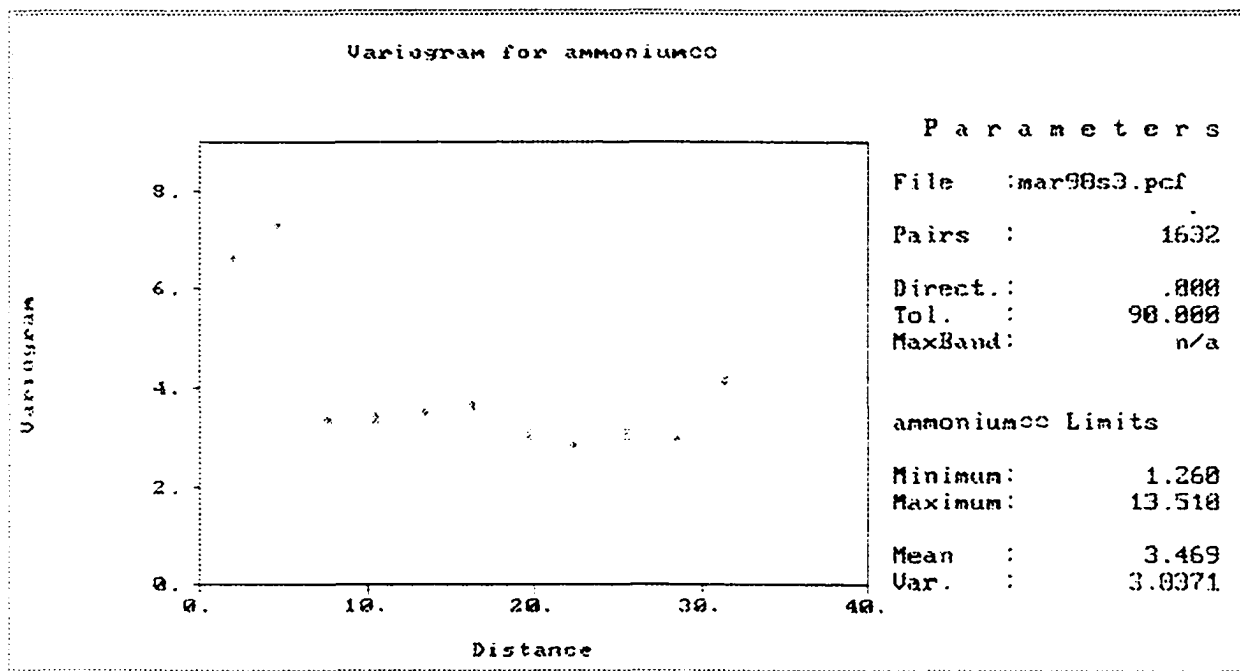


Figure 11. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site A, July, 1998.

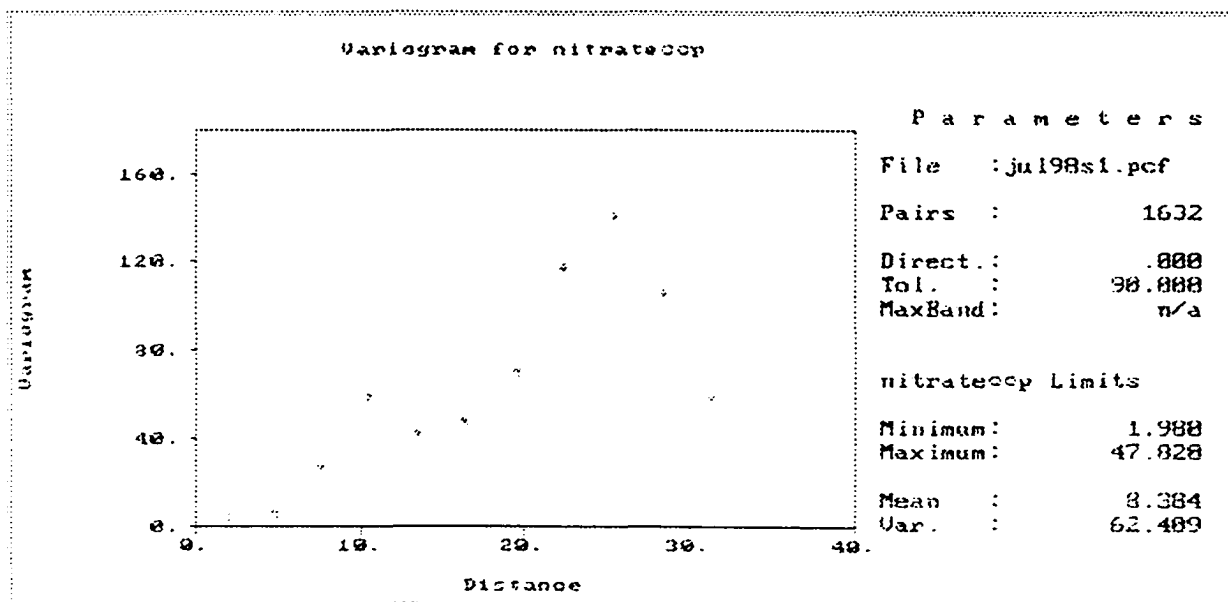
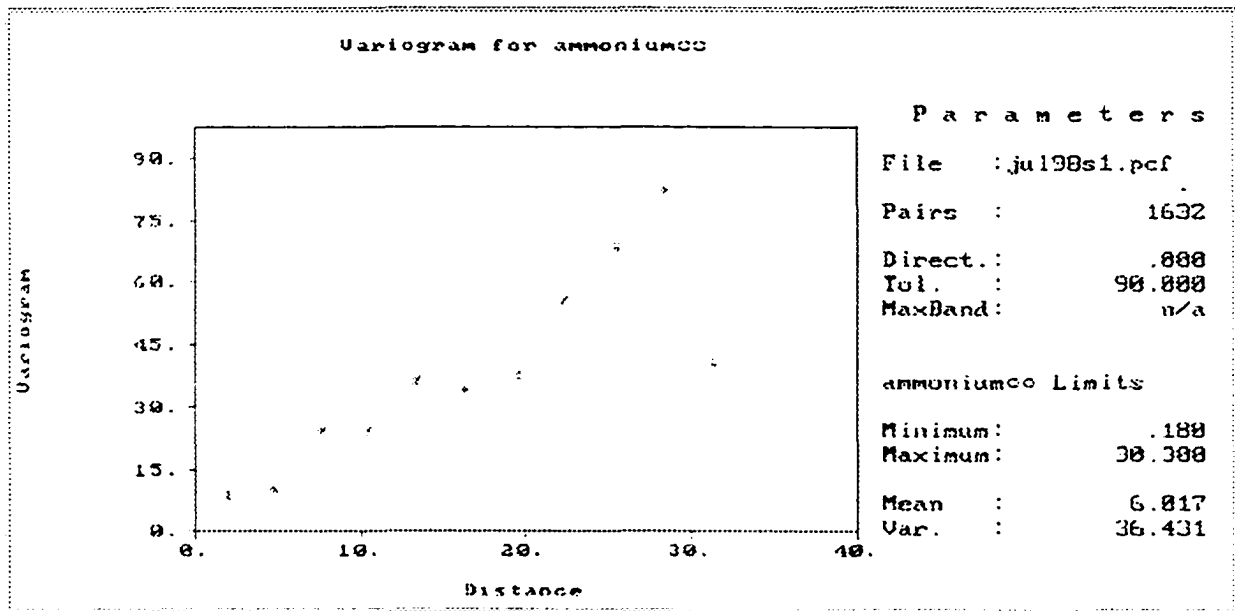


Figure 12. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site B, July, 1998.

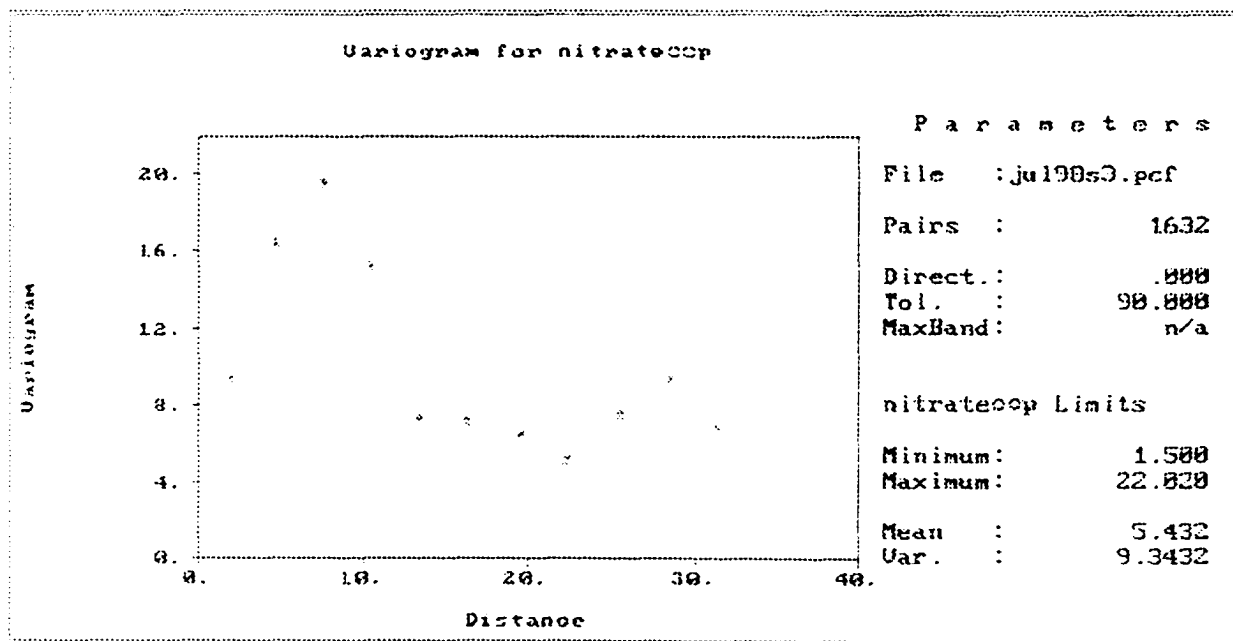
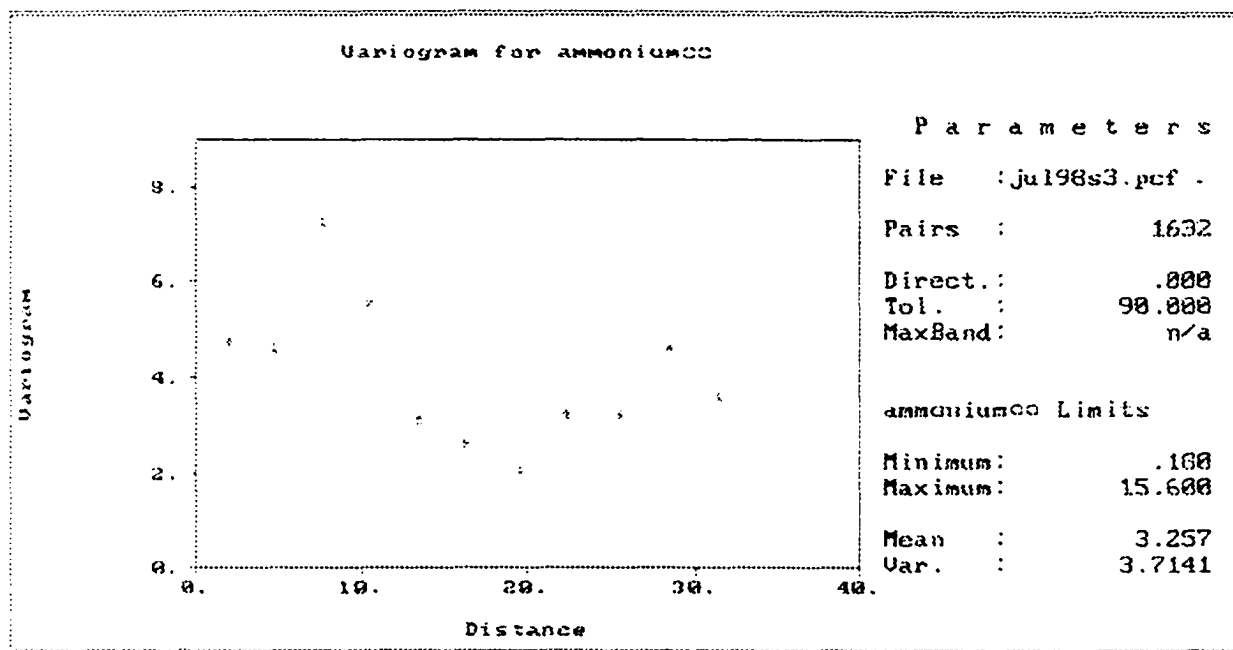


Figure 13. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site A, October, 1998.

