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**Fire effects and vegetation response in a Madrean oak  
woodland, southeastern Arizona**

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The University of Arizona, 1994

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FIRE EFFECTS AND VEGETATION RESPONSE IN A MADREAN  
OAK WOODLAND, SOUTHEASTERN ARIZONA

by

Anthony Conger Caprio

---

A Thesis Submitted to the faculty of the  
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For the Degree of  
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In the Graduate College  
THE UNIVERSITY OF ARIZONA

1994

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### **DEDICATION**

This thesis is dedicated to my parents:

Evelyn and Eugene Caprio

and to all scientist who are more then just good  
researchers but also mentors for a new generation.

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### ABSTRACT

Following a June wildfire on the south slope of the Santa Catalina Mountains, vegetation was sampled to determine how composition, and fine fuels were affected. Spring and fall samples were taken in burned and unburned plots at three sites on south, east and north aspects. Twenty-one common species were selected for intensive analysis.

Burning caused compositional changes with the most significant occurring on the north slope. Woody species and *Selaginella* were reduced while herbaceous species recovered rapidly. Total cover was generally greater in burned than unburned areas by 2½ yr postfire. Recovery was rapid on south slopes dominated by herbaceous perennials and slower on north slopes dominated by woody species and *Selaginella* preburn. Oaks resprouted well after being topkilled, with *Quercus oblongifolia* more resistant than *Q. emoryi* to fire injury. Total herbaceous and litter biomass varied between 272-622 g · m<sup>-2</sup> at unburned and 253-370 g · m<sup>-2</sup> at burned sites 2½ yr postfire.

## INTRODUCTION

The presence and prevalence of fire in southwestern plant communities have been recognized since the late 19th century (Holsinger 1902; Rothkugel 1909; Blumer 1910a; Leopold 1924; Pearson 1931). Its role and effects have been investigated within several biotic communities in the area: semi-desert grassland, interior chaparral, and ponderosa pine forest. However, there is presently a lack of adequate information on the role, effects, and plant species response to fire in the Madrean evergreen woodland, an important vegetational constituent of the region that extends into central Mexico. Fire's presence within the woodland is often noted in the literature and easily detected in the field from charcoal and many fire scarred trees. The nearly ubiquitous evidence of fire throughout the woodland suggests that fire played an important role in determining natural selection processes, plant population dynamics, community composition and diversity, and species distributions. However, it remains unclear how the various attributes of fire might affect these variables over both differing spatial and short and long-term time scales. This study attempted to begin answering some of these questions by comparing vegetation and associated changes caused by fire in burned areas relative to associated unburned areas.

Fire is recognized as a significant factor in shaping many plant communities around the world through its differential effects on individual species (West et al. 1981; Wright and Bailey 1982; Sousa 1984; Pickett and White 1985; Trabaud 1987a; Naveh 1990; van Wilgen et al. 1992; Scifres and Hamilton 1993). Fire's important role in these communities both historically and contemporarily has only recently begun to be well understood. Its influence in modifying the landscape is produced by both naturally-occurring and by human-caused fire. The effects of fire can be found from polar to equatorial ecosystems in a variety of vegetation types from grasslands

to forests. Though not widely recognized or understood fire has undoubtedly significantly influenced the long term evolution of many species.

Most attributes of fire: severity, intensity, duration, frequency, size, and season of burning, are particularly important in determining the precise fire effects on a species or in a given community. These, plus the specific characteristics of the species or plant community being burned, combine to vary the actual effects of any fire or of repeated burns. Fires will vary between vegetation assemblages while their effect on the same species or plant community may differ greatly depending on the interaction of various fire, species, community, and climate/weather characteristics. As a result, a complex of poorly understood outcomes is often possible after fire. Accurately predicting outcomes involves a knowledge of the particular life history traits and the fitness consequences of the potential burning regimes on the flora of a given area (Noble and Slatyer 1977; Catellino et al. 1979; Noble and Slatyer 1981; Trabaud 1987b)

Because fire has been a part of many ecosystems for such long time many residing species have evolved mechanisms or life history strategies for resistance or escape. Whittaker and Woodwell (1972) suggest the development of grasslands, shrublands, and woodlands in semi-arid climate regions may be an evolutionary response of the vegetation to the effects of fire, as influenced by factors such as climate, soils, topography, and fire frequency. It has also been proposed that some species within fire prone communities possess fire facilitating characteristics, an outcome of natural selection processes, giving them a competitive advantage over less well adapted species for a particular fire regime (Mutch 1970; Rundel 1981; Dickinson and Kirkpatrick 1985), though there has been a great deal of debate about the hypothesis (Christensen 1985). Existence of such fitness consequences may have profound influences on species assemblages. Evolution of fire adaptations are possible when natural fire regimes (or other disturbance/disaster

regimes) overlap generation time and consequently have a significant impact on fitness. With this overlap fire acts to strongly affect survival and thus natural selection (Harper 1977; Rogers and Steele 1980; Malanson 1987; Rourke 1988). In some ecosystems with frequent fire it has been debated whether fire should even be called a disturbance (Evens et al. 1989). These regimes are in contrast to regimes with rare or "catastrophic" disturbances, occurring at intervals longer than the generation time, that would have only a small fitness consequence for future generations (Harper 1977).

In much of the United States fire began to be viewed as an enemy to trees and human utilization of natural resources in the latter part of the nineteenth century (Hough 1882; Pinchot 1898; Anon. editorial in *The Forester* 1898). Although fire was recognized as having had a long association with many forests it was viewed as detrimental to the full utilization of forest resources (Sterling 1905; Silcox 1911; Hofmann 1920; Show and Kotok 1924). Fire suppression, begun in the 1870's, was considered a necessity in resource management by the early 1900's within organizations such as the Forest Service and National Park Service. It became an integral part of their mission (Graves 1910a, 1910b, 1910c; Clapp 1911; Silcox 1911; Leopold 1920; Peyton 1926; Holbrook 1943; Pyne 1982) although this policy was debated in the early years (Blumer 1910a; Kitts 1919; Leopold 1924; Koch 1935 [see Loveridge (1935) for response to Koch]). Leopold's publication of 1924 shows a striking rethinking of his views presented in the 1920 article cited above. The negative attitude toward fire appeared to be well entrenched in the Forestry Division of the United States Department of Agriculture by the late 1800's (Hough 1882; Ensign 1888; James 1888; Pinchot 1898, 1900) and was publicized by organizations such as the American Forestry Association (Anon. editorial in *The Forester* 1898, 1901; Anon. editorial in *American Forestry* 1910; Graves 1910b, 1910c; Clapp 1911; Pratt 1919; Hofmann 1920;

Hutchinson 1921), various timberland protective associations (Allen 1911; Sterling 1911), The Ecological Society of America (Wolcott 1926), and the emphasis of the chief foresters of the United States, Henry Graves and William Greeley (Flader and Callicott 1991). In contrast, the Division of Agrostology from the same department was going so far as to promote the use and advantages of fire in some vegetation types (Smith 1899). This latter group seemed very aware of the vegetation changes that were taking place due to overgrazing in combination with reduced burning frequency (because of herbaceous fuel loss from grazing), with many of the observed changes considered to be having a negative impact on resources.

Much of this interesting historical debate centered on what became known as the practice of "light burning" or "Piute Forestry" in pine forests of the West and Southeast and is excellently summarized by Vankat (1977) for the California area. Light burning was being used by timber owners as a way of protecting their merchantable trees from destructive crown fire such as had been experienced in the Lake States during the latter half of the nineteenth century and by ranchers to maintain or improve grazing. However, it was zealously apposed by forest managers who felt that total fire exclusion was the only method of forest protection that should be used (Pinchot 1898; Sterling 1905; Anon. editorial in *American Forestry* 1910; Clapp 1911; Pratt 1911; Silcox 1911; Boerker 1912; Plummer 1912; Show 1916, 1920; Dunning 1919; Hofmann 1920; Pearson 1920; Leopold 1920; Hutchinson 1921; Show and Kotok 1924, 1925; Wolcott 1926; Loveridge 1935). What I found to be an enlightening account of the attitudes in the early years of fire suppression is provided by the following passage by Show and Kotok (1924), extracted from a USDA Bulletin that was considered to be the final word in the light burning debate (Kilgore 1973). The passage plainly states it was apparent to some managers, even at that time, that changes in forest structure and increases in forest fuels were occurring as a result of the

fire suppression policies instituted with the establishment of the national forest reserve system at the end of the Nineteenth Century.

*"The establishment of the national forests in California, beginning as early as 1891, thus found forest burning an established practice. The idea that fires could be excluded entirely from millions of acres was generally regarded as preposterous and the most gloomy pictures were drawn of any attempt. It was claimed that the uncontrollable crown fire was to be expected as the inevitable consequence of allowing ground cover and litter to accumulate. Thus, in the early years of protection of the national forests, the forests were still open as a result of the repeated fires of the past. The great outbreak of incendiarism and agitation for light burning did not come until later. As fire protection became an accomplished fact and the young growth began to fill up the open forest, the amount of inflammable material in the forest increased greatly. Thereupon renewed efforts were made to return to the unrestricted use of fire. The incendiary who desired an open forest and had no concern for the forest itself, and the light burner who honestly desired to protect the merchantable timber with fire, now became two of the most serious obstacles to successful protection, not only because of their direct action, but even more so because of their open preaching of fire."*

The publicized view of the forestry community was that light burning was being used by timber interests, such as the Southern Pacific Railroad, to protect current stands of mature timber for economic profit while ignoring future regeneration (Anon. *American Forestry* editorial 1910; Leopold 1920). With passage of state and federal legislation such as the Clarke-McNary Forestry Law in 1923 (Peyton 1926), the policy of total fire exclusion generally prevailed but with strong contention about the universal application of this policy by researchers in the Southeast (Chapman 1926, 1932a, 1932b; Greene 1931; Stoddard 1935; Heyward 1939), and to a lesser extent in the West (Weaver 1943, 1951).

. By the 1940's relatively effective fire control was achieved with the advent of aerial suppression tactics. However, absolute fire suppression was still being questioned and in places reversed, particularly in the Southeast with respect to an understanding of fire's role in *Pinus*



*palustris* (longleaf pine) forests (Garren 1943; Chapman 1947, 1950; Bruce 1951). Changes in plant community structure and composition were becoming apparent and not necessarily desired. Suppression efforts continue today but a growing understanding of fire's role in various ecosystems has led to new fire suppression practices by land managers. These changes have involved an effort to allow fire to play a larger role in these ecosystems. Recent policy shifts by many resource agencies have emphasized that management of natural areas be based on ecosystem processes rather than being simply structurally orientated (Parsons et al. 1986). The use of either natural prescribed fire or intentional ignitions under specific prescription conditions to either mimic the natural fire regime in areas where the natural regime can no longer operate or to promote a certain management goal is becoming more common. As research progresses the importance of fire as a natural component and important management tool is becoming more widely accepted. Researchers and resource managers need information on the biological, physical and ecological effects of fire in many regions of the world (Nelson 1979; Parsons et al. 1986; Trabaud 1987a; van Wilgen et al. 1992) beyond a simple knowledge of how an area or organism will respond to the postfire environment. It is becoming increasingly apparent that multiple outcomes are possible, given the varied burning conditions and species compositions of an area. Understanding the role and history of fire in an ecosystem is important in management planning and in identifying whether fire effects and responses are beneficial or detrimental to a resource given a desired management objective.

The ecological consequences of the decisions about fire suppression 80 to 90 years ago have had dramatic effects on the dynamics and structure of many ecosystems throughout western North America (Parsons and DeBenedetti 1979; Dodge 1972). The ultimate biological ramifications from these have still not been concluded and are leading us into an unpredictable

future, a future that undoubtedly has multiple outcomes which we cannot presently predict or understand. Even if we do initiate changes in management practices today the past will carry forward be with us due long lasting persistence effects because of organisms such as trees that can survive for hundreds of years.

Within the Madrean evergreen woodland there is evidence of vegetation changes having taken place during the last 100 years, with fire control suggested as one reason. Because of this the Forest Service, National Park Service, and private organizations, like the Nature Conservancy, have begun or are planning prescribed burns in the woodland. Prerequisite for a wide-spread and fine-tuned burning program is a better understanding and knowledge about fire effects (Kickert et al. 1976; Trabaud 1987a; NPS 1992; USDA 1993). This includes fire's influence on ecological relationships and how plants respond to it as a population and as part of a specific vegetation assemblage. This knowledge will allow the best fire management alternatives to be identified to achieve desired resource management objectives such as in development of the new policy on Ecosystem Management being initiated within the Forest Service (Moody et al. 1993).

## Objectives

This study focuses on the effects and postfire response of flora in a Madrean oak woodland community that burned during the natural fire season, although the fire was human caused. Quantitative results were sought allowing judgments to be made about the ecological role of fire and predictions about fire effects and plant responses in this community. Of special interest were specific effects of fire on individual plant species and their postfire response for two years following the burn. Broader, more complex postfire recovery patterns will also be

examined and how these might relate to the overall role of fire in evergreen woodlands will be discussed.

Specific study objectives were to:

- 1) Assess fire impact on individual plant species by comparing burned and unburned sites. This included estimating mortality, damage, and tolerance of species to fire.
- 2) Determine postfire response of individual plant species to burning and identify early postfire vegetation trends and patterns within the lower Madrean evergreen woodland.
- 3) Obtain data on biomass of litter and herbaceous species that are major fuel components in the oak woodland.
- 4) Use this information to ascertain the ecological role of fire in Madrean evergreen woodland, both presently and historically, and to determine the possibility of accurately predicting fire effects and the usefulness of fire in achieving sound management of this community.

Lastly, besides the information on the role of fire in Madrean oak woodland, the research provided details on floristic composition and stand structure, resulting in a better understanding of ecological dynamics in this biotic community; all areas of research need in Madrean oak woodland (Lotan et al. 1981).