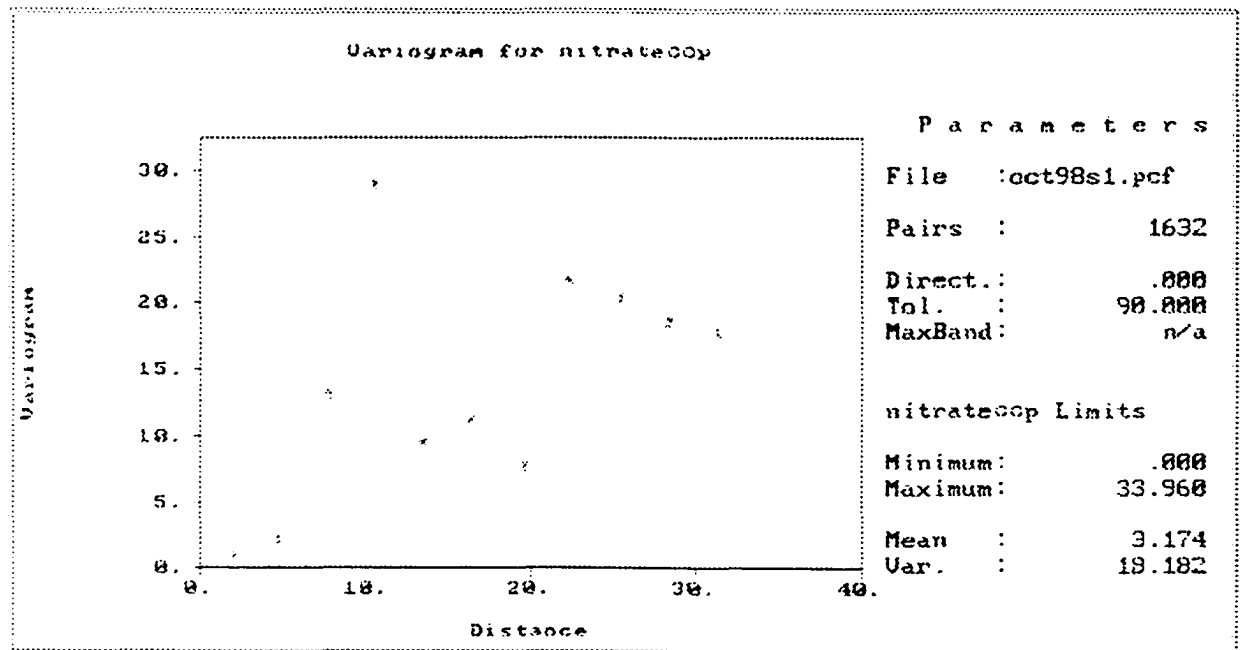
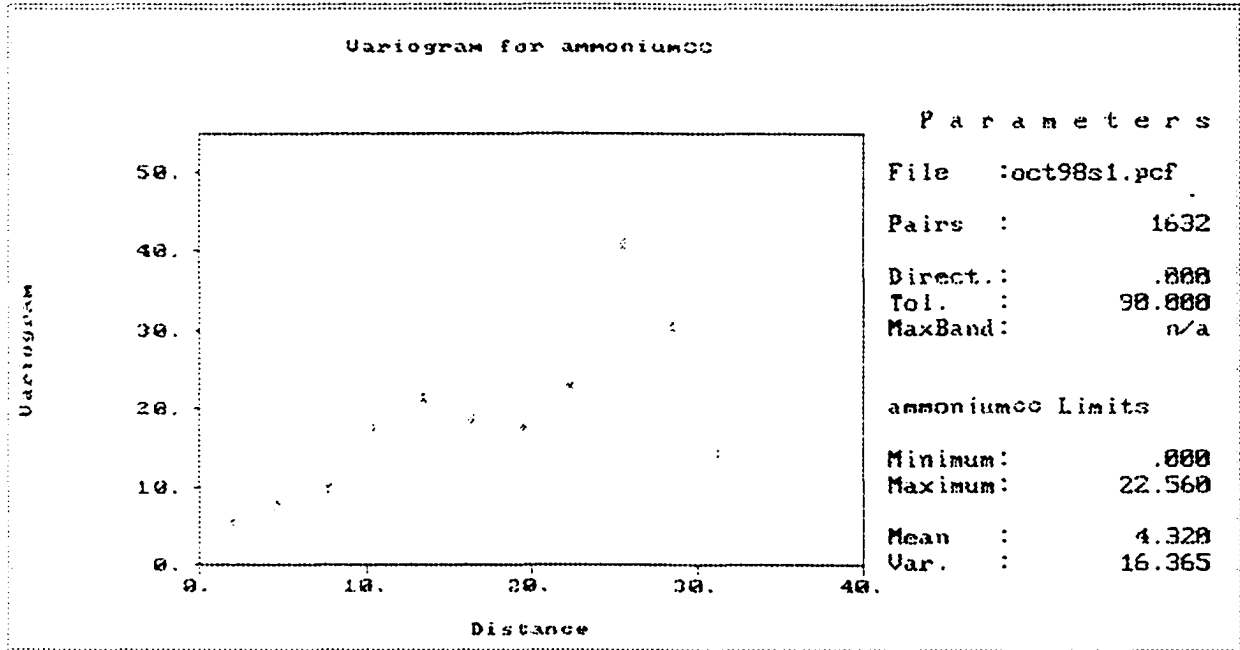


Figure 14. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site B. October, 1998.

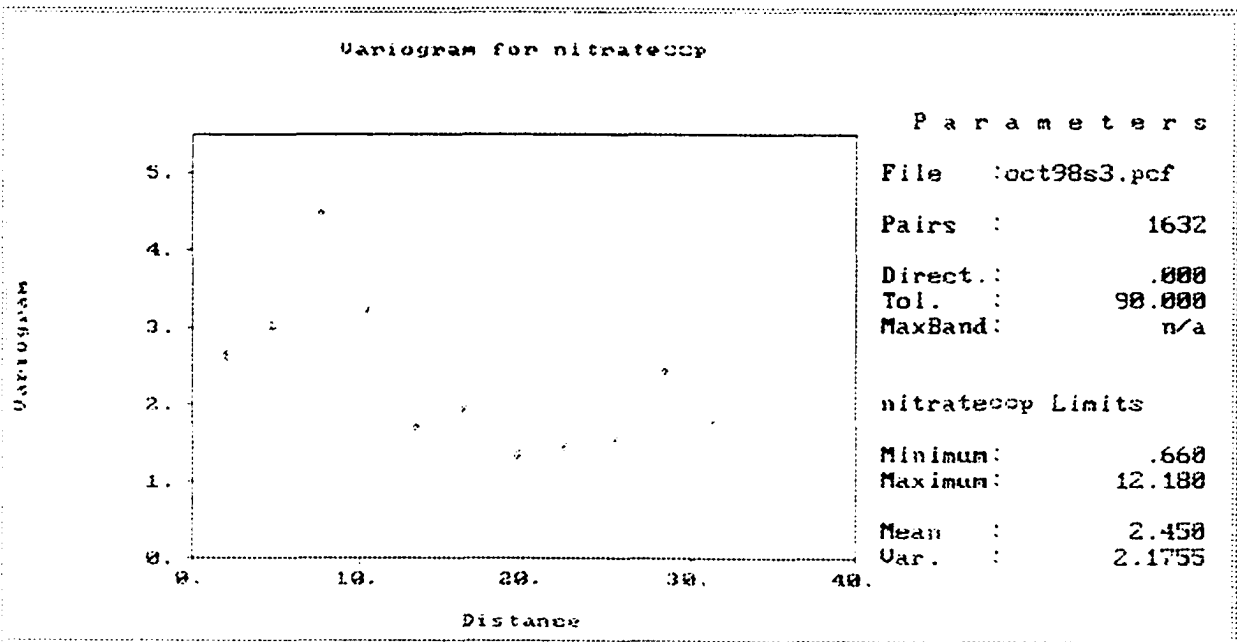
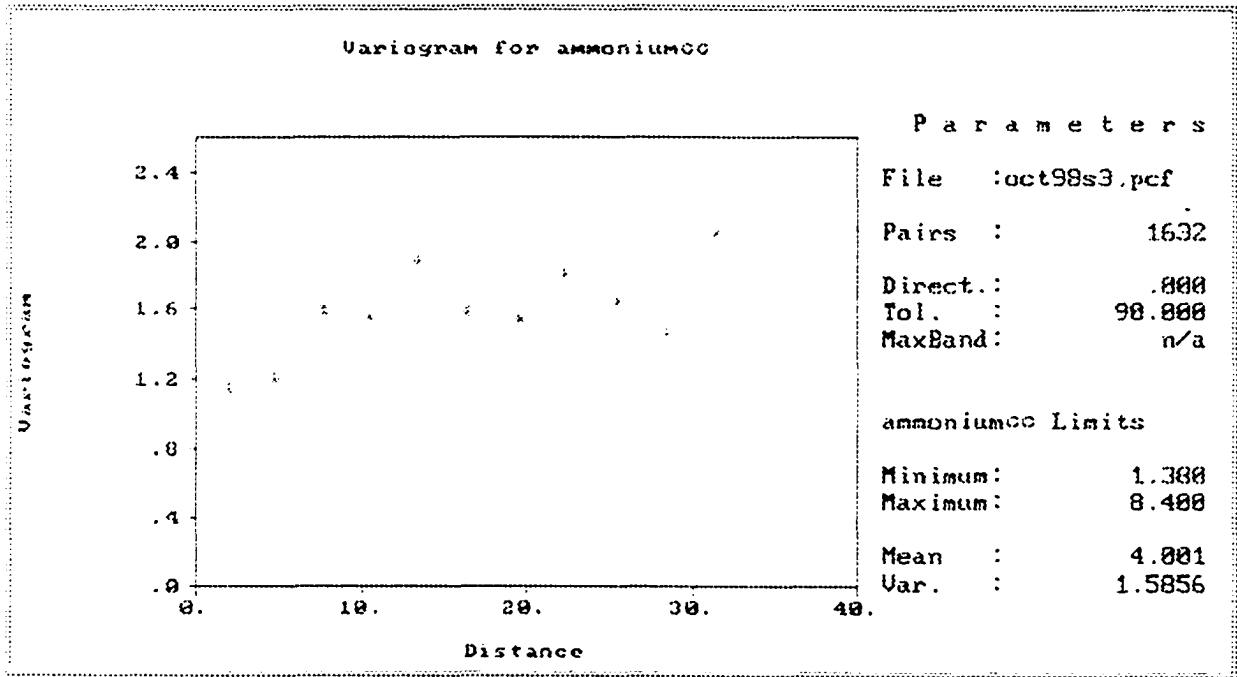


Figure 15. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site A, January, 1999.

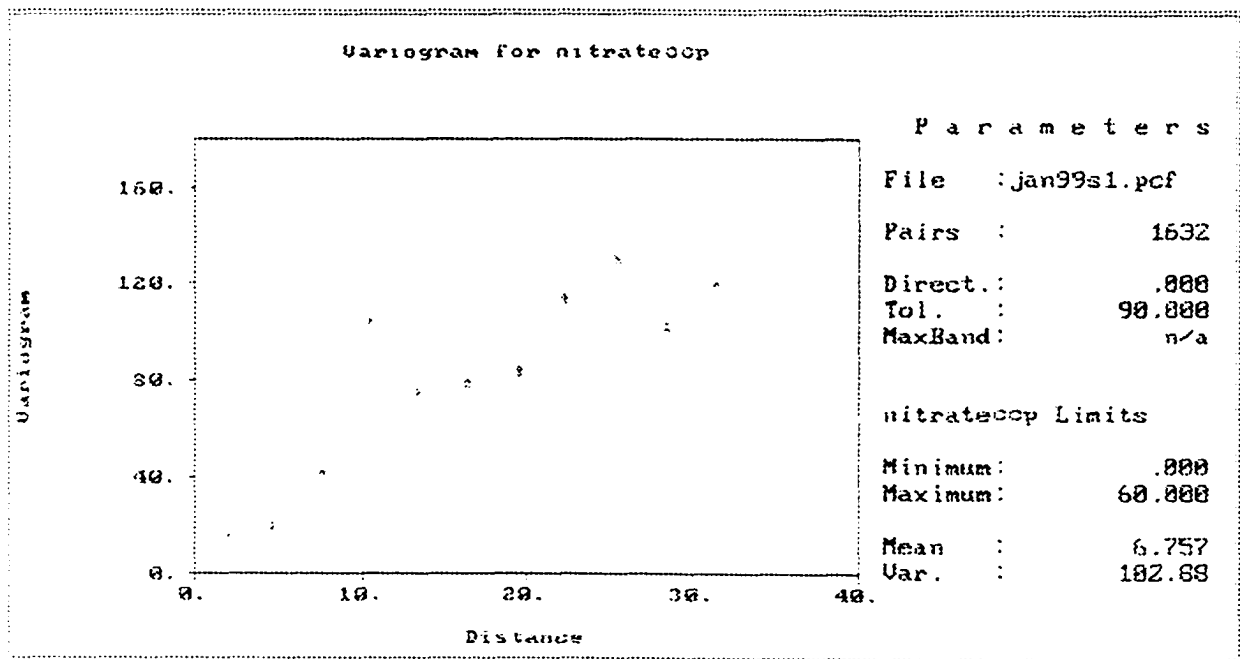
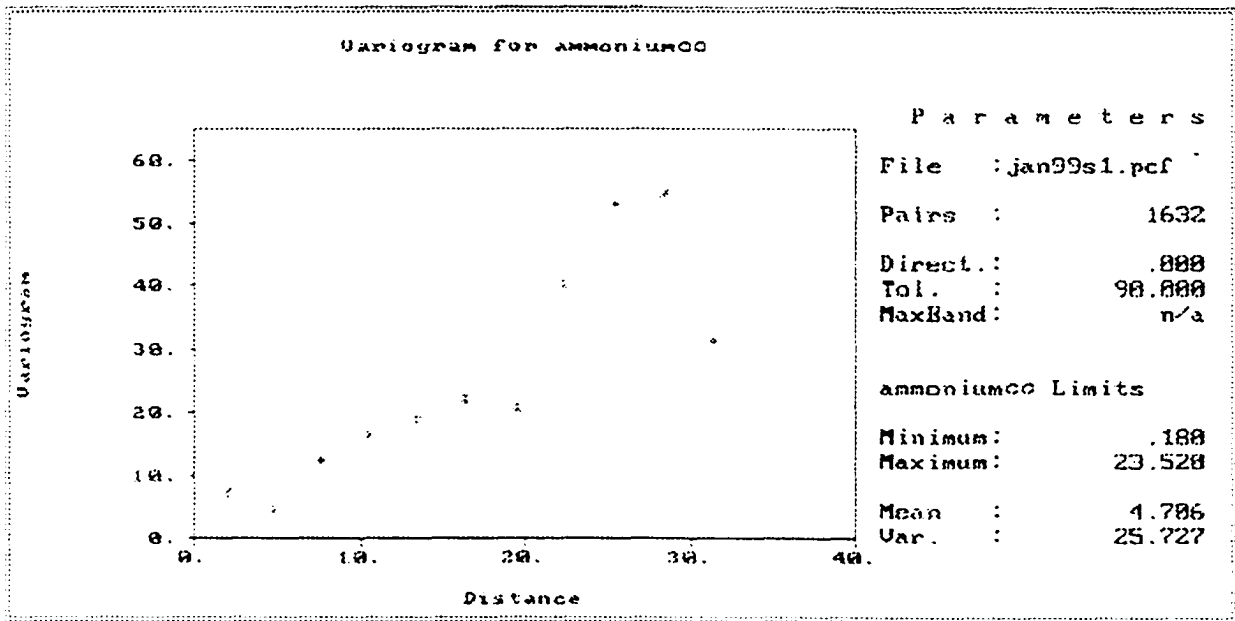


Figure 16. Semi-variograms of soil ammonium (top) and nitrate (bottom) for Site B, January, 1999.

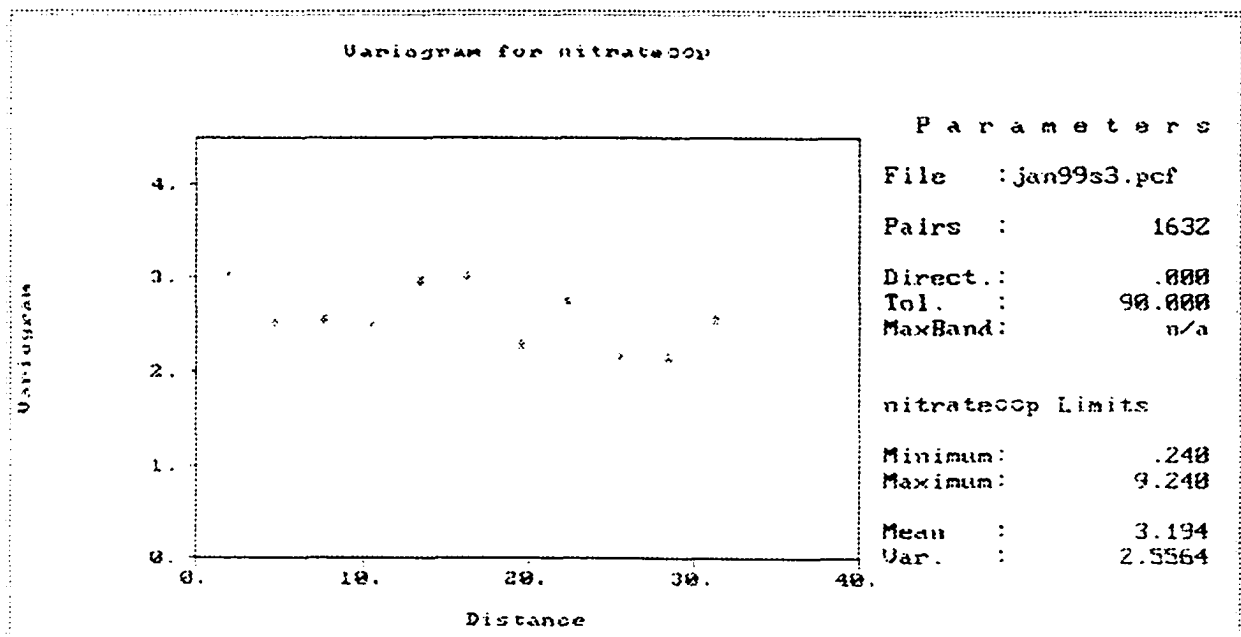
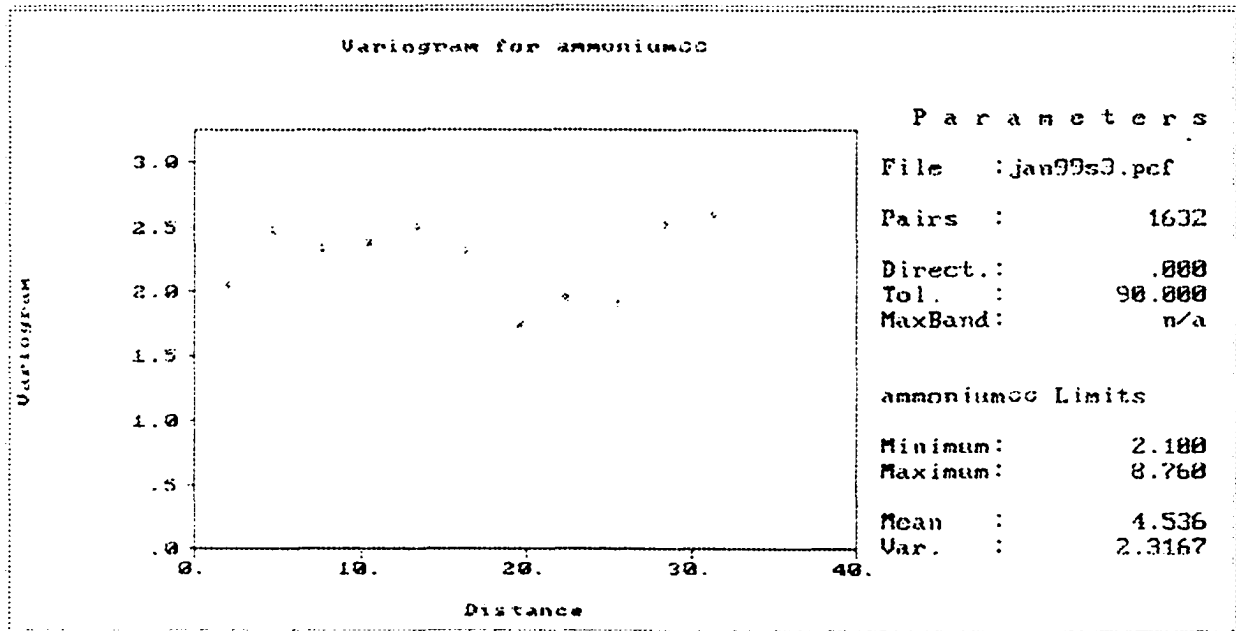