## LITERATURE REVIEW

### 2.1 Madrean Evergreen Oak Woodland Vegetation

Description - Madrean evergreen oak woodland is characterized as a mild winter - wet summer woodland (Axelrod 1958, 1975, 1979; Brown 1982), found in areas where precipitation usually exceeds 400 mm per year (Brown 1982). Winters are warmer than areas of equivalent precipitation further north that support piñon-juniper vegetation. Mean annual rainfall varies between 300 and 600 mm with most of it falling during a summer monsoon period (Hendricks 1985). Woodland vegetation, in contrast to forest vegetation, can be characterized as having trees of low stature with canopies that seldom touch or overlap (Dick-Peddie 1993). Such woodland vegetation can be found throughout much of western North America, including most of Mexico, and often has oak or conifer species as an important constituent.

The Madrean oak woodland is frequently broken into an upper and lower encinal (oak) zone (Shreve 1915, 1919; Dice 1943). The Mexican oak-pine woodland at higher elevations (upper encinal) has been treated as an ecotone in south-central Arizona, but forms a distinct community in the Sierra Madre (Marshall 1957; Lowe 1961; Wagner 1977). Whittaker and Niering (1965) and Niering and Lowe (1984) divided the woodland into a lower "open oak woodland" community, a mid-elevation "pygmy conifer-oak scrub," and an upper "pine-oak woodland." Moir (1986) has further divided these into habitat types. Other authors have treated these subdivisions differently (Pearson et al. 1926; Whitfield and Anderson 1938a; Gentry 1942, 1946; LeSueur 1945; Leopold 1950; Nichol 1952; Axelrod 1958, 1975; Lowe 1961, 1964; Martin 1963; Wauer 1973; Brown and Lowe 1974; Layser and Schubert 1979; Bowers and McLaughlin 1987a; Dick-Peddie 1993).

General descriptions of Madrean evergreen woodland vegetation in Mexico and the United States can be found in Shreve (1942), Axelrod (1958, 1975), Martin (1963), Axelrod and Raven (1985), Brown (1980 - map, 1982), and Gehlbach (1981). Descriptions for Mexico are given by Leopold (1950), Marshall (1957), Zavala (1991), and Hernandez et al. (1992) with Muller (1947) describing woodland in Coahuila; Arriaga (1988), León de la Luz and Dominguez-Cadena (1989), Arriaga et al. (1989, 1992) in Baja California Sur; Islas (1992) in Sonora; and by Brand (1936, 1937), Shreve (1939), LeSueur (1945) and Perez-Garcia (1978) for Chihuahua. The work by Perez-Garcia provides a detailed look at 36 sites sampled repeatedly over a period of two years in the eastern foothills of the Sierra Madre Occidental. In the Río de Bovispe region of northeast Sonora, Landres and MacMahon (1983) give a brief description while White (1948) made an extensive survey. Gentry (1942) describes oak woodland for the valley of the Río Mayo in Sonora, an area where it borders thorn scrub, and also for the Sierra Surotato in northern Sinaloa (Gentry 1946).

Much of the research on the Madrean evergreen woodland has taken place in southeastern Arizona where the largest area of this biotic community occurs in the United States. General descriptions are given by MacDougall (1908), Shreve (1942), Nichol (1952), Marshall (1957, 1963), Humphrey (1965, 1987), Hastings (1963), Hastings and Turner (1965), Lowe (1961, 1964, 1973), Brown (1972, 1978), Brown and Lowe (1977), Layser and Schubert (1979), Wentworth (1983), Hendricks (1985), McLaughlin (1986), Ffolliott and Guertin (1987), McPherson (1992). Woodland vegetation in the **Santa Catalina Mountains** has been extensively investigated and described (Blumer 1911; Shreve 1915, 1919, 1922; Niering and Whittaker 1963; Whittaker and Niering 1964, 1965, 1968a, 1968b, 1975; Whittaker et al. 1968; Patton et al. 1966; Niering and Lowe 1984). Other regions of Arizona where descriptions or

investigations about the woodland have been reported include the **Santa Rita Mountains** (Blumer 1910b, 1911; Bowers 1981), **Rincon Mountains** (Blumer 1911; MacDougall 1937; Marshall 1956; McLaughlin and Van Asdall 1977; Bowers 1984; NPS 1985; Bowers and McLaughlin 1987b), **Huachuca Mountains** (Toumey 1895b, Wallmo 1955; Brady 1973; Brady and Bonham 1976; Cockrum et al. 1979; Toolin 1980; Sanchini 1981; Wentworth 1983, 1985; Law [no date]; Ruffner and Johnson 1991; Pieper 1992), **Atascosa Mountains** (Cummings 1951, 1953; Kincaid 1959; Nevin et al. 1990), **Pinaleno Mountains** (Martin and Fletcher 1943; Johnson 1988), **Mule Mountains** (Wentworth 1976, 1981, 1983), **Chiricahua Mountains** (Toumey 1895a; Blumer 1909a, 1909b, 1909c, 1911; Roseberry and Dole 1939; Martin 1963; Balda 1969, 1970; Moir 1975; Reeves 1976; Leithliter 1980; Bowers 1981; Barton 1991, 1993), **Pajarito Mountains** (Toolin et al. 1980, Bowers 1981), **Patagonia Mountains** (Nevin et al. 1990) and the **Canelo Hills** (Bonham 1972; Bahre 1977; Sanchini 1981; Bock and Bock 1986a, 1986b, 1992a, 1992b).

Elsewhere within the southwestern United States, Madrean evergreen woodland has been described in the **Chisos Mountains** in west Texas (Muller 1937; Wauer 1971, 1973; Whitson 1974; Bunting and Wright 1977; Moir 1980b, 1982; Plumb 1991) and from the Texas-New Mexico border on the **Guadalupe Escarpment and Mountains** (Gehlbach 1966, 1967; Robinson 1969; Kittams 1972; Bunting 1978; Northington and Burgess 1979). In other areas of New Mexico encinal woodlands have been investigated to a varying degree in the central **Peloncillo Mountains** (Moir 1979), **Organ Mountains** (Townsend 1893; Moir 1963; Dick-Peddie and Moir 1970), **Animas Mountains** (Wagner 1977) and for the area of **Fort Baynard**, south of the Tres Pinos Mountains (Medina 1987).

Madrean woodland typically has an open aspect although it can be quite brushy. Its lower boundary typically intergrades with plains or semi-desert grasslands but can also contact interior chaparral, subtropical deciduous forest or rarely Chihuahuan Desert scrub. The upper woodland boundary contacts the Ponderosa pine community of the Rocky Mountain - Madrean montane conifer forest (Gentry 1942; Leopold 1950; Brown 1982). Floristic affinities of the Madrean oak woodland and oak-pine communities are primarily to the south, although the woodland in south-central Arizona is strongly influenced by interior chaparral found to the north. The major community groups it contacts in Arizona are of wide geographic origin. Mountain coniferous forest has northern affinities, semi-desert grassland is of eastern Great Plains affinity, and Sonoran desert vegetation has affinities to the south and west (Whittaker and Niering 1965; Wagner 1977; Wentworth 1981).

Encinal woodland in the southwestern United States and northern Mexico is characterized by trees of short stature (6 to 15 m in height), such as evergreen oaks, alligator juniper (*Juniperus deppeana*), and Border piñon pine (*Pinus discolor*) [formerly Mexican piñon (*Pinus cembroides*)]. Evergreen oaks at higher elevations are usually accompanied by Madrean pines (such as *Pinus engelmannii*, *P. leiophylla*, *P. ponderosa*, and *P. lumholtzii*) and a few deciduous oaks. Prevalent oaks in Arizona's lower encinal are Emory (*Quercus emoryi*), Arizona white (*Q. arizonica*), and Mexican blue (*Q. oblongifolia*). Further east in New Mexico and southwest Texas, Emory and gray oak (*Q. grisea*) are common. In higher elevation woodlands, silverleaf (*Q. hypoleucoides*) and netleaf (*Q. rugosa*) are characteristic (Brown 1982). Tree species change to the south in Mexico. Perez-Garcia (1978) found five important tree species in Chihuahua, *Q. arizonica*, *Q. emoryi*, *Q. grisea*, *P. cembroides* and *J. deppeana*.

Oak species found in Madrean woodland are often called "live" oaks because they retain their leaves during the winter months. However, it has been noted that *Q. emoryi* and *Q. arizonica* may partially or completely drop their leaves in April/May during the spring dry season before flowering (Shreve 1915; Marshall 1957; Balda 1970; Faeth 1986). I observed this in *Q. emoryi* during the present study but not *Q. oblongifolia*. During the severe winter-to-early summer drought of 1988/1989 both species at various locations in the southern part of Arizona lost all leaves.

The major understory component of the woodland in this region is bunch grass, particularly species of muhly (*Muhlenbergia emersleyi*) and grama (*Bouteloua curtipendula*), along with cane beardgrass (*Andropogon barbinodis* [*Bothriochloa*]), wolftail (*Lycurus phleoides*), bluestems (*Andropogon* spp. [*Schizachyrium*]), plains lovegrass (*Eragrostis intermedia*), tanglehead (*Heteropogon contortus*), and green spangletop (*Leptochloa dubia*). Common forbs are taxa such as penstemons (*Penstemon* spp.), lupines (*Lupinus* spp.), bricklebushes (*Brickellia* spp.), indigobushes (*Dalea* spp.), buckwheats (*Eriogonum* spp.), and sagebrush (*Artemisia ludoviciana*). There are also many cacti and leaf succulents usually associated with semi-desert grassland. Taxa include *Echinocereus*, *Ferocactus*, *Opuntia*, *Agave*, *Nolina*, and *Dasyllirion*. Shrubs can vary from scattered individuals to near dominance, particularly near the northern and eastern ends of the Madrean woodland. Common species are manzanita (*Arctostaphylos* spp.), turpentine bush (*Haplopappus* spp.), mountain-mahogany (*Cercocarpus* spp.), ceanothus (*Ceanothus* spp.), silktassel (*Garrya wrightii*), and rosewood (*Vauquelinia* spp.) (Whittaker and Niering 1965; Brown 1982; Niering and Lowe 1984). Perez-Garcia's (1978) research in Chihuahua shows some differences with the following seven grass species comprising 52.1% of the herbaceous layer; *Andropogon gerardi*, *Lycurus phleoides*,



*Muhlenbergia emersleyi*, *M. montana*, *M. rigida*, *Elyonurus barbiculmis* and *Aristida schiendiana*. Common shrubs were *Mimosa biuncifera*, *M. dysocarpa*, *Rhus trilobata*, *Quercus depressipes* and *Arctostaphylos pungens*.

In the 1960's research by Whittaker and associates in the Santa Catalina Mountains described some attributes of the oak woodland and associated communities (Whittaker and Niering 1964, 1965, 1968a, 1968b, 1975; Whittaker et al. 1968; Niering and Lowe 1984). Along a rising elevational gradient they report an increase in productivity, biomass, vegetation cover, N content, and soil organic matter while pH, Ca, Mg, K and annual and diurnal amplitudes of soil temperatures decreased. The same results are found along a topographic moisture gradient. A pattern of increased frequency of C<sub>4</sub> plants (relative to C<sub>3</sub>) was found from mesic to xeric communities in the Mule and Huachuca Mountains by Wentworth (1983). Plant diversity is highest at mid-elevations in the woodland and semi-desert grassland, partially a function of increased moisture and decreased temperature, creating better growing conditions in comparison to higher or lower elevations (Whittaker and Niering 1975). Both were also found to have a high relative species richness by Bowers and McLaughlin (1982), while floras from Sonoran desert communities and chaparral were low. This richness is due to many annual and perennial herbs that proliferate during and immediately after the summer rainy season in combination with the occurrence of a spring flora following winter rains when temperatures begin to rise. Brady (1973), Wentworth (1979) and Bowers and McLaughlin (1982) all suggest that scattered canopies of oaks at oak woodland - desert grassland margin create a heterogenous habitat where many herbs can survive, increasing diversity. Wagner (1977) reports similar trends in the Animas Mountains in southwestern New Mexico. This increased diversity may also be partially a result of increased carbon and nitrogen under *Quercus* trees (Jackson et al. 1990; McPherson et al.

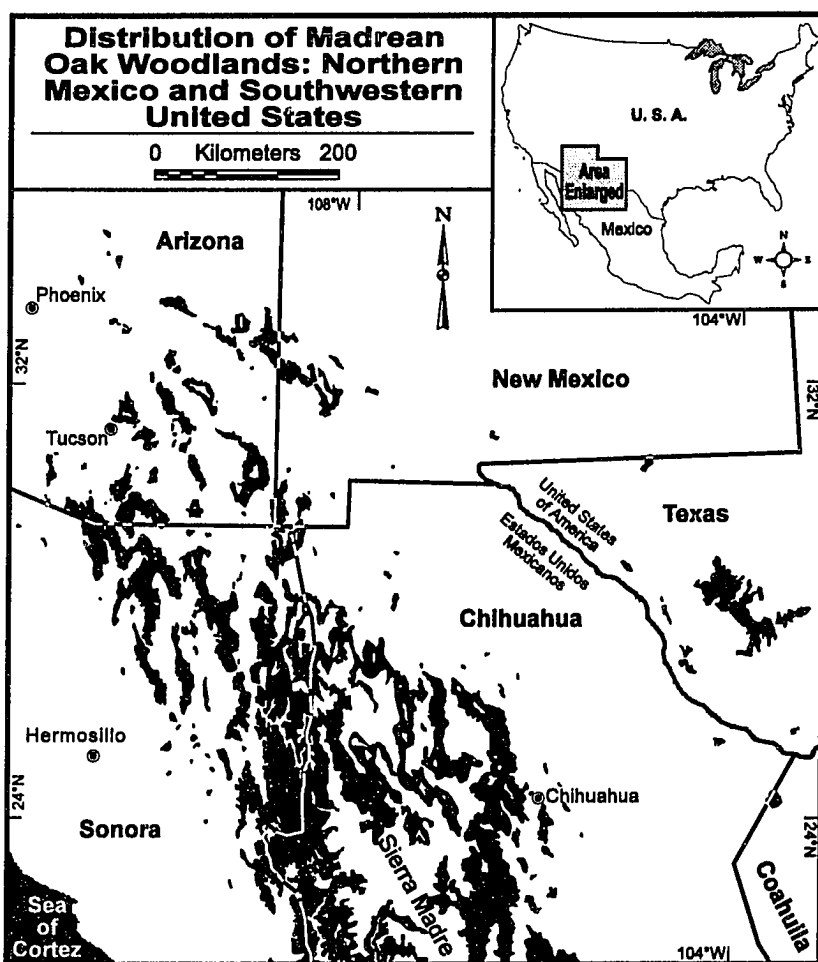
1993). Perez-Garcia (1978) describes some similarities and also some differences. Herbaceous basal cover and biomass are lower at higher elevations than low elevations while tree canopy cover and density increase with increasing elevation and moisture availability.