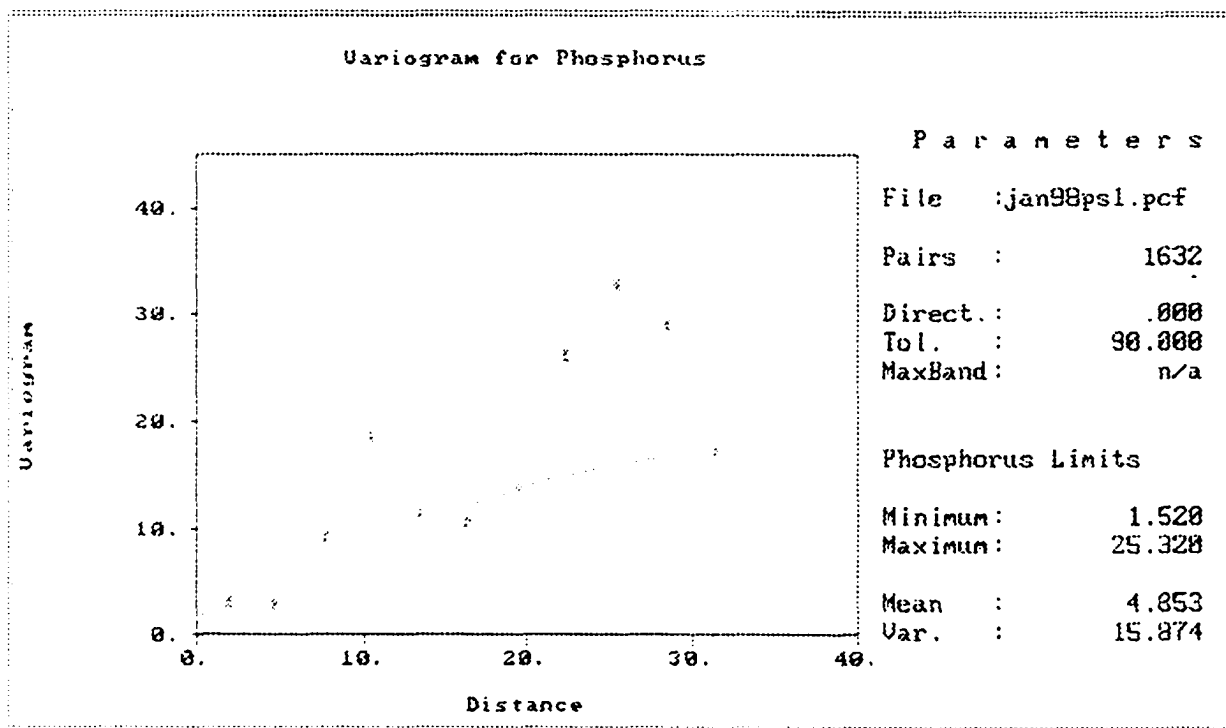
Figure 17. Semi-variogram with a spherical model fitted of soil PO_4^{3-} for Site A, January, 1998.

Figure 18. Semi-variogram with an exponential model fitted of soil PO_4^{3-} for Site B, January, 1998.

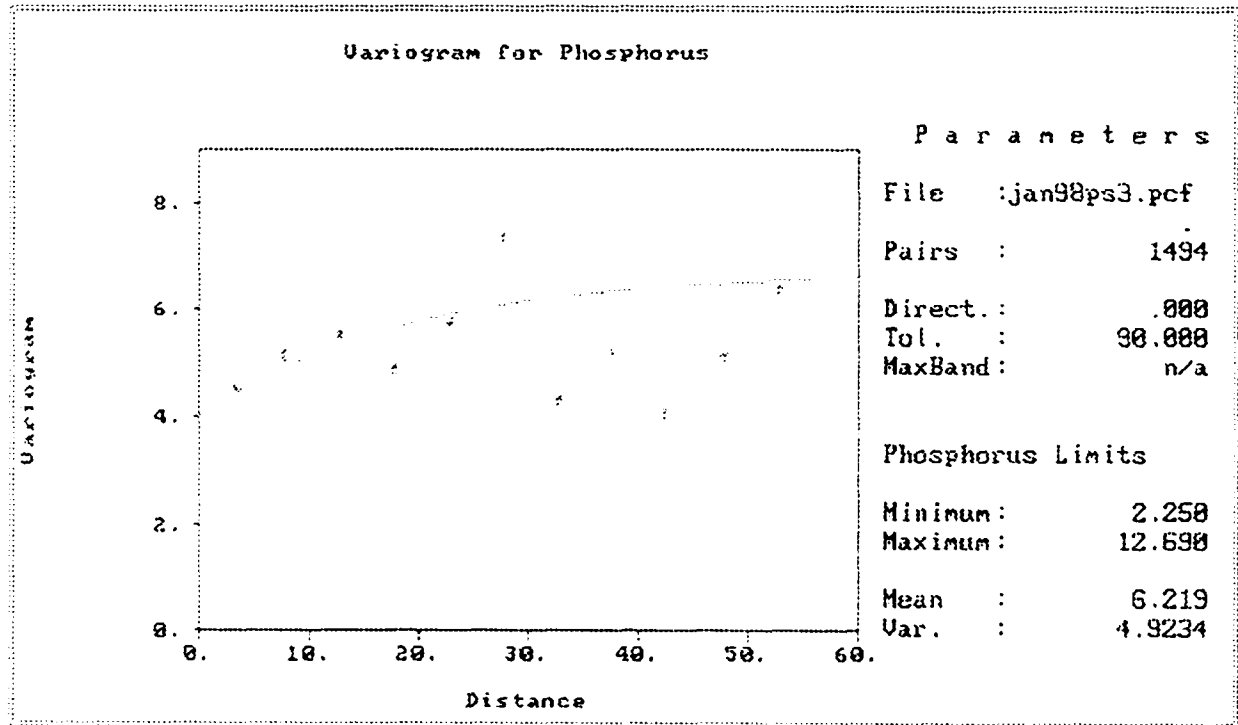


Figure 19. Semi-variograms with a linear model fitted of soil total N (top) and total organic C (bottom) for Site A, January, 1998.

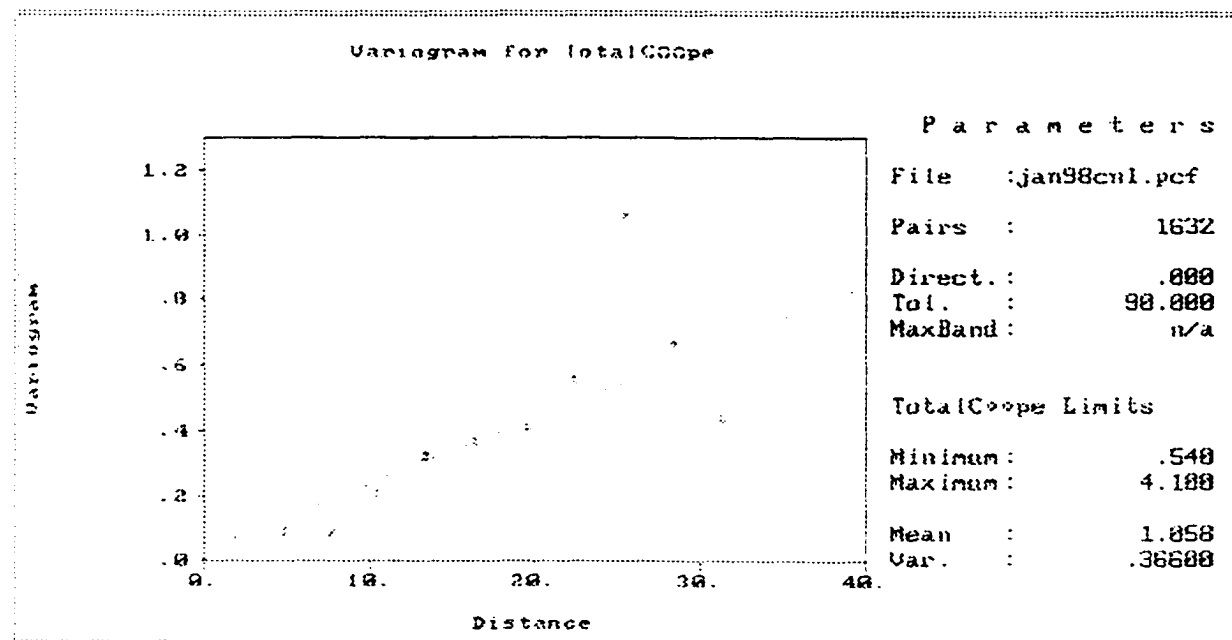
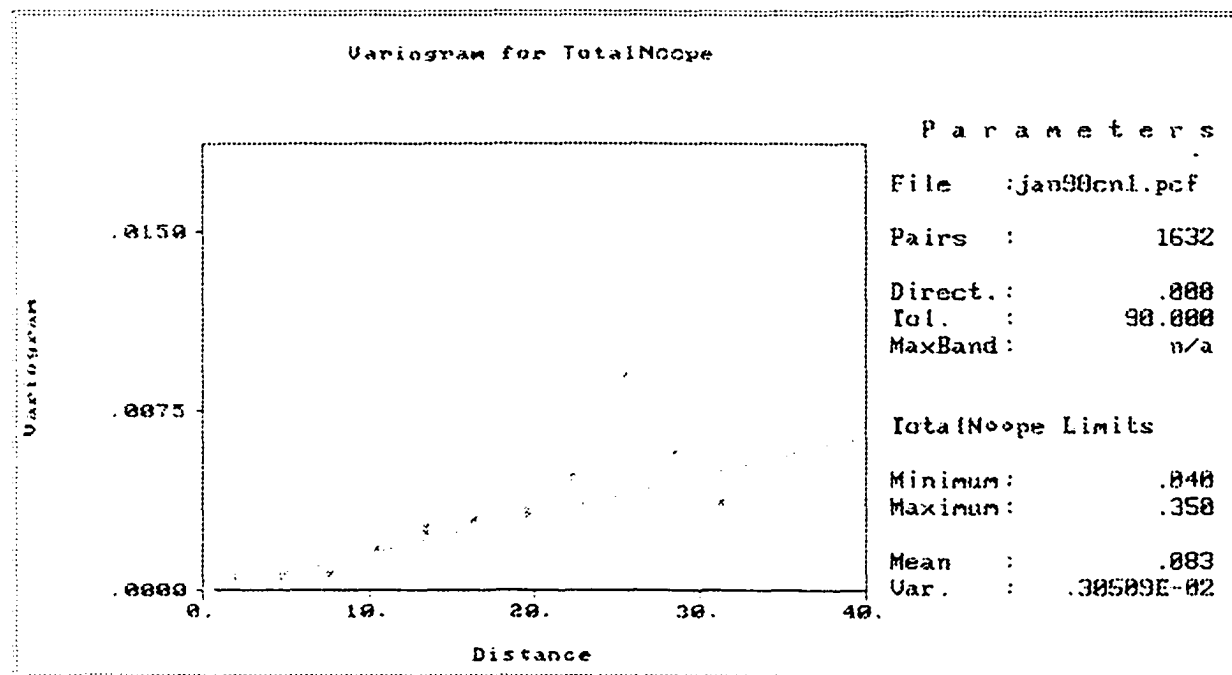
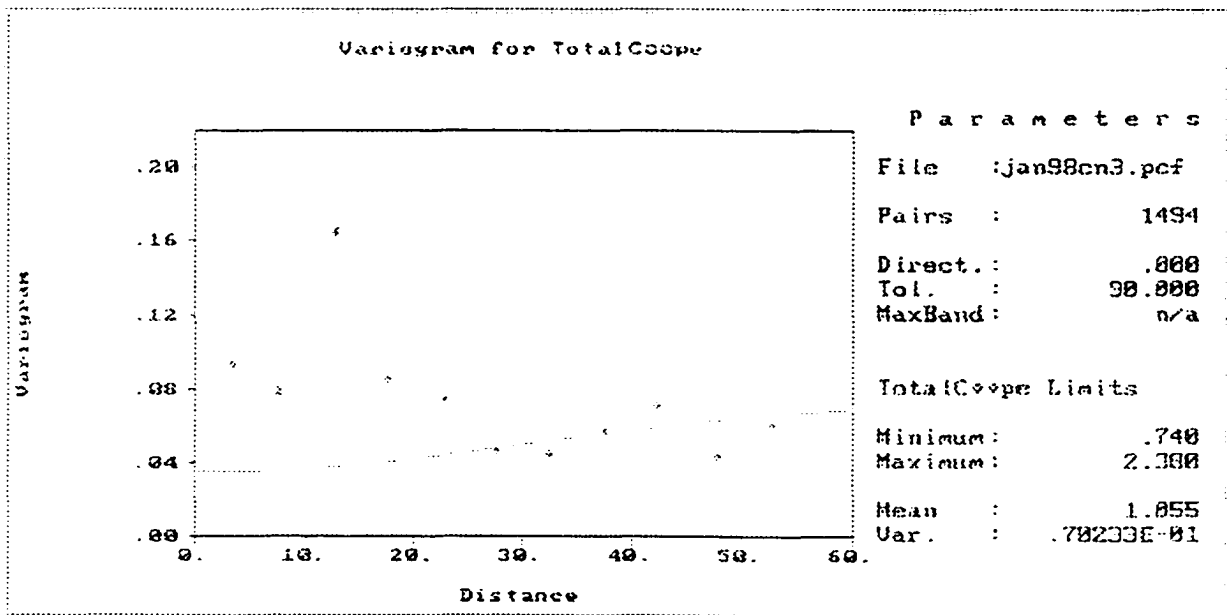
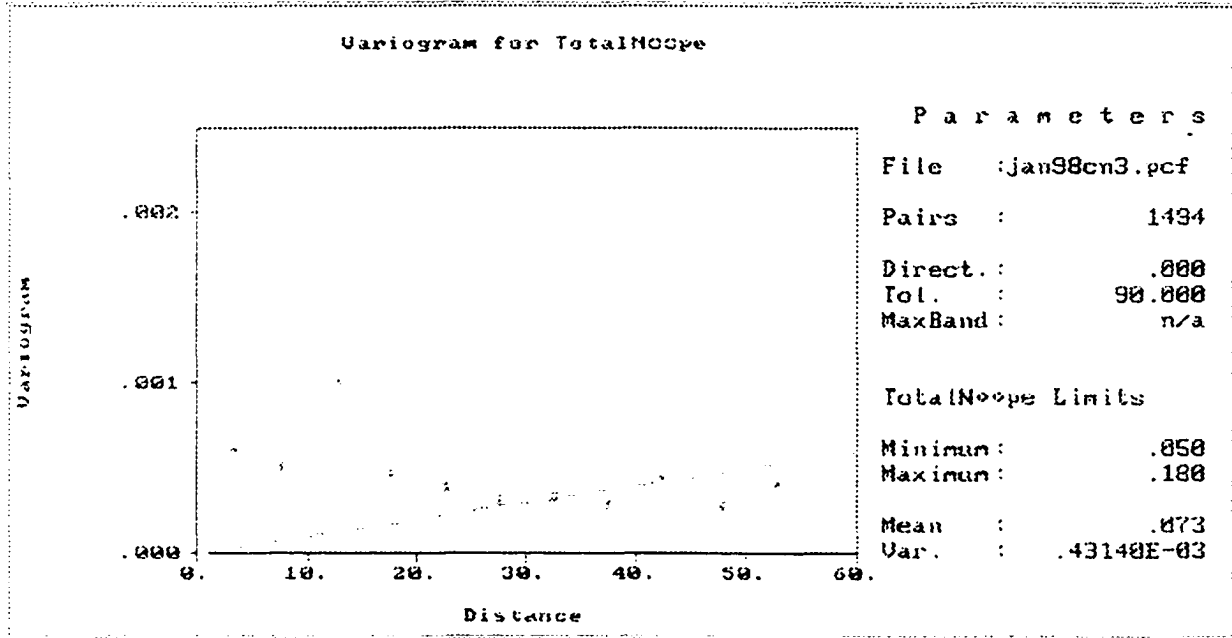


Figure 20. Semi-variograms of soil total N (top, with a linear model fitted) and total organic C (bottom, with a gaussian model fitted) for Site B, January, 1998.



APPENDIX E:

Raw data set from fire history and soil nutrient status at Fort Huachuca military reservation, Arizona manuscript

Table 1. Raw data for plant-available (Olsen) P (mg/kg).

| Sample | FIRE FREQUENCY (fires/decade) | | | | | | | | |
|--------|-------------------------------|--------|-------|-------|-------|------|------------------|-------|------|
| | Pleistocene surface | | | | | | Holocene surface | | |
| | 0 | 1 | 2 | 3 | 4 | 5 | 0 | 2 | 5 |
| 1 | 4.56 | 8.859 | 8.31 | 8.02 | 4.37 | 6.70 | 26.67 | 27.99 | 6.56 |
| 2 | 5.60 | 4.859 | 9.51 | 6.73 | 5.15 | 4.82 | 24.14 | 20.08 | 8.69 |
| 3 | 5.57 | 5.535 | 13.95 | 2.66 | 6.59 | 2.72 | 25.29 | 27.26 | 5.52 |
| 4 | 4.04 | 7.507 | 4.85 | 4.64 | 4.55 | 2.91 | 20.45 | 19.43 | 6.44 |
| 5 | 5.38 | 7.281 | 4.21 | 2.69 | 3.66 | 9.14 | 19.44 | 15.60 | 7.90 |
| 6 | 7.31 | 4.971 | 3.78 | 3.89 | 4.82 | 2.30 | 23.69 | 19.33 | 4.88 |
| 7 | 6.19 | 6.898 | 3.59 | 6.66 | 4.54 | 4.88 | 21.91 | 18.22 | 3.59 |
| 8 | 3.01 | 3.428 | 2.59 | 10.17 | 2.81 | 3.33 | 33.02 | 20.30 | 5.71 |
| 9 | 5.42 | 4.971 | 3.45 | 10.45 | 7.01 | 2.73 | 17.72 | 16.12 | 5.46 |
| 10 | 2.96 | 3.304 | 2.93 | 4.70 | 3.17 | 2.19 | 17.43 | 13.14 | 2.48 |
| 11 | 4.43 | 3.811 | 4.64 | 4.81 | 3.90 | 3.28 | 23.52 | 20.70 | 4.13 |
| 12 | 5.07 | 5.388 | 4.79 | 4.34 | 5.66 | 1.70 | 24.50 | 15.50 | 6.50 |
| 13 | 4.49 | 5.648 | 6.34 | 5.94 | 6.55 | 1.01 | 33.63 | 14.46 | 5.84 |
| 14 | 5.54 | 5.332 | 3.56 | 9.10 | 4.29 | 3.05 | 29.30 | 17.94 | 7.42 |
| 15 | 3.48 | 3.315 | 7.36 | 4.53 | 4.65 | 1.76 | 29.82 | 21.40 | 6.27 |
| 16 | 7.18 | 3.022 | 14.35 | 3.68 | 5.86 | 3.55 | 25.94 | 15.54 | 4.95 |
| 17 | 2.93 | 3.394 | 7.39 | 5.98 | 5.37 | 2.63 | 26.81 | 15.14 | 4.74 |
| 18 | 3.61 | 4.059 | 4.30 | 2.56 | 15.71 | 2.83 | 22.01 | 18.59 | 5.55 |
| 19 | 4.34 | 13.107 | 5.60 | 4.45 | 4.52 | 2.24 | 24.91 | 13.63 | 8.34 |
| 20 | 4.64 | 4.307 | 2.09 | 3.72 | 4.43 | 3.77 | 29.71 | 10.03 | 3.61 |
| 21 | 7.58 | 6.887 | 5.27 | 3.98 | 2.98 | 5.41 | 30.01 | 17.19 | 6.62 |
| 22 | 3.86 | 3.045 | 3.04 | 9.58 | 3.34 | 2.64 | 22.41 | 13.31 | 5.26 |
| 23 | 4.12 | 2.402 | 3.60 | 3.97 | 3.94 | 2.93 | 14.45 | 17.66 | 4.01 |
| 24 | 3.72 | 3.326 | 2.48 | 4.97 | 2.76 | 3.41 | 17.92 | 14.96 | 2.53 |
| 25 | 3.63 | 2.402 | 3.08 | 2.45 | 4.40 | 3.41 | 21.83 | 15.60 | 1.95 |

Table 2. Raw data for total N (%).

| Sample | FIRE FREQUENCY (fires/decade) | | | | | | | | |
|--------|-------------------------------|------|------|------|------|------|------------------|------|------|
| | Pleistocene surface | | | | | | Holocene surface | | |
| | 0 | 1 | 2 | 3 | 4 | 5 | 0 | 2 | 5 |
| 1 | 0.06 | 0.06 | 0.06 | 0.06 | 0.10 | 0.09 | 0.07 | 0.09 | 0.08 |
| 2 | 0.07 | 0.09 | 0.06 | 0.10 | 0.07 | 0.06 | 0.07 | 0.07 | 0.09 |
| 3 | 0.08 | 0.09 | 0.14 | 0.04 | 0.09 | 0.06 | 0.06 | 0.09 | 0.08 |
| 4 | 0.14 | 0.06 | 0.08 | 0.06 | 0.08 | 0.06 | 0.06 | 0.08 | 0.06 |
| 5 | 0.08 | 0.09 | 0.08 | 0.05 | 0.07 | 0.11 | 0.06 | 0.08 | 0.08 |
| 6 | 0.07 | 0.09 | 0.06 | 0.05 | 0.08 | 0.08 | 0.06 | 0.05 | 0.07 |
| 7 | 0.10 | 0.09 | 0.08 | 0.07 | 0.07 | 0.10 | 0.05 | 0.09 | 0.09 |
| 8 | 0.07 | 0.07 | 0.06 | 0.08 | 0.08 | 0.08 | 0.09 | 0.06 | 0.08 |
| 9 | 0.07 | 0.09 | 0.06 | 0.06 | 0.07 | 0.11 | 0.09 | 0.06 | 0.06 |
| 10 | 0.07 | 0.10 | 0.09 | 0.05 | 0.06 | 0.07 | 0.06 | 0.07 | 0.10 |
| 11 | 0.08 | 0.12 | 0.07 | 0.05 | 0.07 | 0.07 | 0.07 | 0.07 | 0.07 |
| 12 | 0.09 | 0.09 | 0.07 | 0.06 | 0.08 | 0.06 | 0.08 | 0.07 | 0.09 |
| 13 | 0.08 | 0.09 | 0.06 | 0.06 | 0.09 | 0.09 | 0.08 | 0.07 | 0.08 |
| 14 | 0.10 | 0.11 | 0.07 | 0.07 | 0.06 | 0.07 | 0.07 | 0.08 | 0.08 |
| 15 | 0.08 | 0.13 | 0.07 | 0.05 | 0.08 | 0.07 | 0.06 | 0.07 | 0.09 |
| 16 | 0.14 | 0.11 | 0.08 | 0.05 | 0.06 | 0.08 | 0.08 | 0.08 | 0.11 |
| 17 | 0.08 | 0.12 | 0.07 | 0.05 | 0.08 | 0.07 | 0.08 | 0.07 | 0.09 |
| 18 | 0.09 | 0.11 | 0.07 | 0.05 | 0.07 | 0.12 | 0.08 | 0.08 | 0.09 |
| 19 | 0.08 | 0.11 | 0.07 | 0.06 | 0.06 | 0.06 | 0.07 | 0.07 | 0.07 |
| 20 | 0.10 | 0.15 | 0.06 | 0.06 | 0.07 | 0.09 | 0.07 | 0.06 | 0.11 |
| 21 | 0.09 | 0.09 | 0.07 | 0.06 | 0.06 | 0.07 | 0.09 | 0.07 | 0.11 |
| 22 | 0.09 | 0.17 | 0.05 | 0.07 | 0.04 | 0.08 | 0.07 | 0.06 | 0.09 |
| 23 | 0.07 | 0.12 | 0.07 | 0.05 | 0.05 | 0.07 | 0.08 | 0.11 | 0.07 |
| 24 | 0.07 | 0.09 | 0.08 | 0.05 | 0.08 | 0.08 | 0.05 | 0.08 | 0.09 |
| 25 | 0.11 | 0.12 | 0.06 | 0.05 | 0.05 | 0.08 | 0.07 | 0.08 | 0.11 |