Distribution and evolution - Madrean evergreen woodland has a wide distribution with a geographic center in the Sierra Madre of Mexico (figure 1). The biotic community extends from central Mexico, north into the southern portions of the American Southwest (Brown 1982). Related pine-oak forest vegetation ("encinal") is found south into southern Mexico (Leopold 1950) and as montane *Quercus* forests further south in Central America and northern South America (Kappelle et al. 1992). In the United States, Madrean oak woodland vegetation ranges from southeastern Arizona (extending north-westward to the Tonto Basin in Gila County), to southwest New Mexico, and eastward into Trans-Pecos Texas in the Davis and Chisos Mountains. Related oak woodlands are found to the east in Texas, in the southern regions of the state and on the Edwards Plateau (Amos and Galhbach 1988; Axelrod 1958, which he described as Madrean woodland), and to the west, in California, forming a band around the Central Valley (Axelrod 1958, 1975, Allen-Diaz and Holzman 1991). California oak woodlands are partially differentiated by existing in a Mediterranean climate with cool wet winters and hot dry summers. Madrean evergreen woodland can be found at elevations between 880 m and 2,300 m (Brown 1982). Woodlands in Arizona have been estimated to occupy from 726,656 ha (Lowe and Brown 1973) to 870,270 ha (Hendricks 1985).

Madrean oak woodland has a long evolutionary history. Fossil evidence suggests it evolved from broadleaved evergreen sclerophyllous taxa that were derived from even older laurophyllous forests adapting to a spreading dry climate during the Tertiary (Axelrod 1958,

1975, 1979; Lowe and Brown 1982). By the middle Eocene this Tertiary Madrean-Tethyan sclerophyllous vegetation ranged across southern Laurasia (present day North America and Eurasia), forming a belt north of the closing Tethys Ocean, and into parts of northwest Africa. Contemporary biotic communities developed from remnants of this vegetation isolated by continental drift and climatic change. They can be found in the western hemisphere in Central America and in the western and southwestern parts of North America (Madrean Province). *Quercus* only recently migrated into the Columbian Andes (340,000 yr BP) with the forming of the Panamanian Isthmus (Kappelle et al. 1992; also see Gentry 1985; and Hooghiemstra and Sarmiento 1991). In Eurasia these biotic communities are found around the Mediterranean and east into Iran (Tethyan Province) (Axelrod 1975) and eastern India along the southern flanks of the Himalayas (Gopal and Meher-Homji 1983). The broadleaved sclerophyllous evergreen vegetation in these two provinces is similar physiognomically and shares many taxa. Related taxa include *Arbutus*, *Cercis*, *Cupressus*, *Juniperus*, *Pinus*, *Platanus*, *Quercus* (evergreen), *Rhus*, and *Rhamnus* (Axelrod 1975). According to Axelrod (1958) interior or petran chaparral and woodlands exist under a climate similar to what they existed under in the past whereas California chaparral and woodlands came under new selective pressures as they were influenced by a Mediterranean climate.

Reconstructions of the Quaternary environment in northwestern Mexico and the American Southwest have been made by Wells (1976, 1978, 1979), Van Devender (1977, 1987), Van Devender and Spaulding (1979), Axelrod (1979), Baker (1983), Lomolino et al. (1989), Betancourt et al. (1990). This period has been one of significant biogeographical changes in elevation and latitude for the woodland. A mesophytic evergreen woodland derived from a general Madrean-Tertiary woodland dominated the landscape during pluvial periods in the late



yr (Van Devender and Spaulding 1979) with the current communities occupying their present locations for about the last 4,000 yr (Moir 1983).

Related vegetation and oak woodlands - Oak woodland vegetation in the American Southwest has close floristic affinities with semi-desert grassland, interior chaparral, some elements of Chihuahuan desert mountain scrub, and pine forest at higher elevations. The complex relationship between interior chaparral and Madrean oak woodland has led some investigators to group these two into a broad "chaparral type." However, this does not consider major floral and faunal differences between these distinct biomes (Brown 1982). The relationships between upper encinal woodland and pine forest have been treated by Marshall (1957). Wagner (1977) lists a similarity index of 0.43 between lower encinal and semi-desert grassland, 0.78 between upper encinal and pine forest, and 0.51 between lower and upper encinal. Though similarity between grassland and lower encinal is high, a large portion of the flora within each community is restricted to that community, 38% and 45% respectively, showing a high degree of integrity for each.

Madrean oak woodland has strong affinities to oak woodlands located to the east on the Edwards Plateau in Texas (Foster 1917; Axelrod 1958; Fonteyn et al. 1984; Fowler and Dunlap 1986) and south into the state of Nuevo Leon, Mexico (Muller 1939). In addition, the Madrean woodland also bears a resemblance to oak woodlands in California, although these are dominated by herbaceous annuals and winter rainfall (Lathrop and Zuill 1984; Brown 1982; Barbour and Major 1977; Baker et al. 1981; Allen-Diaz and Holzman 1991), and the Mediterranean region of Eurasia (Axelrod 1975; Ovington 1983) which also receives most of its precipitation in winter. Comparisons of oak woodlands at a site in central California (Carmel)

and at a site with Madrean oaks in northeast Sonora (Purica) suggests strong structural similarities exist (Landres and MacMahon 1983) as did comparisons to areas of Spain (Huntsinger and Bartolome 1993). Madrean oak woodland also has some relationships to California chaparral which has affinities to vegetation found in mediterranean climates around the world, viz. the Mediterranean, Cape Colony, central Chile, and southwestern and southern Australia (Axelrod 1958; Specht 1969). Growth form and other structural traits of oaks in these arid climates show similarities in adaptations to environmental stresses (Rundel 1980). For example, shrubby taxa dominate in areas of drought, short growing season, and nutrient deficiencies.

These relationships permit some information on fire effects and plant response in these related communities to be usable in interpreting impacts of fire on Madrean woodland. This is especially important since little information is presently available on fire effects and postfire response of plants in Madrean oak woodland.

## 2.2 Fire In The Southwest

Southeast Arizona's natural fire season occurs in late spring and early summer, particularly on lower elevation grasslands and woodlands (Pearson 1922; USDA 1924; Claveron 1967; Bock et al. 1976; Murray 1982). Peak occurrence of lightning fires in New Mexico and Arizona occurs from May to July, proceeding the onset of summer rains (Pearson 1922; Kormarek 1969; Barrows 1978; Smeins 1980). This pattern is also generally observed in fire-scars from the area (Weaver 1951; Ahlstrand 1980; Caprio et al. 1989; Baisan 1990; Swetnam and Stokes 1983; Swetnam et al. 1991, 1992a, 1992b; Ortloff 1992). The natural fire climate is defined by interaction of summer and winter precipitation, the annual cycle of herbaceous vegetation, primarily graminoids as the principal fuels, and seasonal probability of lightning

strikes as ignition sources. This period follows the driest annual months when herbaceous plants are cured, creating dry flashy fuels, and when temperatures are high. Fire spread rates are often rapid. Dry thunderstorms, developing from weak storm cells and often associated with virga and lightning, can occur in April, May, June and early July and are important in making this the primary natural fire season. They form as a shallow layer of moist air from the Gulf of Mexico enters the region at high elevations (3000 - 5500 m). This moist air lifted by thermal convective cells over heated desert surfaces and high mountains produces sporadic local storms.

Precipitation accompanying these storms is often insignificant but they often produce many cloud-to-ground lightning strikes. Historic fire complexes have followed such bursts of spring and early summer lightning (Pyne 1984). As monsoon development progresses, moisture increases with fire occurrence decreasing as herbaceous vegetation greens up and fuels become less amenable to burning. This is analogous to south Florida which also experiences a comparable annual weather pattern and has a peak in naturally occurring fires at the close of the spring dry season (Taylor 1980).

Barrows (1978) found elevational occurrence of lightning fires peaks between 1650 and 2300 m elevations when fire records between 1960 and 1974 were analyzed. Fires were also randomly distributed by aspect. Review of modern fire records, recorded since 1937 at Saguaro National Monument, by Baisan (1990) shows a concentration of lightning fires in the Rincon Mountains at high elevations with a secondary concentration of lightning starts at between 1000 - 1500 m on a fore-ridge composed of grassland/oak woodland vegetation. Distribution of lightning throughout Arizona and even southeastern Arizona may not be random. Concentrations of lightning flashes were detected in higher elevation areas in southeastern Arizona, particularly in the Huachuca to Galiuro Mountain areas during July and August of 1989 and 1990 (King and

Balling 1994). They also state that this pattern was positioned relative to the main axis of the moisture flow from the south.

The influence of anthropogenic burning on fire occurrence and ultimately its impact on Madrean woodland vegetation in the Southwest is unknown. However, ethnographers and early accounts from visitors and residents of the area tell of frequent and widespread burning by native Americans (Hough 1926; Stewart 1951, 1956; Dobyns 1981; Pyne 1984). Its influence may vary from location-to-location and from time period-to-time period making interpretation difficult. Thus, this impact should not be ignored when attempting to understand vegetation patterns and changes on the landscape but we may never be able to fully differentiate the effects of anthropogenic from lightning caused fires in many localities.

The association of past fire occurrence as recorded as fire scars and the record of climate derived from tree rings have been investigated by several researchers (Keen 1937; Laven et al. 1980). Recent evidence from fire statistics and tree-ring fire-scar chronologies suggests a longer term interannual pattern in fire activity in the Southwest associated with El Niño-Southern Oscillation (ENSO) events (Swetnam and Betancourt 1990). A reduction in activity is often correlated with these synoptic weather events that increase precipitation and may affect fuel moisture. Strong links have also been found between ENSO occurrence and seasons of increased fire activity in eastern Australia (Skidmore 1987) or decreased fire activity in the southeastern United States (Simard et al. 1985; Brenner 1991), similar to the Southwest (during ENSO events it is dry in the western Pacific and wet in the southern United States). Additionally, Baisan (1990) reports significantly positive reconstructed June PDSI values for the two years preceding major fires when 35 major fire years, reconstructed from tree-ring fire-scar chronologies in the Rincon Mountains, Arizona, were analyzed. Similarly, though with a slightly weaker



relationship, Ortloff (1992) found a positive reconstructed July PDSI value for a single year preceding 32 fire years from a fire history in the Santa Rita Mountains. This trend suggests fine fuels, such as grasses, are important in carrying fires and that wet years may inhibit fire spread through increased fuel moisture while increasing fine fuel production, such that if the following year is dry, larger than normal fires can occur. Similar patterns have also been reported for lower Sonoran desert areas where the probability of fires appears to increase following two wet winters (Rogers and Steele 1980; McLaughlin and Bowers 1982; Rogers and Vint 1987), Great Basin (West 1979) and Great Plains grasslands (Wright and Bailey 1982).

### 2.3 Effects And Response Of Vegetation To Fire

General effects and responses - Factors predisposing plant communities to fire and ultimately regulating fire effects in them are reviewed by Lyon and Stickney (1974). They include the production of organic matter (biomass) faster than decomposition allowing fuel accumulations. The type and speed of organic matter accumulations determine such fire parameters as frequency, intensity and severity. Other factors predisposing a community to fire are regional weather patterns that provide adequate ignition sources (lightning) and fuel moisture conditions permitting ignition. This would include the presence of a climate suitable for the development of flammable vegetation or certain soils and topographical conditions.

Fire interacts with various environmental components with its effects being direct, occurring immediately, or indirect, occurring over a short or long period of time. The influence of many factors affect vegetation response to fire. The main characteristics of fire important in determining these effects are: fire type and severity, frequency, size, predictability, and season of burning. Acting together the historical pattern of these factors constitute an areas' fire regime

(Gill and Groves 1981; Van Wagner 1983; Rowe 1983; Christensen 1985). Their importance in determining vegetation response to fire varies with each particular burning situation. Variables would include the specific plant community involved, its physical and historical characteristics, and individual species and their heat tolerance (Volland and Dell 1981). The fire regime of an area has inherent variability and an overall distributional pattern that for biotic or climatological reasons may change over both millennial-length and century-length time scales (Clark 1988, 1989; Swetnam 1993; Caprio and Swetnam 1993).

Specific plant responses to fire are affected by fire intensity, duration, and frequency. Heat energy released per unit time per unit area defines intensity (Rowe 1983). Duration or fire residence time is a time-temperature relationship related to total fuel consumed and heat yield (McArthur and Cheney 1966). Frequency refers to how often an area burns. Plant response can be short term, to a particular fire, or long term, to the fire regime as a whole. Response to a particular fire event is most dependent on fire severity as a function of total heat yield and duration of this heating, while fire intensity is of lesser importance (Rowe 1983; Ryan and Noste 1983; Trollope 1984; Morgan and Neuenschwander 1985). However, under some circumstances fire severity and fire intensity can be synonymous, for example, when looking at crown foliage damage. Long term vegetation response would be determined by the severity of an area's fire regime. This depends on individual burn severity, frequency and season in which these burns occur. Frequency and season would affect floral composition by selecting for species that could continue to maintain themselves under this fire regime (Chandler et al. 1983).