Table 3. Raw data for NH_4^- (mg/kg).

| Sample | FIRE FREQUENCY (fires/decade) | | | | | | | | |
|--------|-------------------------------|------|------|------|------|------|------------------|------|------|
| | Pleistocene surface | | | | | | Holocene surface | | |
| | 0 | 1 | 2 | 3 | 4 | 5 | 0 | 2 | 5 |
| 1 | 1.73 | 1.21 | 0.35 | 0.00 | 0.00 | 0.00 | 1.73 | 0.00 | 0.69 |
| 2 | 1.55 | 1.73 | 0.86 | 0.52 | 0.00 | 0.00 | 1.73 | 0.00 | 2.93 |
| 3 | 1.73 | 0.69 | 1.38 | 0.00 | 0.00 | 0.00 | 0.52 | 0.00 | 0.52 |
| 4 | 1.90 | 0.35 | 2.24 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.69 |
| 5 | 1.90 | 0.86 | 2.59 | 0.00 | 0.52 | 0.00 | 0.86 | 0.00 | 0.17 |
| 6 | 1.73 | 0.86 | 0.52 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.86 |
| 7 | 1.73 | 0.52 | 1.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.17 | 0.86 |
| 8 | 2.07 | 0.52 | 0.17 | 0.17 | 0.00 | 0.00 | 1.04 | 0.00 | 0.52 |
| 9 | 2.93 | 0.86 | 0.17 | 1.55 | 0.00 | 0.00 | 0.69 | 0.17 | 0.69 |
| 10 | 0.52 | 0.52 | 1.38 | 0.69 | 0.00 | 0.00 | 0.00 | 0.00 | 0.52 |
| 11 | 0.00 | 0.69 | 0.00 | 0.52 | 0.00 | 0.00 | 0.86 | 0.00 | 1.90 |
| 12 | 0.17 | 0.69 | 0.86 | 0.00 | 0.52 | 0.00 | 0.00 | 0.00 | 1.55 |
| 13 | 0.86 | 0.52 | 0.00 | 2.07 | 0.52 | 0.52 | 0.35 | 0.17 | 1.73 |
| 14 | 0.52 | 0.69 | 0.52 | 0.17 | 0.00 | 0.00 | 0.00 | 1.04 | 1.21 |
| 15 | 1.38 | 0.86 | 0.69 | 0.00 | 0.00 | 0.00 | 0.00 | 1.90 | 0.52 |
| 16 | 3.97 | 1.55 | 0.00 | 0.00 | 0.17 | 0.35 | 0.35 | 0.00 | 1.21 |
| 17 | 0.86 | 1.38 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.17 | 0.52 |
| 18 | 3.97 | 1.73 | 0.52 | 0.17 | 0.00 | 0.35 | 0.00 | 0.00 | 1.21 |
| 19 | 1.21 | 2.07 | 0.00 | 0.00 | 0.35 | 0.00 | 0.00 | 0.00 | 1.90 |
| 20 | 1.73 | 4.14 | 0.00 | 0.35 | 0.00 | 0.35 | 0.00 | 0.00 | 2.07 |
| 21 | 2.07 | 2.76 | 0.00 | 1.04 | 0.00 | 0.00 | 1.38 | 0.52 | 1.73 |
| 22 | 1.73 | 3.80 | 0.00 | 0.52 | 1.73 | 0.00 | 0.00 | 0.35 | 1.04 |
| 23 | 1.90 | 1.73 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.69 | 0.69 |
| 24 | 1.38 | 1.38 | 0.00 | 0.00 | 2.42 | | 0.00 | 0.00 | 0.00 |
| 25 | 1.90 | 2.24 | 0.52 | 0.00 | 0.00 | | 0.00 | 0.00 | 1.21 |

Table 4. Raw data for NO_3^{2-} (mg/kg).

| Sample | FIRE FREQUENCY (fires/decade) | | | | | | | | |
|--------|-------------------------------|------|------|------|------|------|------------------|------|------|
| | Pleistocene surface | | | | | | Holocene surface | | |
| | 0 | 1 | 2 | 3 | 4 | 5 | 0 | 2 | 5 |
| 1 | 3.28 | 1.21 | 3.97 | 0.86 | 1.21 | 1.04 | 1.73 | 0.69 | 1.55 |
| 2 | 3.45 | 1.21 | 1.73 | 1.04 | 1.04 | 0.35 | 1.55 | 0.69 | 0.00 |
| 3 | 4.66 | 1.55 | 2.07 | 1.21 | 3.28 | 0.00 | 2.07 | 0.86 | 1.73 |
| 4 | 5.87 | 1.55 | 0.86 | 0.17 | 0.86 | 0.00 | 2.59 | 0.35 | 1.73 |
| 5 | 3.62 | 1.73 | 0.52 | 0.17 | 0.69 | 0.86 | 0.35 | 0.35 | 1.73 |
| 6 | 2.76 | 1.21 | 0.69 | 1.73 | 0.35 | 1.55 | 1.90 | 1.73 | 1.38 |
| 7 | 4.49 | 4.31 | 2.24 | 0.00 | 0.86 | 0.35 | 1.73 | 0.86 | 1.73 |
| 8 | 1.38 | 1.21 | 1.55 | 2.59 | 2.59 | 1.04 | 1.73 | 1.21 | 1.55 |
| 9 | 3.45 | 1.73 | 0.69 | 0.69 | 0.69 | 0.35 | 2.24 | 0.52 | 1.21 |
| 10 | 1.73 | 1.73 | 0.52 | 1.04 | 1.38 | 0.35 | 2.07 | 0.52 | 3.97 |
| 11 | 1.21 | 0.69 | 0.69 | 0.35 | 0.86 | 1.73 | 1.38 | 0.17 | 0.00 |
| 12 | 10.87 | 2.76 | 2.59 | 0.35 | 1.38 | 0.69 | 0.86 | 0.00 | 3.11 |
| 13 | 6.21 | 1.21 | 0.69 | 3.28 | 1.04 | 0.00 | 1.21 | 1.04 | 1.90 |
| 14 | 1.55 | 1.90 | 0.17 | 0.52 | 0.86 | 0.00 | 1.38 | 1.38 | 1.38 |
| 15 | 12.59 | 2.07 | 1.04 | 0.35 | 0.69 | 4.31 | 1.90 | 1.04 | 1.21 |
| 16 | 11.04 | 2.42 | 3.28 | 0.17 | 5.87 | 1.73 | 0.86 | 0.35 | 1.73 |
| 17 | 14.32 | 2.07 | 0.86 | 1.21 | 1.73 | 1.04 | 1.55 | 0.35 | 2.76 |
| 18 | 3.11 | 2.07 | 0.69 | 0.52 | 1.55 | 2.93 | 1.38 | 2.76 | 0.00 |
| 19 | 2.42 | 2.76 | 0.35 | 0.86 | 1.73 | 2.76 | 2.07 | 0.52 | 2.07 |
| 20 | 2.59 | 4.14 | 0.86 | 0.86 | 1.38 | 3.80 | 0.86 | 0.00 | 3.11 |
| 21 | 2.24 | 3.11 | 2.59 | 1.55 | 1.55 | 0.00 | 2.24 | 1.55 | 1.55 |
| 22 | 4.31 | 3.45 | 0.69 | 4.31 | 0.00 | 0.00 | 2.07 | 1.04 | 0.00 |
| 23 | 1.73 | 2.93 | 1.38 | 0.86 | 1.04 | 1.21 | 1.04 | 0.00 | 3.11 |
| 24 | 3.11 | 1.90 | 0.86 | 0.52 | 5.69 | 0.00 | 1.04 | 3.45 | 0.00 |
| 25 | 5.69 | 3.11 | 1.38 | 1.04 | 0.86 | 0.00 | 1.38 | 0.35 | 1.55 |

Table 5. Raw data for total organic C (%).

| Sample | FIRE FREQUENCY (fires/decade) | | | | | | | | |
|--------|-------------------------------|------|------|------|------|------------------|------|------|------|
| | Pleistocene surface | | | | | Holocene surface | | | |
| | 0 | 1 | 2 | 3 | 4 | 5 | 0 | 2 | 5 |
| 1 | 0.81 | 0.65 | 0.62 | 0.64 | 1.03 | 0.98 | 0.92 | 1.12 | 1.11 |
| 2 | 0.77 | 1.01 | 0.69 | 1.33 | 0.75 | 0.72 | 0.83 | 0.81 | 1.17 |
| 3 | 0.94 | 0.98 | 1.73 | 0.46 | 1.02 | 0.63 | 0.76 | 1.15 | 1.06 |
| 4 | 1.75 | 0.65 | 0.94 | 0.68 | 0.79 | 0.61 | 0.70 | 0.96 | 0.76 |
| 5 | 0.82 | 0.89 | 0.80 | 0.51 | 0.66 | 1.36 | 0.75 | 1.04 | 1.09 |
| 6 | 0.82 | 0.99 | 0.80 | 0.51 | 0.77 | 0.91 | 0.64 | 0.67 | 0.87 |
| 7 | 1.08 | 0.88 | 0.83 | 0.79 | 0.68 | 1.05 | 0.64 | 1.14 | 1.16 |
| 8 | 0.75 | 0.74 | 0.61 | 0.82 | 0.78 | 0.98 | 1.01 | 0.75 | 0.97 |
| 9 | 0.82 | 0.94 | 0.68 | 0.65 | 0.83 | 1.44 | 1.16 | 0.72 | 0.76 |
| 10 | 0.82 | 1.02 | 1.10 | 0.53 | 0.78 | 0.91 | 0.71 | 0.85 | 1.33 |
| 11 | 0.96 | 1.37 | 0.72 | 0.59 | 0.82 | 0.76 | 0.76 | 0.85 | 0.90 |
| 12 | 1.10 | 0.94 | 0.83 | 0.65 | 1.31 | 0.59 | 0.88 | 0.79 | 1.15 |
| 13 | 0.89 | 0.93 | 0.64 | 0.65 | 1.06 | 1.01 | 0.99 | 0.91 | 0.97 |
| 14 | 1.07 | 1.25 | 0.73 | 0.87 | 0.77 | 0.79 | 0.79 | 0.92 | 0.97 |
| 15 | 0.97 | 1.28 | 0.75 | 0.60 | 0.98 | 0.79 | 0.65 | 0.84 | 1.02 |
| 16 | 1.71 | 1.21 | 0.90 | 0.55 | 0.75 | 0.93 | 0.90 | 0.97 | 1.31 |
| 17 | 0.87 | 1.24 | 0.75 | 0.58 | 0.90 | 0.75 | 0.88 | 0.86 | 1.09 |
| 18 | 1.09 | 1.07 | 0.74 | 0.62 | 0.83 | 1.47 | 0.85 | 0.95 | 1.11 |
| 19 | 0.89 | 2.02 | 0.72 | 0.71 | 0.66 | 0.69 | 0.82 | 0.82 | 0.97 |
| 20 | 1.17 | 1.63 | 0.78 | 0.71 | 0.86 | 0.99 | 0.87 | 0.76 | 1.37 |
| 21 | 1.18 | 0.87 | 0.82 | 0.64 | 0.75 | 0.78 | 1.07 | 0.87 | 1.25 |
| 22 | 1.12 | 1.74 | 0.57 | 0.79 | 0.46 | 0.96 | 0.83 | 0.79 | 1.09 |
| 23 | 0.75 | 1.21 | 0.77 | 0.51 | 0.69 | 0.82 | 0.89 | 1.35 | 0.89 |
| 24 | 0.82 | 0.91 | 0.88 | 0.60 | 0.99 | 0.909 | 0.68 | 1.07 | 1.10 |
| 25 | 1.33 | 1.13 | 0.71 | 0.58 | 0.53 | 0.909 | 0.88 | 0.93 | 1.37 |