Response of plants to fire in a particular area depends on the fire adaptive traits of the plants. These traits enhance fitness, survivability and reproduction. Gill (1981) defines them as, *"those traits contributing to the successful completion of the life cycle of a species in a fire-prone*

*environment.*" Autoecological traits important for survival are described by Lyon and Stickney (1974) and synthesized by Noble and Slatyer (1977), Catellino et al. (1979), Noble (1981) and with some modification by Rowe (1983) into three "vital attributes". These attributes make up the dimensions of a species "regeneration niche" which includes: mode of regeneration and reproduction, competition or communal relationships among species, and life cycle or over time those historical events critical in a species life history. Based on the first two attributes they categorized the mode of persistence of plants in relation to fire as invaders, evaders, avoiders, resisters, or endurers. These are defined in Rowe (1983) as:

- **Invaders** - highly dispersive, pioneering fugitive species with short lived disseminules.
- **Evaders** - species with relatively long-lived propagules that are stored in soil or in the canopy.
- **Avoiders** - shade-tolerant species that slowly reinvade burned areas: late successional, often with symbiotic requirements.
- **Resisters** - shade-intolerant species whose adult stages can survive low-severity fire.
- **Endurers** - resprouting species, shade-intolerant or tolerant, with protected perennating buds.

Use of these traits in association with specific fire cycle information (fire history) can provide a means of modelling and exploring the multiple pathways of succession in various vegetation assemblages.

Although the literature on fire effects on plants is not new (see Blumer 1910a; Buttrick 1912; Hensel 1923; Wolcott 1926) a growing number of symposia, reviews and texts have been published over the last 35 years summarizing effects and the ecological response of vegetation to fire. These have included the important contributions of the Tall Timber Fire Ecology Conferences over many years and the work of many researchers (Garren 1943; Ahlgren and Ahlgren 1960; Daubenmire 1968a; Kozlowski and Ahlgren 1974; Wells et al. 1979; Mooney and Conrad 1977; Lotan et al. 1981; Wade et al. 1980; Mooney et al. 1981; Wright and Bailey 1982; Chandler et al. 1983; Wein and MacLean 1983; Booysen and Tainton 1984; Lotan et al. 1985; Goldammer and Jenkins 1990).

#### 2.4 Madrean Evergreen Oak Woodland

Fire effects - The role of fire and its importance as one of the primary factors defining vegetation distributions in the Madrean evergreen woodland has been receiving increasing attention over the past few years. Fire is important not simply through its local vegetation effects but also because it acts as a dynamic link among various vegetation communities over a landscape. Vegetation changes, natural or human induced, in one plant community resulting in alteration of the fire regime may have indirect impacts on nearby plant communities through changes in how fire interacts between the two communities. In the American Southwest such interactions may extend from low elevation desert grasslands to ponderosa pine/mixed conifer forests at higher elevations. So an understanding of the relationship between fire and the many vegetation communities in the Southwest cannot be achieved without a knowledge of past and current fire history and effects in a variety of often linked communities (USDA 1993).

Fire occurrence within the oak woodland has often been noted (Rothkugel 1909; Blumer 1910a; Phillips 1912; Foster 1917; Leopold 1924; Gentry 1942; LeSueur 1945, Wallmo 1955; Marshall 1957, 1963; Hastings 1963; Hastings and Turner 1965; Whittaker and Niering 1965; Thames and Doran 1968; Reeves 1976; Wagner 1977; Sawyer and Kinraise 1980; Niering and Lowe 1984; Johnson 1988; León del la Luz and Domínguez-Cadena 1989). In areas of oak woodland Leopold (1924) notes there are, "*Universal fire scars on all the junipers, oaks, or other trees old enough to bear them.*". In Mexico, with a different history of fire suppression, frequent widespread fires are still occurring. In woodland on the southern end of Baja California Sur, Mexico, León de la Luz and Domínguez-Cadena (1989) state that "*this plant association is constantly disturbed by fire; there are practically no areas of forest without recent evidence of fire from both natural and human causes*". In the Sierra de los Ajos, Sonora, Mexico, just south of Arizona, fire histories from fire scarred trees are evidence of the occurrence of many fires in the twentieth century (Dieterich 1983b; Laboratory of Tree-Ring Research unpublished data).

Hastings (1963) and Hastings and Turner (1965) address the question of fire's role in the oak woodland and speculate on its importance, particularly as a regulator in oak regeneration. They felt its presence at any frequency would prohibit oak reproduction and destroy the woodland. In contrast, Marshall (1963), surveying birds in the pine-oak woodlands, felt fire occurred naturally at a frequent interval and played an important role in the development of this community as it occurred historically before fire suppression. He compared woodlands in Mexico to those in the United States and found the woodlands in Mexico, where fire suppression was minimal, to be open with a dense grass understory. Across the border in the United States where fire suppression was sophisticated and effective, the woodlands were stunted, with heavy fuel accumulations and little grass understory. Fires that do occur were severe and burned the

woodland back to the ground. Leopold (1937) made similar observations in Chihuahua and stated, "... *the watersheds (of Mexico) are intact, whereas our own watersheds, sedulously protected from fire, but mercilessly grazed before the (national) forests were created, and much too hard since, are a wreck*". Minnich (1983) cites an analogous situation in California chaparral communities, with larger more severe fires occurring north of the border due to suppression efforts whereas south of the border fires are small and patchy.

When describing the vegetation ecology in northwestern Chihuahua, Mexico, LeSueur (1945) states that burns within oak woodlands cause little damage because mature oaks are almost unhurt by fire when past the seedling stage. He adds that fire within the pine forest-oak woodland ecotone works to the advantage of *Quercus glaucophylla*, *Arbutus arizonica* and *Arctostaphylos pungens*, woodland species. Gentry (1942) made the following statement about fire in oak woodlands of the Río Mayo Valley region of Sonora but does not say whether the fires are lightning or man caused although they occurred during the peak period of lightning caused fire:

*"Grass fires are common in the Oak Forest belt during the height of the dry season in May and the early part of June. In 1935 they were observed burning for days at a time on the slopes of the Cedros range east of Tesopaco, on the range of the Sierra Baroyeca, and on Sierra de Alamos. The natives at night watch the bright, lurid paths of the flames with indifference. Except for occasional patches where shrubbery has closely pressed upon the oaks, the fire does not mount to the forest trees, and usually only the dry stalks of perennials are affected, in many instances being burned back to the root crown or wholly destroyed.*

*It is probable that on the whole the grass fires do more good to the natural cover than harm, clearing the ground of old dead grass, eliminating senile plants, depositing potash and phosphorus in the soil, and assisting in the germination and spread of young plants. In July 1935 we found that grass and many young herbs and shrubs had sprung anew after the spring fires. The dark, boulder-strewn stream of Arroyo Hondo was dull black with its charge of cinders. Many plants which had appeared rarely on the previous year's trip were now conspicuous owing to the elimination of choking grass. Two perennial species which had apparently gained a new*

*foothold on the mountain in burnt-over areas are Acacia crinita and Tephrosia leucantha."*

Similar observations were made by Leopold (1937) for the Chihuahua Sierras;

*"The Chihuahua Sierras burn over every few years. There are no ill effects, except that the pines are a bit further apart than ours, reproduction is scarcer, there is less juniper, and there is much less brush..."*

These observations suggest that in the past fires may have occurred at very frequent intervals in oak woodland, in the range of over 3-4 years, and that a high frequency fire regime occurred well into the twentieth century in northern Mexico.

A study by Johnson et al. (1962) in an area of the Santa Rita Mountains found Emoryi oak (*Quercus emoryi*) and Arizona white oak (*Q. arizonica*) susceptible to fire damage but able to resprout vigorously. They also state that beargrass (*Nolina microcarpa*) is moderately tolerant of and resprouts following fire. Niering and Lowe (1984) report on sampling carried out by Whittaker and Niering in upper Molino Basin (near the sites sampled in the present investigation) following a 1963 fire. They found Mexican blue oak (*Q. oblongifolia*) to sprout vigorously after being stem killed and that ocotillo (*Fouquieria*), turpentine bush (*Haplopappus*), sotol (*Dasylirion*), manzanita (*Arctostaphylos*), rosewood (*Vauquelinia*), beargrass (*Nolina*), and shindagger (*Agave schottii*) decreased after a fire, with some barrel cactus (*Ferocactus*) being killed and others, though charred to survive. Graminoids such as *Bouteloua* spp. and *Andropogon* spp. increased markedly while shrubs generally declined. They felt fire and drought were the two salient factors responsible for species shifts in the oak woodlands.

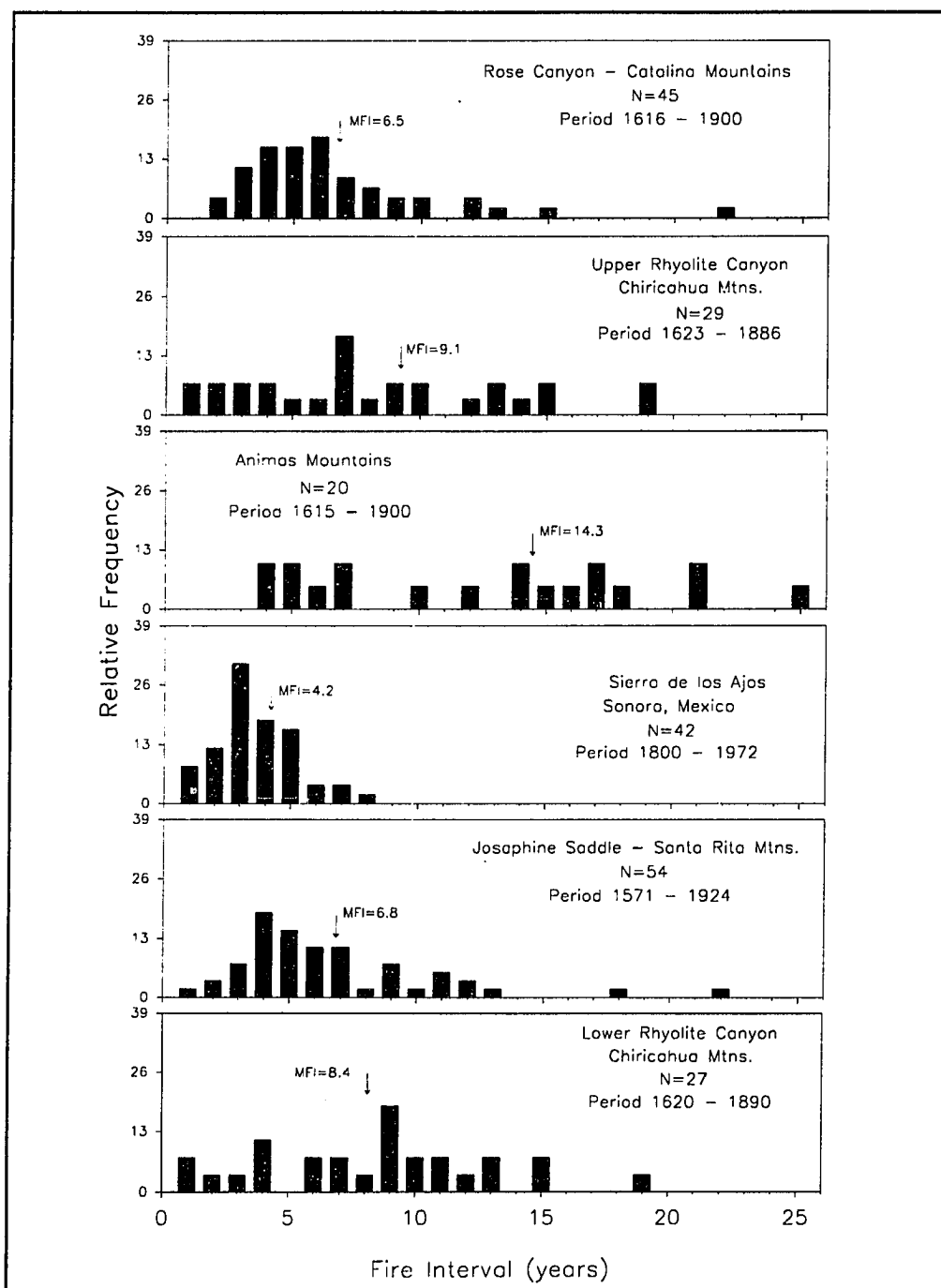
Bock and Bock (1986a) describe effects of a cool, fast moving, early summer prescribed burn in 1983 on plant density in open oak woodland and associated semidesert grassland at the Audubon Appleton-Whittell Research Ranch near Elgin in southeast Arizona. They report the fire as a whole had only a transitory effect on their study site. The scattered oaks

and oak seedlings (*Q. emoryi* and *Q. arizonica*) and woodland shrubs (*Baccharis pteronioides*, *Mimosa biuncifera* and *M. dysocarpa*) were little affected by burning while *Agave palmeri* and *Opuntia engelmannii* were more severely impacted. Herb abundance increased the first season postfire but were similar to unburned areas the second season although the same prescribed burn in semidesert grasslands had showed the opposite response (Bock and Bock 1992b). Graminoids were reduced on burned plots the first season but nearly equivalent the second season when compared to unburned controls. *Eragrostis intermedia*, *Bouteloua curtipendula*, and *Panicum hallii* all decreased the first season but recovered by the second. After a July wildfire in the same area Bock and Bock (1992a) observed that burning substantially, but only temporarily, reduced grass cover while forbs responded positively but again only temporarily.

Historic fire occurrence. Pre-European settlement fire frequency estimates for lower elevation oak woodland are non-existent although some estimates from pine-oak woodland, where fire-scarred conifers could be sampled, have recently been made that probably provide some estimate for lower woodlands. Understanding the fire history of an area is important because it is a component of the fire regime that has a unique pattern and has a very strong influence on the current vegetation of an area (Fox and Fox 1987).

Moir (1982) studied the fire history of the high Chisos Mountains in Big Bend National Park whose vegetation has been classified as Madrean evergreen woodland (Brown1982). Ring counts from scars on *Pinus cembroides* indicate at least 10 fires between 1770 and 1940 in Boot Canyon. These episodic surface fires were important for regeneration of some treespecies. He suggests a 50 yr return interval would be needed to maintain the vegetation





**Figure 2.** Fire interval distributions at six pine-oak or pine forest locations in southeastern Arizona and Sonora. Interval distributions provide information on both the mean fire interval and on how this interval varies, both important parameters in understanding the fire regime of an area.

in a natural fire regulated condition. He also suggests that fire frequency was the same before 1880 as today.

A number of dendrochronological crossdated fire histories have also been completed in the mountain ranges in southeastern Arizona, southwestern New Mexico, and surrounding regions that possess oak woodlands very similar to Molino Basin. Among these fire event chronologies were some developed from fire-scarred pines in areas of pine-oak woodland that border lower open-oak woodland or lower elevation pine forest (Figure 2 - data from Dieterich 1983b; Ortloff 1992; Swetnam and Stokes 1983; Swetnam et al. 1989, 1991, 1992a, 1992b; Baisan and Swetnam in press; Laboratory of Tree-Ring Research unpublished data). A composite picture of the fire-interval distributions from many of these sites may give some idea of fire frequency in the adjoining woodland and semi-desert grasslands. Several possess interesting fire occurrence patterns although these have not all been fully explained. In Rhyolite Canyon, Chiricahua National Monument it has been speculated that source areas for many fires might be the lower woodlands and grasslands. To the south in Sonora, Mexico, fire history studies in the Sierra de los Ajos, a range dominated by oak woodland vegetation, are of particular interest because widespread fires have continued to occur throughout the twentieth century (3.2 yr average 1900-1972) in contrast to nearby mountain ranges of the southwestern United States where fire frequency decreased in the late 1800's. Differences in vegetation structure between the two countries resulting from differing fire suppression policies was also observed by Marshall (1957, 1963). Many of the fires in this range burned in pine-oak and lower elevation oak forests with several recent fires burning during the 1989 drought (personal observation during August 1993) The Animas Range is also unusual with frequent fires occurring into the twentieth century except for a period of several decades when under the jurisdiction of the U.S. Forest Service.

Large lightning fires in 1959 and 1989 ignited in low elevation semi-desert grasslands where they spread and burned into higher elevation oak woodland and montane forest.

Reviewing newspaper accounts of fires in southeastern Arizona between 1859 and 1890, Bahre (1985, 1991) reports that fires were more frequent and of much larger areal extent than presently. He cites the occurrence of fires on the south slope of the Catalina Mountains in 1877, 1880 and 1889. The 1877 fire(s) was reported to have been burning in the Tortolita Mountains and to have carried across the Santa Catalina Mountains and burned to the summit of the Santa Rita Mountains to the south of Tucson (*Arizona Star* June 23, 1877). The 1889 fire was more localized on the south slope of the Catalina Mountains.

*A large fire is raging in the Santa Catalina Mountains. A party who has been on the scene states that it has gone over an area of about ten square miles and that it is making its way toward the valley on this side [Tucson].*  
- *Arizona Daily Star*, June 22, 1889.

Bahre (1985, 1991) estimates fire frequency in oak-juniper woodland to be similar to pine forest and roughly twice as common as in semi-desert grassland but gives no return interval. Fires in semi-desert grasslands declined significantly after 1882, corresponding to the start of heavy overgrazing in the region.

Large twentieth century fires on the south slope of the Santa Catalina Mountains in 1910 and 1936 are described by Lauver (1938). The 6,050 ha 1910 fire burned approximately 3240 ha in the "oak type" between June 4 and June 22 in an area two miles south of Soldiers Camp. Suppression attempts were only moderately successful. The fire report she quotes also states that the last fire in this area occurred 23 years previously which approximately corresponds to the 1889 burn mentioned above. The 1936 burn in the middle reaches of Sabino Canyon burned from June 11 to June 15 and was actively and successfully suppressed by 355 fire fighters. More recent burns occurred in this area in 1985 and 1987 (personal observation).

A decreasing fire frequency, usually associated with increased grazing, has been cited as occurring since the end of the last century (Holsinger 1902; Cook 1908; Foster 1917; Leopold 1924; Mehrhoff 1955; Humphrey 1958; Pyne 1984; Bahre 1985, 1991) and is supported by fire history studies for much of the southwest (Dieterich 1980, 1983a; Swetnam and Dieterich 1985; Swetnam et al. 1989, 1992a; 1992b; Caprio et al. 1989; Baisan 1990; Ortloff 1992). In some instances heavy grazing has been promoted as a means of fire protection through the reduction of fine fuels (Korstian 1926). The change in the fire regime has been put forward as one possible cause for the shrub invasion and other vegetation changes noted in a variety of southwestern biotic communities including the Madrean woodland (Hough 1882; Bentley 1898; Smith 1899; Bray 1901; Holsinger 1902; Cook 1908; Griffiths 1910; Foster 1917; Hensel 1923; Leopold 1924; Clements 1934; Whitfield and Beutner 1938b; Humphrey 1949, 1958, 1974; Stewart 1951; Ellison 1960; Harris 1966; Cable 1972). Although most accounts indicate the shift in fire regimes and vegetation occurred late in the 19<sup>th</sup> century, comments by Gregg (1844) suggest that in at least some areas these changes were happening at an earlier time.

*"Indeed there are parts of the southwest now thickly set with trees of good size, that, within the remembrance of the oldest inhabitants, were as naked as the prairie plains; and the appearance of the timber in many other sections indicates that it has grown up within less than a century... It is unquestionably the prairie conflagrations that keep down the woody growth upon most western uplands... In fact, we are now witnessing the encroachment of timber upon prairies wherever the devastating conflagrations have ceased their ravages... Yet may not the time come when these vast plains will be covered with timber?"*

The areas referred to, such as the upper Rio Grande River Valley, were settled by the Spanish and under intense grazing pressure by livestock (primarily sheep) by the late 1700's (Denevan 1967).

Grazing influence was to reduce herbaceous fuels, which along with active fire suppression, acted to reduce the total area being burned. Holsinger (1902) noted drastic changes in Arizona pine forests due to grazing and reduced fire frequency (fires he believed were set by Native Americans) after he questioned what he called the "oldest reliable pioneers". He states:

*"...when first invaded by the white man the forests were open, devoid of undergrowth, and consisted in the main of matured trees, with practically no forest cover. Instead of forest undergrowth, the ground was well set with perennial grasses and other herbage, which being undisturbed, maintained what may be termed a normal condition, or such as existed when the country was first settled and such as is now so much to be desired. It was not an uncommon thing for the early settlers to cut native hay in the pine forests and fill large government contracts at the different military posts."*

He felt that the frequent fires of the past caused little damage but were being replaced by fires of reduced frequency that were more damaging to the forests. In Madrean woodland, Leopold (1924) reports that fire scars suggested the 1880's as the period when these changes began. He states fire frequency up to that point had been about every 10 yr and believes fires were usually ignited by lightning or Indians. Woodland vegetation up to this time was believed to be composed of scattered shrubs and large trees with graminoids dominating. Graminoids were dense enough to carry fire at frequent intervals and then recover quickly. Leopold further states that total fire control causes great damage to watershed and range resources, contrary to administrative policy and popular opinion of the day. An analogous pattern with a reduction in fire frequency as a result of heavy grazing in grasslands has been documented by Mace (1991) for the Borana plateau in Ethiopia. In his research heavy grazing was found to decrease perennial grass dominance while also producing a concurrent increase in woody species and a decrease in the risk of fire.

As an alternative to the grazing hypothesis, Dobyns (1981) suggests that *"... stopping Indoamericans from hunting with fire, and restricting them to reservations, had more to do with the disappearance of Sonoran Desert grasslands than did biomass removal by grazing."* He felt the distribution of vegetation in the region of the Sonoran Desert was almost exclusively determined by native American burning practices usually associated with hunting. The change in this cultural practice rather than the imposition of heavy livestock grazing in the latter half of the nineteenth century produced the vegetation changes we are seeing today.

Repeat photography has been used in several studies of vegetation change in southeastern Arizona with particular emphasis placed on the stability of woodland/grassland boundaries (Leopold 1951; Hastings 1963; Hastings and Turner 1965; Bahre and Bradbury 1978; Humphrey 1987; Bahre 1991). Hastings (1959, 1963) and Hastings and Turner (1965) support the hypothesis of shrub invasion in low elevation woodland but do not believe a decrease in fire frequency is responsible for the vegetation changes. Rather, they feel fire frequency increased in the twentieth century. They raised the question as to how fires were able to limit mesquite invasion in semi-desert grassland while in adjacent oak woodland, with a similar fuel structure and similar fire regime, fire did not keep out oaks. Humphrey (1966) responded that this question could be answered if one knew the fire susceptibility of each species and suggested that mesquite was less fire resistant than oaks. Research by Claveron (1967) who investigated bark characteristics of the two species supports this hypothesis. Hastings and Turner (1965) also report an upward retreat of the lower woodland boundary contrary to Leopold (1924) who states it appeared to be dropping. Humphrey (1987) also made extensive use of repeat photographs to show woody plant increases in many oak woodland areas. When I reviewed his historic photographs it was striking how heavy the grazing had been at the end of the 19<sup>th</sup> Century in most areas pictured. Most grassland and oak woodland areas appear to have had nearly all herbaceous forage consumed. As noted by Leopold (1951) this points to a problem with many of the historic photographs in that most were taken after heavy grazing had begun in southeastern Arizona and so do not actually give a clear picture of the original undisturbed vegetation. Direct evidence providing support for the increase in woody vegetation comes from a recent investigation using stable carbon isotope analysis of soil organic matter across the grassland/woodland ecotone (McPherson et al. 1993). It indicates that both *Prosopis juliflora* and *Quercus emoryi* are recent

components of former grassland. This study used  $\delta^{13}\text{C}$  values to infer dominance of woody ( $\text{C}_3$ ) and grassland species ( $\text{C}_4$ ) over time.

Associated communities - The Madrean evergreen woodland is bounded by several biotic communities where the role and effects of fire on vegetation have been investigated. Principal among these are interior chaparral, semi-desert grassland, desert mountain scrub in the Chihuahuan Desert, and Rocky Mountain - Madrean montane conifer forest where ponderosa pine forests contact oak woodland. Each shares certain floristic characteristics with the woodland at various locations and elevations.

Because of the open aspect of Madrean oak woodland, especially at lower elevations, it is often associated with grassland. Frequently it cannot be told where one begins and the other ends (Hastings and Turner 1965). A great deal of attention and much research on fire in the semi-desert grassland has been conducted (Humphrey 1949, 1953, 1958, 1962, 1963, 1974; Glendening 1952; Glendening and Paulsen 1955; Reynolds and Bohning 1956; Blydenstein 1957; Cable 1959, 1961, 1965, 1967, 1972; Buffington and Herbel 1965; White 1965, 1969; Claveron 1967; Martin 1975; Bock et al. 1976; Bock and Bock 1978, 1992a, 1992b; Bunting et al. 1980; Wright 1980; Sourabie 1982; Wright and Bailey 1982; Martin 1983; Kenney et al. 1986; Bahre 1985; Schmutz et al. 1985; Grover and Musick 1990; Bahre 1993).

Dramatic increases in shrub cover have occurred on these grasslands as has been suggested for the Madrean woodland. At the start of Anglo settlement in the mid-to-late 19<sup>th</sup> Century these grasslands are described as being vast and open. While travelling through the Rio Grande River (Rio del Norte) valley in 1835 Gregg (1844) comments that, "*...The plains and highlands are generally of a prairie character and do not differ materially from those of all Northern Mexico, which are almost everywhere completely void of timber*". Several additional accounts below are based on reports furnished by commanding officers stationed at military

outposts in southeastern Arizona to the Commissioner of Agriculture via the War Department on the forestry conditions in the western states and territories in 1878 (USDA 1879). The brief reports are interesting because they predate the advent of heavy cattle grazing in the region.

Captain J.H. Coster, Eighth Cavalry, A.D.C., acting engineer officer for the Military Division of the Pacific, provided the following descriptions for grassland-oak woodland areas of southeastern Arizona at several locations:

- Camp Grant, on the west side of the Peloncillo Mountains.

*"Situated 4,833 feet above sea-level, on the northwestern base of Graham or Sierra Bonita Mountains, on a sort of mesa sloping towards an extensive plain about fifteen miles wide and over one hundred miles long. On this plain there are no trees of any kind south of Camp Grant, but scattered mesquite (bush) to the northward and to the valley of the Gila River. Abundant mesquite is to be found on the mesa between elevations 4,000 and 6,000 feet. This timber is intermixed with varieties of oak and one juniper, up to an elevation of 7,000 feet."*

- For the mesa areas near Camp Lowell (called Ft. Lowell today), located on the banks of the Rillito River near Tucson.

*"With few exceptions the mesquite trees are very small and stunted in the mesa, but in the valley of the Rillito, and in that part of the Santa Cruz Valley north of the San Xavier mission, south of Tucson, they grow quite large --"*

- Camp Thomas,

*"Mesquite .... grows in fair quantities in the vicinity of the post, but sparingly on the adjoining plains."*

The awareness of the vegetation changes in the Southwest is not new but was recognized by the end of the last century and early in this century (Toumey 1891; Bentley 1898; Smith 1899; Bray 1901; Cook 1908; Griffiths 1901, 1910; Thornber 1910; Foster 1917; Hensel 1923; Leopold 1924, 1937; Barnes 1936). Maintenance of these grasslands in an open condition was historically an important role played by fire (Martin 1983). Areas may have burned at approximately 10 year intervals. Active suppression of fire began during the latter half of the 19th century as settlement of the region increased. This in combination with factors relating to



grazing intensification in the 1880's and climatic changes, including atmospheric CO<sub>2</sub> enrichment over the last century, has been cited as responsible for the vegetation changes (Humphrey 1958; Hastings and Turner 1965; Claveron 1967; Korarek 1969; Wright 1980; Idso and Quinn 1983; Archer 1989, 1994, Mayeux et al. 1991, Idso 1992; Bahre 1993). Today fires are nearly nonexistent in many areas of former semi-desert grassland that are now mesquite or creosote shrublands so we have little data on frequency and extent of burns (Grover and Musick 1990).