Table 6. Raw data for pH.

| Sample | FIRE FREQUENCY (fires/decade) | | | | | | | | |
|--------|-------------------------------|------|------|------|------|------|------------------|------|------|
| | Pleistocene surface | | | | | | Holocene surface | | |
| | 0 | 1 | 2 | 3 | 4 | 5 | 0 | 2 | 5 |
| 1 | 6.10 | 6.34 | 6.07 | 6.14 | 5.98 | 5.77 | 6.67 | 6.24 | 6.16 |
| 2 | 5.90 | 6.62 | 6.06 | 6.50 | 5.74 | 5.22 | 6.04 | 6.55 | 6.28 |
| 3 | 5.59 | 6.66 | 6.01 | 6.30 | 5.60 | 5.22 | 6.54 | 6.13 | 6.58 |
| 4 | 5.70 | 6.80 | 5.96 | 6.15 | 5.88 | 5.40 | 6.30 | 6.11 | 6.61 |
| 5 | 5.90 | 6.87 | 5.91 | 6.25 | 6.06 | 6.21 | 6.39 | 6.33 | 6.51 |
| 6 | 5.64 | 6.73 | 6.00 | 6.18 | 5.82 | 5.99 | 6.41 | 6.41 | 6.29 |
| 7 | 6.08 | 7.05 | 6.00 | 6.16 | 5.80 | 5.90 | 6.45 | 6.37 | 6.38 |
| 8 | 6.16 | 6.54 | 6.06 | 5.98 | 5.59 | 5.63 | 6.44 | 6.52 | 6.27 |
| 9 | 6.05 | 6.79 | 6.11 | 6.07 | 5.88 | 5.80 | 6.44 | 6.35 | 6.23 |
| 10 | 6.03 | 6.96 | 6.14 | 6.06 | 5.87 | 5.88 | 6.59 | 6.22 | 6.56 |
| 11 | 5.92 | 7.36 | 6.01 | 6.11 | 5.92 | 5.94 | 6.58 | 6.21 | 6.36 |
| 12 | 5.94 | 7.07 | 5.91 | 6.18 | 5.78 | 5.99 | 6.72 | 6.37 | 6.46 |
| 13 | 5.92 | 7.39 | 5.99 | 6.27 | 6.04 | 6.12 | 6.45 | 6.25 | 6.47 |
| 14 | 5.94 | 7.07 | 6.08 | 5.92 | 5.92 | 5.97 | 6.34 | 6.28 | 6.58 |
| 15 | 6.42 | 7.16 | 5.89 | 6.07 | 5.92 | 5.81 | 7.02 | 6.43 | 6.89 |
| 16 | 5.69 | 6.90 | 5.73 | 6.17 | 5.22 | 6.30 | 6.63 | 6.30 | 6.85 |
| 17 | 6.18 | 7.30 | 5.75 | 6.16 | 5.23 | 5.21 | 6.46 | 6.28 | 6.58 |
| 18 | 6.28 | 7.21 | 6.10 | 6.19 | 5.65 | 5.80 | 6.62 | 6.25 | 6.56 |
| 19 | 6.09 | 7.48 | 6.02 | 6.12 | 5.78 | 5.83 | 6.58 | 6.27 | 6.47 |
| 20 | 5.97 | 7.37 | 6.01 | 6.07 | 6.18 | 6.00 | 6.76 | 6.22 | 6.43 |
| 21 | 6.09 | 6.92 | 6.03 | 6.23 | 6.04 | 5.75 | 6.58 | 5.62 | 6.45 |
| 22 | 6.16 | 7.34 | 6.05 | 6.36 | 5.67 | 5.86 | 6.73 | 6.42 | 6.45 |
| 23 | 6.13 | 7.23 | 5.85 | 6.27 | 5.94 | 6.26 | 6.46 | 6.30 | 6.46 |
| 24 | 6.13 | 7.17 | 6.13 | 6.25 | 5.29 | 5.82 | 6.23 | 6.48 | 6.49 |
| 25 | 6.49 | 7.23 | 5.85 | 6.25 | 5.84 | 5.82 | 6.44 | 6.34 | 6.59 |

Table 7. Raw data for gravel content (%).

| Sample | FIRE FREQUENCY (fires/decade) | | | | | | | | |
|--------|-------------------------------|-------|-------|-------|-------|-------|------------------|-------|-------|
| | Pleistocene surface | | | | | | Holocene surface | | |
| | 0 | 1 | 2 | 3 | 4 | 5 | 0 | 2 | 5 |
| 1 | 31.51 | 19.86 | 14.60 | 12.86 | 18.21 | 24.19 | 23.22 | 28.42 | 12.32 |
| 2 | 21.07 | 39.97 | 19.81 | 18.68 | 14.07 | 27.47 | 20.49 | 31.63 | 18.68 |
| 3 | 32.71 | 30.76 | 14.93 | 12.15 | 12.28 | 40.85 | 20.32 | 20.46 | 21.66 |
| 4 | 20.41 | 12.68 | 19.00 | 11.48 | 16.09 | | 12.85 | 27.49 | 16.19 |
| 5 | 17.75 | 21.12 | 31.17 | 15.24 | 17.75 | | 17.24 | 25.96 | 18.81 |
| 6 | 49.41 | 33.35 | 14.75 | 20.38 | 15.54 | 28.51 | 18.66 | 25.76 | 20.23 |
| 7 | 26.08 | 27.76 | 14.09 | 16.12 | 16.89 | 26.55 | 21.80 | 35.32 | 31.24 |
| 8 | 41.91 | 25.68 | 14.17 | 26.22 | 14.22 | 32.36 | 16.55 | 21.19 | 24.03 |
| 9 | 29.02 | 27.52 | 17.30 | 16.00 | 12.17 | 39.90 | 14.11 | 24.47 | 15.01 |
| 10 | 17.66 | 19.47 | 7.79 | 18.43 | 16.60 | 31.74 | 20.14 | 22.41 | 29.35 |
| 11 | 24.01 | 17.95 | 15.87 | 18.20 | 14.70 | 30.38 | 23.60 | 23.18 | 24.73 |
| 12 | 29.94 | 38.95 | 30.67 | 14.96 | 15.62 | 24.60 | 15.74 | 25.39 | 24.12 |
| 13 | 26.70 | 50.63 | 24.73 | 18.35 | 15.06 | 31.15 | 17.73 | 23.63 | 24.48 |
| 14 | 23.31 | 29.09 | 12.46 | 10.47 | 15.66 | 36.60 | 24.50 | 19.52 | 22.54 |
| 15 | 41.02 | 39.32 | 16.49 | 11.70 | 18.95 | 23.88 | 21.52 | 23.88 | 22.28 |
| 16 | 26.05 | 27.98 | 17.50 | 21.15 | 22.58 | 20.37 | 10.57 | 19.22 | 33.40 |
| 17 | 26.56 | 35.36 | 17.10 | 13.70 | 16.52 | 28.84 | 22.49 | 27.60 | 20.77 |
| 18 | 28.73 | 38.10 | 16.40 | 18.08 | 21.54 | 24.49 | 19.20 | 18.86 | 26.55 |
| 19 | 26.90 | 28.19 | 28.93 | 16.24 | 15.98 | 26.29 | 14.57 | 29.09 | 31.92 |
| 20 | 21.81 | 22.84 | 15.25 | 22.65 | 16.10 | 28.08 | 17.40 | 19.83 | 24.20 |
| 21 | 34.86 | 51.42 | 11.27 | 15.29 | 15.19 | 38.37 | 15.89 | 25.88 | 37.84 |
| 22 | 34.10 | 33.07 | 13.49 | 13.27 | 14.44 | 16.50 | 13.36 | 20.52 | 21.67 |
| 23 | 38.96 | 25.44 | 14.97 | 10.44 | 12.94 | 39.53 | 22.43 | 14.62 | 23.23 |
| 24 | 30.68 | 21.78 | 17.70 | 17.58 | 18.60 | 38.35 | 16.00 | 22.12 | 36.21 |
| 25 | 27.72 | 36.95 | 19.77 | 21.36 | 24.43 | 20.60 | 23.70 | 29.54 | 33.90 |

Table 8. Raw data for surface litter aboveground biomass (g/m^2).

| Sample | FIRE FREQUENCY (fires/decade) | | | | | | | | |
|--------|-------------------------------|--------|--------|--------|--------|--------|------------------|--------|--------|
| | Pleistocene surface | | | | | | Holocene surface | | |
| | 0 | 1 | 2 | 3 | 4 | 5 | 0 | 2 | 5 |
| 1.00 | 47.45 | 119.55 | 0.00 | 79.95 | 152.55 | 0.00 | 122.25 | 85.65 | 27.05 |
| 2.00 | 11.25 | 26.25 | 116.55 | 78.55 | 65.05 | 25.75 | 144.05 | 127.05 | 171.15 |
| 3.00 | 34.15 | 1.95 | 176.05 | 63.65 | 361.45 | 35.85 | 193.75 | 203.75 | 45.85 |
| 4.00 | 71.55 | 13.85 | 67.15 | 130.55 | 116.85 | 37.05 | 121.25 | 89.95 | 62.05 |
| 5.00 | 75.25 | 22.85 | 39.35 | 75.75 | 137.60 | 42.45 | 156.25 | 85.55 | 26.45 |
| 6.00 | 65.95 | 112.55 | 95.05 | 64.35 | 29.75 | 42.55 | 157.55 | 108.25 | 45.25 |
| 7.00 | 11.45 | 46.05 | 48.55 | 92.75 | 64.35 | 54.25 | 75.75 | 97.85 | 39.45 |
| 8.00 | 192.95 | 23.45 | 92.55 | 75.25 | 39.25 | 61.95 | 117.05 | 232.15 | 60.95 |
| 9.00 | 21.05 | 31.55 | 77.85 | 47.05 | 286.10 | 62.95 | 173.30 | 91.55 | 111.35 |
| 10.00 | 102.25 | 244.35 | 103.45 | 84.05 | 92.35 | 76.75 | 72.00 | 134.35 | 128.75 |
| 11.00 | 71.25 | 66.15 | 70.85 | 147.10 | 76.45 | 116.75 | 259.80 | 144.65 | 55.35 |
| 12.00 | 15.55 | 121.55 | 102.35 | 22.35 | 184.55 | 136.15 | 59.60 | 56.45 | 78.35 |
| 13.00 | 11.95 | 107.15 | 40.75 | 16.25 | 161.35 | 166.55 | 81.50 | 98.55 | 60.85 |
| 14.00 | 49.55 | 0.00 | 211.65 | 48.25 | 76.05 | 599.75 | 143.30 | 222.55 | 94.55 |
| 15.00 | 0.00 | 0.00 | 113.55 | 0.00 | 33.05 | 0.00 | 244.20 | 175.35 | 257.35 |

Table 9. Raw data for forbs aboveground biomass(g/m^2).

| Sample | FIRE FREQUENCY (fires/decade) | | | | | | | | |
|--------|-------------------------------|-------|-------|--------|-------|-------|------------------|-------|--------|
| | Pleistocene surface | | | | | | Holocene surface | | |
| | 0 | 1 | 2 | 3 | 4 | 5 | 0 | 2 | 5 |
| 1.00 | 69.65 | 6.95 | 31.05 | 10.10 | 9.35 | 20.35 | 95.05 | 9.75 | 48.55 |
| 2.00 | 7.95 | 69.85 | 32.15 | 4.55 | 1.15 | 9.05 | 8.55 | 11.45 | 109.55 |
| 3.00 | 33.25 | 3.25 | 1.25 | 4.65 | 22.95 | 1.95 | 126.75 | 9.85 | 23.15 |
| 4.00 | 9.70 | 33.45 | 16.15 | 7.45 | 47.85 | 19.25 | 84.35 | 27.55 | 20.65 |
| 5.00 | 44.95 | 46.75 | 11.65 | 9.75 | 9.75 | 42.45 | 47.05 | 41.85 | 21.65 |
| 6.00 | 62.35 | 41.95 | 1.75 | 432.15 | 11.95 | 4.30 | 76.95 | 33.15 | 41.35 |
| 7.00 | 0.60 | 33.35 | 10.55 | 34.95 | 11.95 | 20.75 | 8.55 | 0.45 | 68.35 |
| 8.00 | 62.35 | 8.75 | 17.25 | 8.65 | 18.75 | 31.05 | 63.45 | 34.55 | 36.15 |
| 9.00 | 30.85 | 6.35 | 9.95 | 15.95 | 16.55 | 11.65 | 85.70 | 16.35 | 23.25 |
| 10.00 | 36.05 | 33.95 | 34.80 | 25.75 | 9.10 | 0.30 | 17.30 | 6.95 | 13.15 |
| 11.00 | 10.25 | 0.00 | 18.15 | 97.70 | 23.85 | 0.00 | 18.35 | 13.05 | 9.25 |
| 12.00 | 47.25 | 0.00 | 41.45 | 28.35 | 39.25 | 0.00 | 80.70 | 7.45 | 0.75 |
| 13.00 | 6.85 | 0.00 | 0.00 | 14.15 | 9.75 | 0.00 | 24.70 | 44.25 | 15.15 |
| 14.00 | 0.00 | 0.00 | 0.00 | 38.45 | 26.75 | 0.00 | 121.60 | 20.65 | 9.35 |
| 15.00 | 0.00 | 0.00 | 0.00 | 1.85 | 0.55 | 0.00 | 59.65 | 0.00 | 81.70 |

Table 10. Raw data for shrubs aboveground biomass (g/m^2).

| Sample | FIRE FREQUENCY (fires/decade) | | | | | | | | |
|--------|-------------------------------|--------|--------|-------|-------|--------|------------------|---|---|
| | Pleistocene surface | | | | | | Holocene surface | | |
| | 0 | 1 | 2 | 3 | 4 | 5 | 0 | 2 | 5 |
| 1 | 4.35 | 177.85 | 179.95 | 29.85 | 50.05 | 122.3 | 82.5 | 0 | 0 |
| 2 | 20.95 | 196.35 | 32.05 | 9.4 | 126.3 | 97.05 | 0 | 0 | 0 |
| 3 | 143.5 | 64.25 | 189.65 | 5.55 | 0 | 21.45 | 0 | 0 | 0 |
| 4 | 131.65 | 0 | 21.1 | 7.55 | 0 | 7.45 | 0 | 0 | 0 |
| 5 | 0 | 0 | 178.35 | 88.95 | 0 | 142.55 | 0 | 0 | 0 |
| 6 | 0 | 0 | 123.65 | 0 | 0 | 26.15 | 0 | 0 | 0 |
| 7 | 0 | 0 | 108.15 | 0 | 0 | 20.1 | 0 | 0 | 0 |
| 8 | 0 | 0 | 0 | 0 | 0 | 89.45 | 0 | 0 | 0 |
| 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

Table 11. Raw data for native grass aboveground biomass (g/m^2).

| Sample | FIRE FREQUENCY (fires/decade) | | | | | | | | |
|--------|-------------------------------|--------|--------|--------|--------|--------|------------------|--------|--------|
| | Pleistocene surface | | | | | | Holocene surface | | |
| | 0 | 1 | 2 | 3 | 4 | 5 | 0 | 2 | 5 |
| 1 | 25.95 | 154.75 | 211.75 | 93.95 | 15.55 | 159.95 | 259 | 123.05 | 62.65 |
| 2 | 125.85 | 78.95 | 51.95 | 74.95 | 2.55 | 18.45 | 188.15 | 224.35 | 62.65 |
| 3 | 205.75 | 10.55 | 172.75 | 112.05 | 146.95 | 4.2 | 176.65 | 156.75 | 139.35 |
| 4 | 121.05 | 145.55 | 94.55 | 84.45 | 8.05 | 60.15 | 173.35 | 102.85 | 40.15 |
| 5 | 121.25 | 38.15 | 198.95 | 157.75 | 81.95 | 149.35 | 250.65 | 127.95 | 39.55 |
| 6 | 71.85 | 27.75 | 192.75 | 132.25 | 3.95 | 52.55 | 190 | 170.15 | 149.95 |
| 7 | 73.15 | 44.55 | 418.05 | 21.95 | 3.55 | 59.05 | 245.5 | 161.35 | 34.85 |
| 8 | 30.55 | 51.95 | 87.35 | 105.65 | 4.55 | 12.3 | 261.8 | 45.95 | 115.85 |
| 9 | 277.25 | 167.95 | 48.05 | 92.35 | 48.05 | 17.55 | 231 | 136.35 | 230.2 |
| 10 | 65.65 | 107.75 | 39.05 | 71.15 | 0.25 | 2.6 | 143.5 | 104.55 | 350.85 |
| 11 | 106.75 | 139.85 | 82.75 | 97.75 | 52.45 | 6.4 | 136.7 | 121.05 | 181.45 |
| 12 | 0 | 0 | 293.4 | 50.15 | 16.35 | 64.55 | 500.3 | 34.95 | 18.85 |
| 13 | 0 | 0 | 0 | 106.05 | 20.35 | 7.9 | 93.05 | 76.95 | 39.65 |
| 14 | 0 | 0 | 0 | 92.45 | 0 | 0 | 65.5 | 84.35 | 27.95 |
| 15 | 0 | 0 | 0 | 9.35 | 0 | 0 | 167.25 | 223.75 | 248.6 |

Table 12. Raw data for *Eragrostis lehmanniana* aboveground biomass (g/m²).

| Sample | FIRE FREQUENCY (fires/decade) | | | | | | | | |
|--------|-------------------------------|-------|--------|--------|--------|--------|------------------|--------|--------|
| | Pleistocene surface | | | | | | Holocene surface | | |
| | 0 | 1 | 2 | 3 | 4 | 5 | 0 | 2 | 5 |
| 1.00 | 41.15 | 57.05 | 27.05 | 44.05 | 307.50 | 95.05 | 0.00 | 147.45 | 7.25 |
| 2.00 | 163.65 | 42.55 | 149.75 | 118.55 | 255.25 | 233.60 | 0.00 | 19.55 | 28.55 |
| 3.00 | 246.55 | 0.00 | 91.05 | 116.95 | 505.85 | 33.25 | 0.00 | 21.35 | 128.75 |
| 4.00 | 45.45 | 0.00 | 404.80 | 295.40 | 288.50 | 371.80 | 0.00 | 2.75 | 1.95 |
| 5.00 | 54.95 | 0.00 | 16.75 | 22.05 | 192.45 | 68.95 | 0.00 | 9.80 | 33.45 |
| 6.00 | 21.55 | 0.00 | 328.90 | 45.75 | 187.65 | 72.95 | 0.00 | 49.85 | 50.75 |
| 7.00 | 25.15 | 0.00 | 28.95 | 7.15 | 246.75 | 109.75 | 0.00 | 91.75 | 135.65 |
| 8.00 | 17.95 | 0.00 | 124.95 | 9.45 | 256.30 | 244.50 | 0.00 | 0.00 | 184.95 |
| 9.00 | 0.00 | 0.00 | 80.05 | 83.35 | 319.00 | 96.65 | 0.00 | 0.00 | 9.60 |
| 10.00 | 0.00 | 0.00 | 0.00 | 19.45 | 264.15 | 160.25 | 0.00 | 0.00 | 0.00 |
| 11.00 | 0.00 | 0.00 | 0.00 | 71.05 | 0.00 | 96.45 | 0.00 | 0.00 | 0.00 |
| 12.00 | 0.00 | 0.00 | 0.00 | 236.50 | 375.70 | 341.15 | 0.00 | 0.00 | 0.00 |
| 13.00 | 0.00 | 0.00 | 0.00 | 0.00 | 239.95 | 0.00 | 0.00 | 0.00 | 0.00 |
| 14.00 | 0.00 | 0.00 | 0.00 | 0.00 | 400.40 | 0.00 | 0.00 | 0.00 | 0.00 |
| 15.00 | 0.00 | 0.00 | 0.00 | 0.00 | 407.25 | 0.00 | 0.00 | 0.00 | 0.00 |

REFERENCES

- Archer, S., C. Scifres, C.R. Bassham, and R. Maggio. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecol. Mon.* 52: 111-127.
- Biggs, T.H. 1997. Fire frequency, nutrient concentrations and distributions, and ^{13}C of soil organic matter and plants in southeastern Arizona grassland. Ph.D Thesis, Univ. Arizona, Tucson.
- Brown, J.R.; Archer, S. 1989. Woody plant invasion of grasslands: Establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecol.* 80: 19-26.
- Buffington, L.C.; Herbel, C.H. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecol. Mon.* 35: 139-164.
- Hastings, J.R.; Turner, R.M. 1965. The changing mile: an ecological study of vegetation change with time in the lower mile of an arid and semi-arid region. Univ. Arizona Press, Tucson.
- Killingbeck, K.T., and W.G. Whitford. 1996. High foliar nitrogen in desert shrubs: An important ecosystem trait or defective desert doctrine? *Ecol.* 77: 1728-1737.
- Klemmedson, J.O., and A.R. Tiedemann. 1986. Long-term effects of mesquite removal on soil characteristics: II. Nutrient availability. *Soil Sci. Soc. Am. J.* 50:476-480.
- Martin, S.C. 1983. Responses of semidesert grasses and shrubs to fall burning. *J. Range Manage.* 36: 604-610.
- McClaran, M.P. and T.R. Van Devender. 1995. The desert grassland. Univ Arizona Press, Tucson.
- Polley, H.W.; Johnson, H.B.; Mayeux, H.S. 1994. Increasing CO₂: Comparative responses of the C₄ grass *Schizachyrium* and grassland invader *Prosopis*. *Ecol.* 75: 976-988.
- Tiedemann, A.R., and J.O. Klemmedson. 1986. Long-term effects of mesquite removal on soil characteristics: I. Nutrients and bulk density. *Soil Sci. Soc. Am. J.* 50:472-475.
- Wilson, T.B.; R.H. Webb, and T.L. Thompson. 1999. Fire frequency and soil nutrient status on the Southern Gunnery Range at Fort Huachuca military reservation, Arizona. *in* Toward integrated research, land management, and ecosystem protection in the Malpai borderlands: conference summary; 6-8 January 1999; Douglas AZ. Ed. by G. J. Gottfried, L.G. Eskew, C.G. Curtin, and C.B. Edminster. Proc. RMRS-P-10. U.S.D.A Forest Service, Rocky Mountain Research Station, Fort Collins. 81-82.

Wilson, T.B., and T.L. Thompson. In Preparation. Nutrient Topographies of mesquite-dominated desert grasslands: changes in time and space.

Wright, H.A.; Bunting, S.C.; Neuenschwander, L.F. 1976. Effect of fire on honey mesquite. *J. Range Manage.* 29: 461-471.

Zitzer, S.F.; S.R. Archer, and T.W. Boutton. 1996. Spatial variability in the potential for symbiotic N₂ fixation by woody plants in a subtropical savanna ecosystem. *J. Appl. Ecol.* 33: 1125-1136.