Fire can kill many shrub species and inhibit expansion of others, although shrub susceptibility to fire varies depending on species, size, age, season, and quantity of herbaceous fuels present at the time of burning. The postfire response of species is also variable depending on many of these same variables. Cacti are moderately susceptible while perennial graminoids as a group are not harmed and recover within a year or two. However, individual graminoid species such as black grama (*Bouteloua eriopoda*), may suffer adverse effects (Cable 1972, Wright and Bailey 1982; Cornelius 1988). As in the oak woodland, Bahre (1985) felt that fires were larger and more frequent prior to 1890 and that the number of large fires declined after 1882. This was probably a result of overgrazing with the decline in the number of grassland fires preceding shrub invasion.

The shrubby aspect of the Madrean woodland possesses many similarities to interior chaparral in parts of its range. Fire has also been well studied within this biotic community (Cable 1957, 1975; Carmichael et al. 1978; Pase 1965; Pase and Glendening 1965; Pond and Cable 1962; Pase and Lindenmuth 1971; Pase and Pond 1964; Box et al. 1967; Axelrod 1958) although not as well studied as California chaparral (Vogl and Schorr 1972; Barro and Conrad 1991) to which it is closely related (Pase and Brown 1982). A number of species found in both interior chaparral and Madrean woodland have related counterparts in California chaparral, such as *Arctostaphylos* (manzanita), *Garrya* (silktassel), and *Brickellia* (brickellbrush) (Cooper 1922;

Pase and Brown 1982). Interior chaparral has a long association with fire to which it is well adapted (Axelrod 1958). It regenerates quickly without a typical postfire successional sequence (Carmichael et al. 1978). Shrub densities recover within five years of burning (Cable 1957) and cover in about six to seven years (Pond and Cable 1962; Pase and Pond 1964). This quick recovery can prevent long term establishment of graminoids (Carmichael et al. 1978). Chaparral recovery depends on crown/root sprouting ability of particular species, the ability to establish seedlings, relative abundance of species prefire, and season of burn (Cable 1975; Carmichael et al. 1978). Other features of chaparral that Axelrod (1958) felt show its adaption to fire are the production of seed at an early age, production of large numbers and of fire resistant seed, and fire dependent germination.

Madrean evergreen woodland in the Trans-Pecos region of west Texas displays similarities to and shares species with Chihuahuan desert mountain scrub. Limited research on fire effects and species response of this vegetation has been carried out (Kittams 1972; Bunting and Wright 1977; Ahlstrand 1978a, 1978b, 1979a, 1979b, 1980, 1982). Fire frequency has also decreased in the last century in this area due to reductions in fuels, with concurrent increases in shrubs, attributed to grazing. With burning, woody shrubs, rosette shrubs and succulents decrease with a corresponding increase in graminoids and forbs, attributed to reduced competition. However, many shrub and succulent species show good sprouting ability following fire but with more frequent burning would decrease while graminoids that recover quicker increase.

At higher elevations Madrean oak woodland contacts ponderosa pine forest (*Pinus ponderosa*). Low intensity, frequent fires are common in this type, resulting in a relatively open, often park-like forest (Blumer 1910a; Weaver 1951; Cooper 1960; Brown 1982; White 1985). This open forest is similar in many respects to the open Mexican oak-pine phase of the Madrean woodland found in the Sierra Madre of Mexico (Brown 1982). Fire suppression can result in

dense often dog-hair stands of pine and an increase in shrubs (Cooper 1960). Mean fire interval on Mica Mountain in the Rincon Mountains, immediately southeast of the Catalina Mountains, was 6.1 years with a fire return interval of up to 20 years at single sites, for the period 1657-1893 when fire-scars were analyzed for the area (Baisan 1990). Crossdated fire-scar samples from one area of higher elevation pine forest in Rose Canyon in the Santa Catalina Mountains recorded fires in 1702, 1704, 1707, 1722, 1725, 1735, 1748, 1752, 1772, 1785, 1803, 1806, 1819, 1836, 1851, 1857, 1870, and 1887 ( unpublished report on file at the Laboratory of Tree-Ring Research). Similar frequencies are reported by fire history research from the Pinaleno Mountains (Grissino-Mayer and Swetnam 1992) and in the Guadalupe Mountains of Texas where Ahlstrand (1979a, 1980) found the average fire-free interval was 13.8 years (range 2-45 years) and 11.8 years (range 2-37 years) at two sites. Most information about fire effects in these pine forests is not applicable to the Molino Basin area since my study concentrated on the lower edge of the oak woodland. However, I believe they provide some information about fire frequency because fires, at least historically, may have burned across the whole elevational gradient from semi-desert grassland into upper elevation forests.

Other oak woodlands - Related oak woodlands in which fire effects have been studied include the Edwards Plateau region of Texas (Fonteyn et al. 1984) and California oak woodlands (Naveh 1967, Barbour and Major 1977; Baker et al. 1981) where most of the investigations have concentrated on oak management and postfire response (Heady 1973; Minnich 1980; Rundel 1980; Snow 1980; Griffin 1980; Green 1980; Plumb 1963, 1980a, 1980b; Parsons 1981; Plumb and McDonald 1981; Plumb and Gomez 1983; McClaran and Bartolome 1989; Haggerty 1991, 1993). Fire is a common event in California woodlands and affects the probability of an oak species growing in an area. Species in the region differ widely in their tolerance and postfire

response to fire. High but differing survival rates were found for *Quercus douglasii* (blue oak - 93%) and *Q. wislizenii* (interior live oak - 79%) in the Sierra Nevada foothills (Haggerty 1991, 1993). Differing survival rates, primarily of seedlings and saplings, were also observed in two other sympatric California oak species, *Q. engelmanni* (Engelmann oak) and *Q. agrifolia* (coast live oak) (Snow 1980). Tree characteristics affecting survival are bark thickness, relative amount of living and dead bark, and ability to sprout from the bole. Sprouting from the root crown is considered the most important adaptive trait and helps maintain established stands (Plumb and McDonald 1981). McClaran and Bartolome (1989) found an association between tree ages and fire dates in *Quercus douglasii* suggesting a positive role for fire in recruitment.

In sclerophyllous oak woodlands of the Mediterranean basin and regions further east in Eurasia, fire effects and vegetation responses have been reported by Naveh (1967, 1973a, 1973b, 1975, 1977), LeHouerou (1973, 1977), Novo (1977), Trabaud (1973, 1977, 1983, 1991), Liacos (1977), Susmel (1977), Trabaud and Lepart (1980, 1981), Gopal and Meher-Homji (1983), Malanson and Trabaud (1988), Canadell et al. (1991), Gratani and Amadori (1991) and Huntsinger and Bartolome (1993). Naveh (1975) summarized the significance of fire in the Mediterranean region, stating it was a strong selective force and important in maintaining ecological diversity and existence of oak vegetation and savannahs. A 1977 symposium (Mooney and Conrad 1977) brought together much of the then current state of information about fire in Mediterranean ecosystems.

### STUDY AREA

The study I conducted was located in the Santa Catalina Mountains northeast of Tucson in southeastern Arizona (Figure 3). The study area in Molino Basin lies within the Coronado National Forest, Santa Catalina Ranger District. The Santa Catalina Mountains rise from the Santa Cruz valley floor at about 700 m up to 2775 m at Mt. Lemmon. This elevational change creates strong physical and biotic gradients from lower to upper elevations. Precipitation increases with elevation while temperature and evaporation generally decrease with increasing elevation. Plant distribution patterns in the Santa Catalinas have been the subject of several classic studies (Shreve 1915; Whittaker and Niering 1964, 1965, 1968a, 1968b, 1975; Whittaker

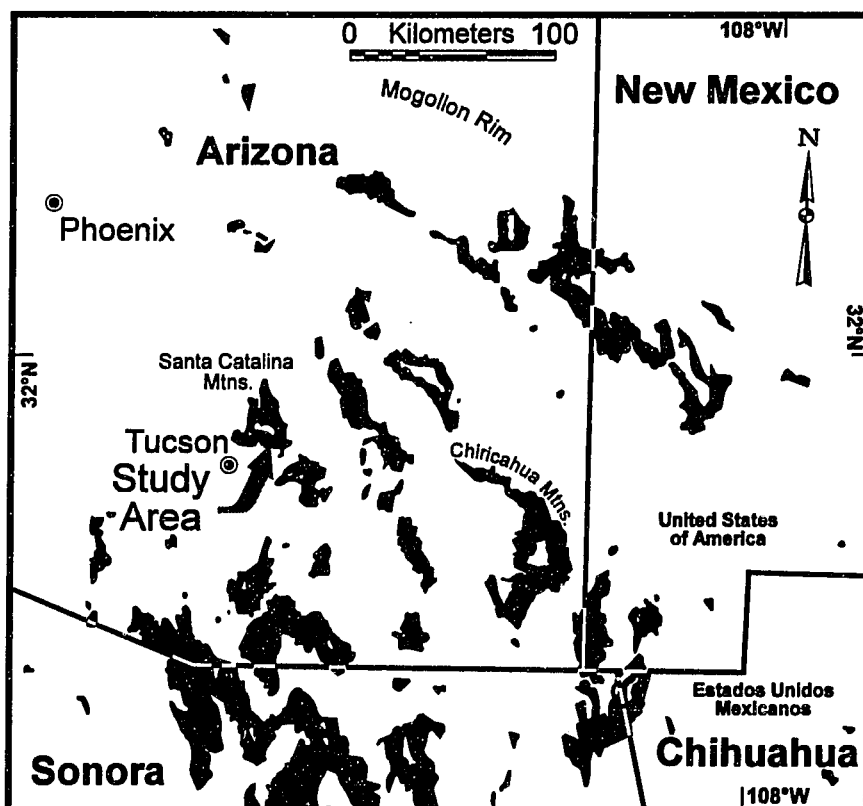


Figure 3. Location of study area in south central Arizona in relation to the distribution of Madrean oak woodland (dark areas) in the surrounding region (from Brown and Lowe 1980).

et al. 1968; Niering and Lowe 1984). These patterns are shown in Figure 4. Whittaker and associates include descriptions of Molino Basin vegetation in the presentation of their investigations on vegetation gradients on the south slopes of the Santa Catalinas .

### 3.1 Location

The study area in Molino Basin was about 40 km (25 mi) northeast of the University of Arizona campus. Three study sites were located between milepost five and seven on the Mt. Lemmon Highway (Figure 5). Much of the basin burned during the end of June 1983. I established plots in burned and unburned areas at three different sites. Sampling was begun in May 1984.

One site (referred to as site "A" on data forms) was situated on a south facing slope in the western and upper part of the basin (this site will be referred to as the south slope or "S" in the text and figures). Plots were located about 400-500 m above the road (Figure 6). Burned plots were located about 75 m below the west end of a line of cliffs forming the ridgetop on the north side of the basin, while unburned plots were located about 200 m west and slightly below the ridge-top. A second site (site "B" on data forms) was on an east-to-southeast facing slope about 1.5 km up Molino Creek from the road crossing in the eastern end of the basin (east slope or "E"). The plots were on a lower slope about 30-40 m above and west of the creek bed. Burned plots were above a small falls on the creek while unburned plots were another hundred meters up the creek and beyond a draw entering from the west. A third site (site "C" data forms) on a north facing slope was established on a ridge above the upper end of the lower Molino Basin campground (north slope or "N"). Both burned and unburned plots were located near the ridge-top.

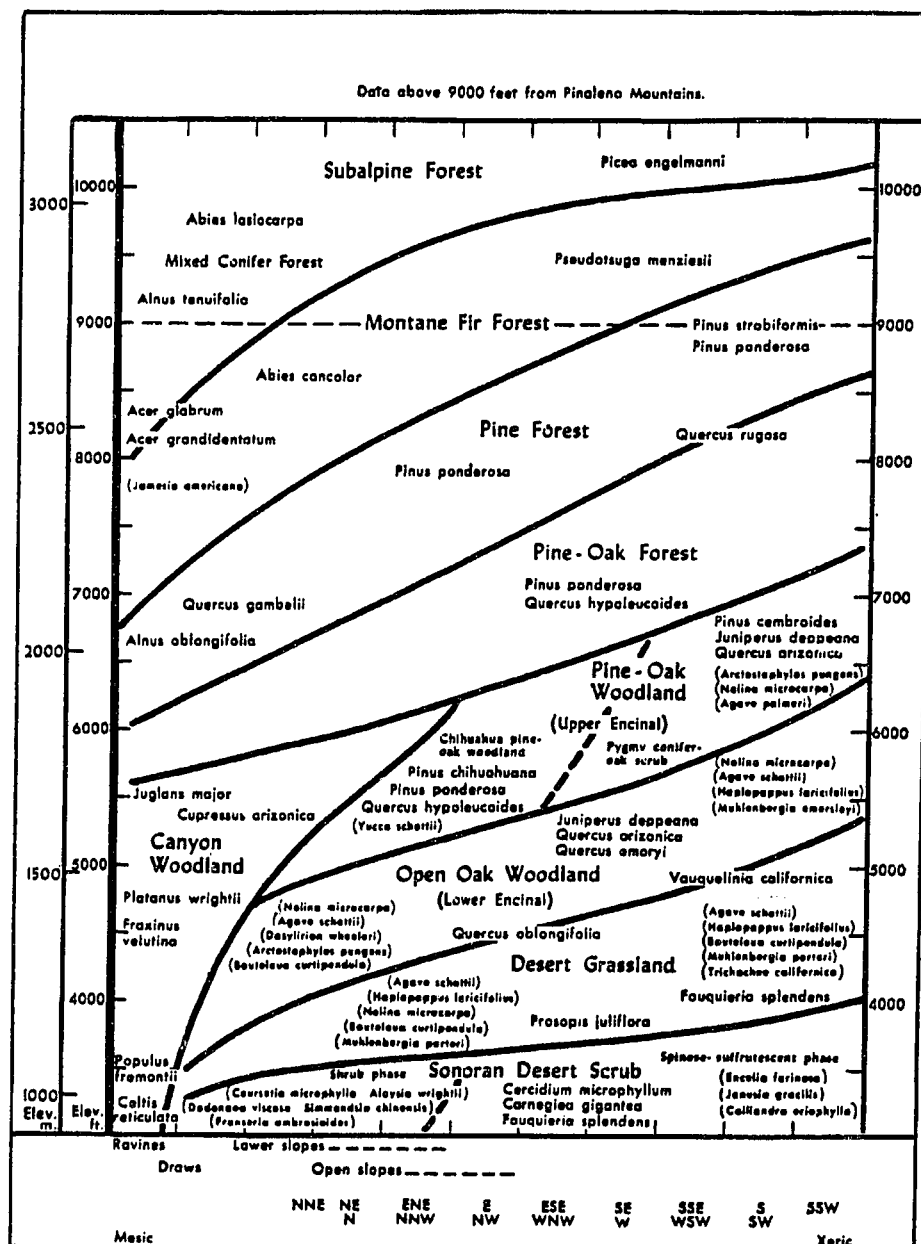
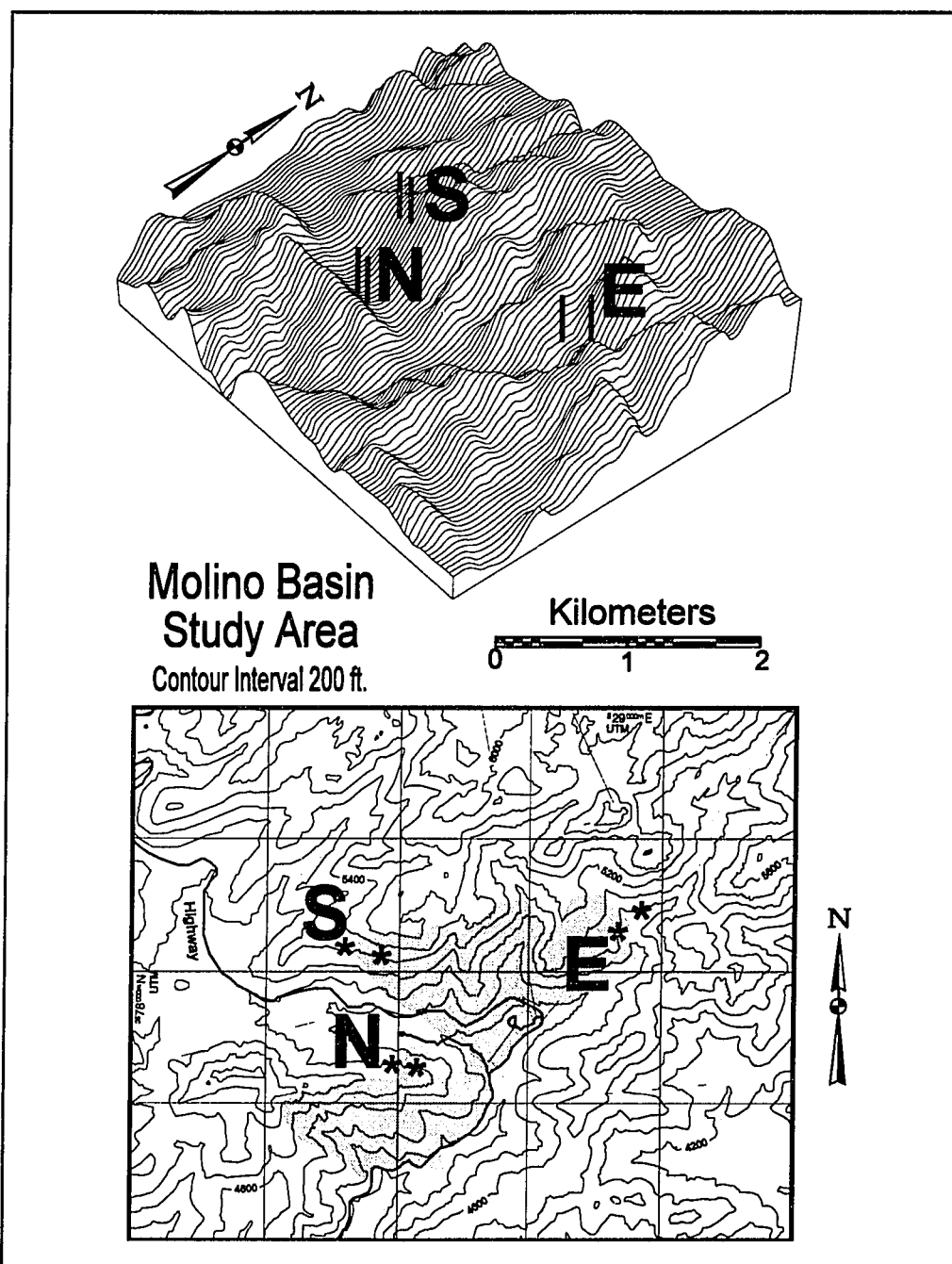
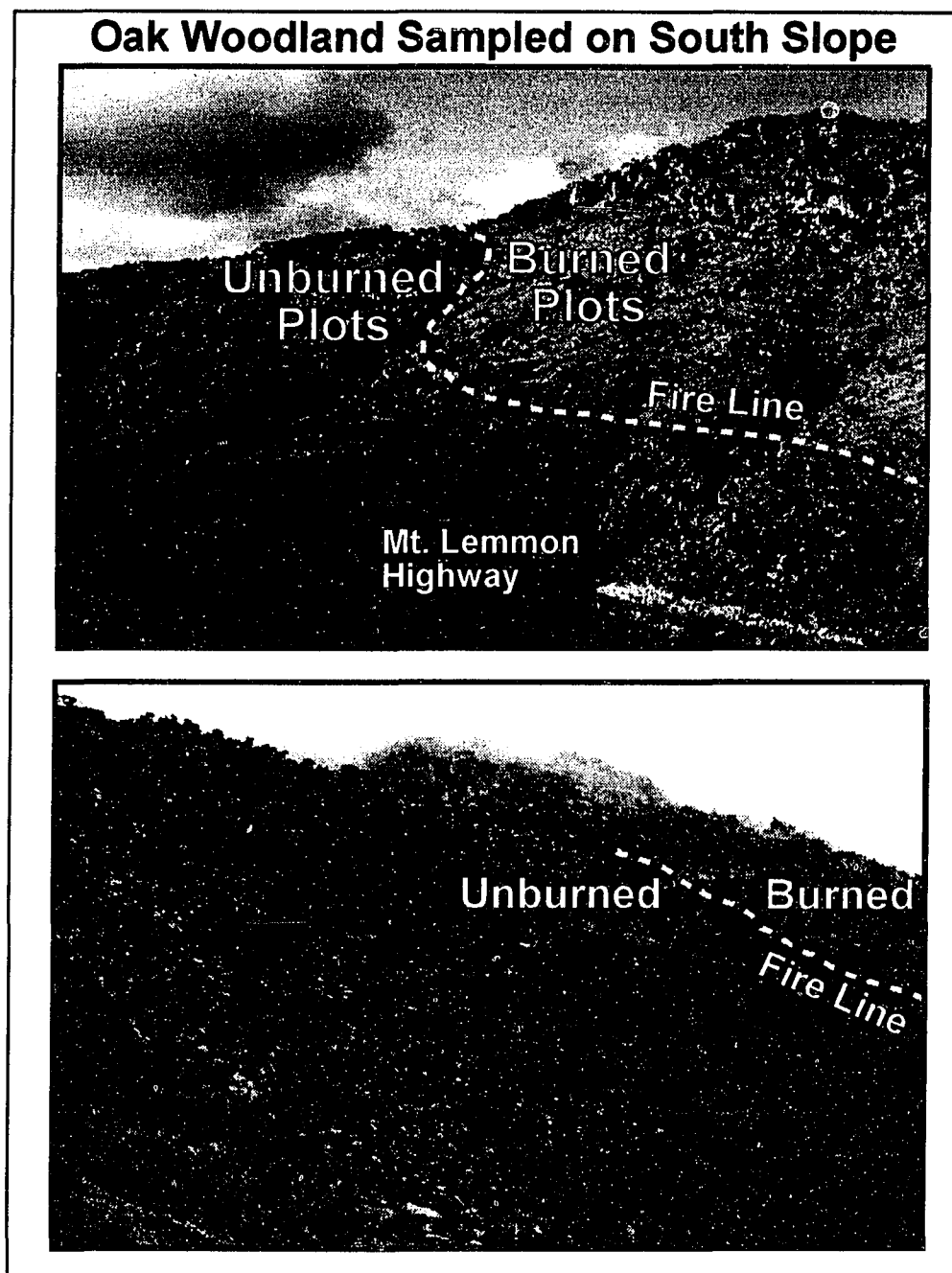


Figure 4. Mosaic chart of vegetation of the Santa Catalina Mountains (and elevations above 2700 m in the Pinaleno Mtns.), Arizona, based on 400 vegetation samples. Major species are indicated by their centers of maximum importance; dominants of lower strata are indicated in parentheses (from Whittaker and Niering 1965).



**Figure 5.** Study area in the Santa Catalina Mountains, Coronado National Forest. Map shows approximate burn boundaries and locations of the three sample sites in Molino Basin - south slope "S", east slope "E", and north slope "N" (in the field the south slope was called "A", the east slope as "B", and the north slope as "C").





**Figure 6.** View of oak woodland and burned and unburned sites sampled on the south slope. Dotted line shows the burn boundary.

The universal transverse mercator (UTM) coordinates for each plot were determined to within 10-20 meters (Table 1). Each plot was permanently with iron rebar posts (25-30 cm high) at each end of four transects.

### 3.2 Climate

Climate of the study area is sub-humid (surrounded by a semi-arid desert), characterized by moderate rainfall, relatively high temperatures, high evaporation and low humidity. No precipitation or temperature records are available from the study area so records from weather stations located nearby and throughout oak woodlands in southeast Arizona were examined.

Precipitation - Precipitation has a distinctly bimodal distribution with wet winters and summers (Blumer 1910b, Wooton 1916; Pearson 1922; Whitfield 1938b; Jurwitz 1953; Whittaker and Niering 1965; Nevin et al. 1990). The Santa Catalina Mountains are in a transition zone between an arid climate to the west and north, with winter rainfall exceeding summer rainfall, and a semi-arid climate to the east and south where summer rainfall exceeds winter rainfall (Pearson 1922; Turnage and Mallery 1941; Whittaker and Niering 1965). About 57% of Tucson's precipitation falls during the summer while at Oracle on the north side of the mountains about 47% falls in the summer (McDonald 1956). Summer rains occur from July to September and winter storms from December to March, with a pronounced seasonal drought during late spring and fall. Summer precipitation in the form of thunderstorms begins with the monsoonal flow of moist air from Gulf of Mexico. This may be augmented later in the season by moisture from the southwest, originating in the Gulf of California and Pacific (Sellers et al. 1985). Thunder-storms

develop when ample moisture in a state of conditional instability is triggered by thermal and orographic lifting to release this instability (Grant 1933; Pyne 1984). These storms are typically of high intensity, of short duration and small in areal extent. Winter moisture is associated with cyclonic frontal systems originating to the northwest in the Pacific. These are widespread in area, tend to last several days and have gentle rainfall with increased infiltration. The amount of summer rainfall varies from point-to-point but not year-to year-while winter rainfall varies from year-to-year but is similar between points within a season (Grant 1933; Humphrey 1933; McDonald 1956; Sellers 1960). The amounts of annual precipitation over southern Arizona is also related to elevation, with greater rainfall at higher elevations (Grant 1933). Overlaying this seasonal pattern of precipitation is a longer term pattern of wet and dry periods closely associated with ENSO or El Niño-Southern Oscillation events (Philander 1983). These global climatic anomalies recur at intervals of 2 to 10 years with varying intensities. In the southwestern United States these events are related to wetter than average fall, winter, and spring seasons (Andrade and Sellers 1988).

The long-term normal and average precipitation from 1982 to 1985 at Oracle and at all major oak woodland stations in southeast Arizona are shown in Table 2. Figure 7 shows monthly precipitation departures from the norm for stations in oak woodlands. An unusual rainfall event occurred during a seven day period between September 28 and October 4, 1983. Precipitation measurements at Oracle and the Tucson Magnetic Observatory, respectively, recorded 171.7 mm and 193.3 mm of rainfall. Flooding occurred in many stream and river channels throughout southeastern Arizona. Scouring of the major ravines and Molino Creek occurred in Molino Basin. It is unknown how the burn affected runoff and erosion. However, soil movement on the slopes did not appear extensive. Rapid recovery of the perennial vegetation plus expansion of

**Temperature** - Temperature differences from the norm for the period of study are shown in Figure 7. Normal and averages at oak woodland stations from 1982 to 1985 are given in Table 2. Highest average temperatures occur during late June and early July, with lowest during January. Based on records from nine oak woodland weather stations (Bisbee, Canelo, Cascabel, Chiricahua National Monument, Coronado National Memorial, Oracle, Portal, Ruby, Santa Rita Experimental Range) average minimum temperature for January was  $-0.2^{\circ}\text{C}$  while average maximum was  $14.7^{\circ}\text{C}$ . For July these temperatures were respectively  $17.4^{\circ}\text{C}$  and  $32.8^{\circ}\text{C}$ .

Seasonal shifts in precipitation and temperatures interact to create two periods of plant growth annually in the oak woodland, early spring and summer. This is similar to the nearby lower deserts (Shreve 1917), but with plant growth following winter rains delayed until spring. Winter temperatures are usually too low to permit growth, while moisture is limiting at other times, except during the short spring, and the period of summer rain. Calculated potential evapotranspiration (cm) averaged for four oak woodland sites (Bisbee, Canelo, Chiricahua

**Table 1.** Average precipitation (mm) and temperature ( $^{\circ}\text{C}$ ) at Oracle and at stations located throughout oak woodlands in southeast Arizona. Period of study was from January 1982 to December 1985.

	SE Arizona Oak Woodlands*		Oracle	
	Normal	Study Period	Normal	Study Period
<b><u>Precipitation</u></b>				
Annual	491 mm	655 mm	528 mm	793 mm
July	109	107	79	92
Jan.	35	60	49	99
<b><u>Temperature</u></b>				
Annual	$15.8^{\circ}\text{C}$	$15.3^{\circ}\text{C}$	$16.8^{\circ}\text{C}$	$15.9^{\circ}\text{C}$
July	25.1	24.5	26.6	25.7
Jan.	7.2	6.8	7.9	6.9

\* Oak woodland precipitation data are from nine stations; Bisbee, Canelo, Chiricahua National Monument, Coronado National Memorial, Oracle, Patagonia, Portal, Rucker Canyon, Santa Rita Experimental Range and Cascabel. Temperature data are from four stations; Canelo, Chiricahua National Monument, Oracle and Santa Rita Experimental Range.

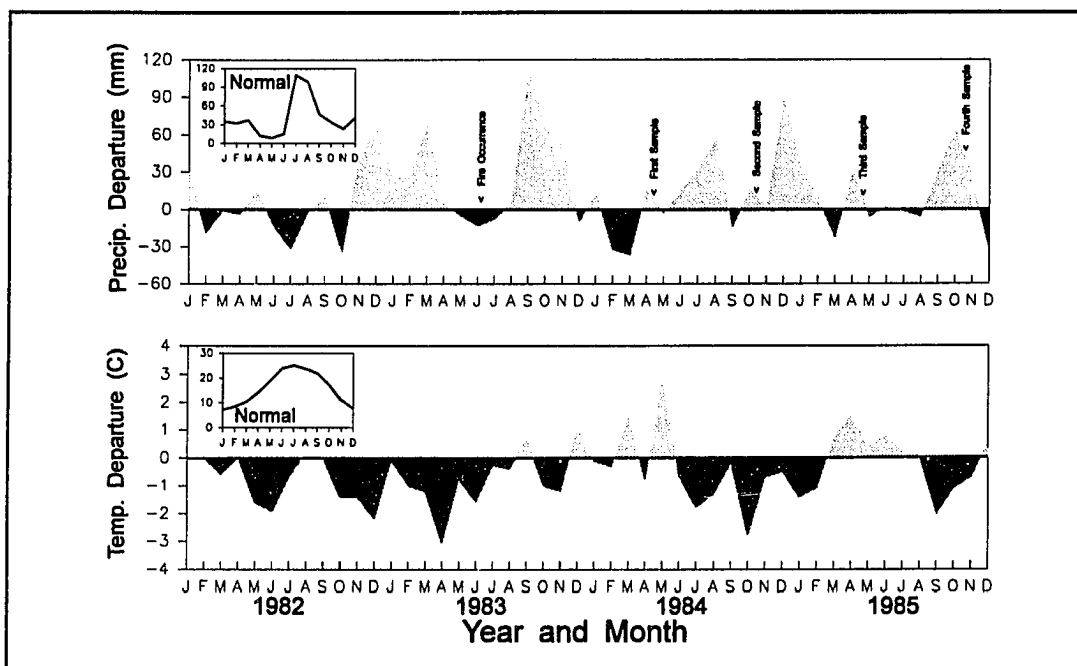


Figure 7. Departure of mean monthly temperature and rainfall from norm for period 1982 to 1985. Dates of fire occurrence and sampling are also shown.

National Monument, Oracle) was 31.90 annually, 0.41 for January and 5.72 for July (Buol 1964).

At a slightly lower 930 m elevation site in desert scrub in the Santa Catalina Mountains, Haase (1970) found the most severe drought conditions on SW aspects during the arid foresummer, on S and SSW aspects during the fall drought, with the warmest and driest aspect during the summer rainy season to be SSE and winter rainy season to be S.

### 3.3 Physical Features

Topography - Molino Basin forms an elongated valley running northwest to southeast.

It is part of a narrow linear valley running WNW that includes Romero Canyon and Sabino Basin and separates a rough forerange from the main mountain mass of the Santa Catalinas. A divided parallel ridge rising about 120 m above the rolling basin floor to the south and curving northeast, forms the basin's south and east flanks. This ridge forms the north facing slope and is cut by Molino Creek flowing into the basin from the northeast and out to the south. To the north a high

rugged ridge dominates. It rises to about 1840 m, forms the south facing slope and is cut by several intermittent drainage. The west boundary of the basin is formed by a low rounded pass separating it from Soldier Creek. Microtopography of the sample sites was rough with many rock outcrops.

Geology - The Santa Catalina Mountains are part of a southern extension of the Basin and Range Province located between the Colorado Plateau and the Sierra Madre in Mexico. They form the western edge of the Mountain Plateau or southeast high section of this province. This section extends eastward into western Texas with many peaks exceeding 3000 m. These peaks are often called "mountain islands" in a "desert sea" (MacDougall 1908; Gehlbach 1981). The dome of the main range of the Santa Catalinas together with a forerange, make up the Catalina section of a huge Rincon-Catalina metamorphic core complex, the largest in the Basin and Range region (Chronic 1983).

Geologically the Santa Catalinas are composed of Precambrian igneous and metamorphic rocks forming the Catalina gneissic complex. The forerange is dominated by layered or banded gneiss with compositional differences between layers, visible as alternating light and dark layers (DuBois 1959b; Wilson et al. 1960; Peterson 1968). This gneiss has a well-defined foliation and lineation structure and is part of a large northeast trending anticline (Laughlin 1959; DuBois 1959a, 1959b). The differential ability of the rocks to resist erosion plus faulting and fracturing has formed the basin. The main range forming the south slope of the basin is composed of granitic gneiss (DuBois 1959b; Wilson et al. 1960; Peterson 1968). It rises steeply, with areas of outcrops and spires, to a dissected upland above 2100 m.

Soils - Soils of the Catalinas are predominantly shallow entisols and inceptisols that tend to be immature with limited profile development. Southern exposures in Molino Basin have

been classified as lithic ustorthents (Galioto 1985) (thermic semiarid) while more mesic north slopes have been classified as lithic haplustolls (Galioto 1985, Hendricks 1985). Soils are shallow, gravelly and moderately coarse, and generally on steep terrain with many rock outcrops.

Characteristics of the soils and their relationship to vegetation on the south slope of the Santa Catalinas has been well described by Whittaker et al. (1968) and are similar to the soil gradient studied in the Pinalenos Mountains by Martin and Fletcher (1943).

### 3.4 Vegetation

Vegetation in Molino Basin forms a gradient from upper semi-desert grassland on south facing slopes to moderately dense oak woodland on north facing slopes. It has components of typical open woodland plus some derived from interior chaparral found in central Arizona. The three sites selected for study represent: 1) very open woodland grading into semi-desert grassland on a south facing slope, 2) "open woodland" (Whittaker and Niering 1965) or "lower encinal" (Shreve 1915) on a southeast to east facing slope and 3) a relatively dense woodland on a north facing slope somewhat characteristic of "pygmy conifer-oak woodland" (Whittaker and Niering 1965).

Habitat types have recently been designated for vegetation in the Madrean oak woodland of New Mexico and Arizona (Moir 1986). The three sites sampled are represented by two types: *Quercus oblongifolia*/*Dasyllirion wheeleri* habitat type (Mexican blue oak/sotal - QUOB/DAWH) on the south and southeast slope, and *Quercus emoryi*/*Dasyllirion wheeleri* habitat type (Emoryi oak/sotal - QUEM/DAWH) on the north facing slope.

The south facing site has a savannah like aspect with grasses dominating, though on a steep slope. Trees are predominantly *Quercus oblongifolia* with a few scattered and generally smaller *Q. emoryi* and a rare *Pinus discolor* or *Juniperus deppeana*. Some *Q. oblongifolia* are

large with DBH's up to 46 cm. These individuals are usually rooted among rocks that may provide some measure of fire protection to the crown and trunks. Scattered clumps of shrubs exist and are mostly *Arctostaphylos pungens* and *Garrya wrightii*. Common subshrubs are *Agave schottii* and *Calliandra eriophylla* with scattered *Dasyllirion wheeleri*, *Haplopappus laricifolius*, and *Selloa glutinosa*. Wet or warm season graminoids dominate the herbaceous vegetation with important species being *Eragrostis intermedia*, *Muhlenbergia emersleyi*, *Bouteloua curtipendula*, *B. hirsuta*, *Andropogon cirratus*, *Lycurus phleoides* and *Heteropogon contortus*. Important forbs include *Gnaphalium wrightii*, *Artemisia ludoviciana* and *Lotus rigidus*.

The east facing site represents a more typical open woodland described by Whittaker and Niering (1965) and Niering and Lowe (1984). Trees are important with both *Quercus oblongifolia* and *Q. emoryi* about equally represented. A few scattered *Pinus discolor*, *Juniperus deppeana* and *Q. arizonica* also occur, the latter indicative of a slightly more mesic site than the south facing slope. Shrubs are also more dominant than on the south slope with *Arctostaphylos pungens* and *Garrya wrightii* common. *Agave schottii* and *Desmodium cinerascens* are the most abundant subshrubs with scattered individuals of *Dasyllirion wheeleri*, *Nolina microcarpa*, *Haplopappus laricifolius* and *Gossypium thurberi*. Herbaceous flora is dominated by graminoids and pteridophytes. Common graminoids include *Eragrostis intermedia*, *Muhlenbergia emersleyi*, *Bouteloua curtipendula*, *B. hirsuta*, *Andropogon cirratus* and *Trachypogon secundus*. *Selaginella rupincola* along with *Cheilanthes wootoni* form the major cover constituent. Common forbs are similar to the south facing site.

On the north facing slope tree cover is slightly greater than at the east site with *Quercus emoryi* dominating and *Q. oblongifolia* a minor constituent. *Q. arizonica*, *Juniperus deppeana* and *Pinus discolor* are more important than at any other site. Shrubs form the major



cover component and give the site a closed canopy aspect with large clumps of *Arctostaphylos pungens* and *Garrya wrightii* predominating. Important shrubs include *Brickellia californica*, *Haplopappus laricifolius*, and *Nolina microcarpa*. Herbaceous plant cover is less than at the other sites with the only important species being *Selaginella rupicola*. Common grasses include *Koeleria cristata*, *Muhlenbergia emersleyi*, *Andropogon cirratus* and *Aristida adscensionis*. Major forbs consist of *Agastache breviflora*, *Gnaphalium wrightii*, *Artemisia ludoviciana* and the fern *Cheilanthes wootoni*.

### 3.5 History

Historically the Santa Catalinas and other southeastern Arizona mountain ranges were the realms of Apache Indians although they too were relatively recent entrants into the region, arriving in the mid-to-late 1600's taking areas occupied by Northern Pimans. By the early 1700's there was a minimal Spanish influence in the Tucson area with limited farming, cattle grazing and mining. In 1776 a Spanish royal garrison was established in the Presidio of Tucson as the northernmost military outpost in this area of the Spanish colony. The garrison acted as an effective deterrent to Apache aggression in the area with a period of general peace ensuing. With the Mexican war of independence ending in 1821 this influence crumbled. By the 1830's this period of peace ended with increasing Apache autonomy and aggression toward Europeans (Dobyns 1981). The area became part of the United States in 1854 with the Gadsden Purchase from Mexico and opened to settlement around 1870. By 1880, extensive sheep and cattle grazing was taking place. Whittaker and Niering (1965) felt the grazing impact was not great above the bajada and probably had little impact on Molino Basin.

The Santa Catalina Mountains (also known historically as the Catarina Mountains) became a forest reserve in 1902 (Catalina Forest Reserve) and a national forest in 1908 (part of

Coronado National Forest). The road to Mt. Lemmon (General Hitchcock Highway) was begun in 1933 and completed in 1947 (Heylmun 1979). Molino Basin was closed to grazing with the opening of the road (Whittaker and Niering 1965) and the construction of a campground. Several small inactive mining prospects are present in the basin.

### 3.6 Fire

Evidence of fire is apparent throughout the basin and at all study sites as charred wood fragments and stumps or fire scarred oaks and junipers. Niering and Lowe (1984) state a fire burned the basin's northwest end during 1963. Presence of old oak snags and fire scarred trees suggest this area may be west of the site located on the south slope. None of the present study sites appears to have burned in the recent past.

The fire whose effects are being studied burned from June 28 - 30, 1983 during a period of extreme fire danger. It was man caused but burned during the period when natural fires are most common. Minimal control efforts were exerted for a period while Forest Service personnel were suppressing other fires. Approximately 259 ha burned by the time suppression was successful (Figure 5) with about 200 ha burned the first day. Suppression was achieved by back-burning and guiding the fire into natural barriers.

Sites on the south and east aspect burned with a head or flanking fire moving upslope (personal observation). Firelines were evident along fire boundaries between burned and unburned plots at these sites. A backing fire moving downslope from the ridgetop burned the north aspect site after crossing the ridge from the south slope below Molino Basin.

## MATERIALS and METHODS

### 4.1 Experimental Approach

Sampling was designed to test for differences in vegetation at three sites of differing aspect, each with a burned and unburned subsite. This choice of sites allowed the examination of a wider range of fire effects since vegetation structure varied with aspect. Vegetation was sampled using permanently placed plots in vegetatively similar areas at each site. Subsites were sampled using three randomly placed plots established on adjacent burned and unburned areas. Individual plots consisted of transects and nested quadrats. Three quadrat sizes were used to sample each of the three life-form strata: herbaceous (microplots), subshrub (macroplots), and shrub-trees (subplots). Sampling was conducted to detect vegetation differences in cover, frequency and density between site and burn factors. Additionally, I took random herbaceous biomass and fuel samples immediately adjacent to each plot. I began sampling one year postfire and continued it for two consecutive years. This permitted me to measure the first year response, along with some longer term implications of the fire's effect (Britton and Clark ND).

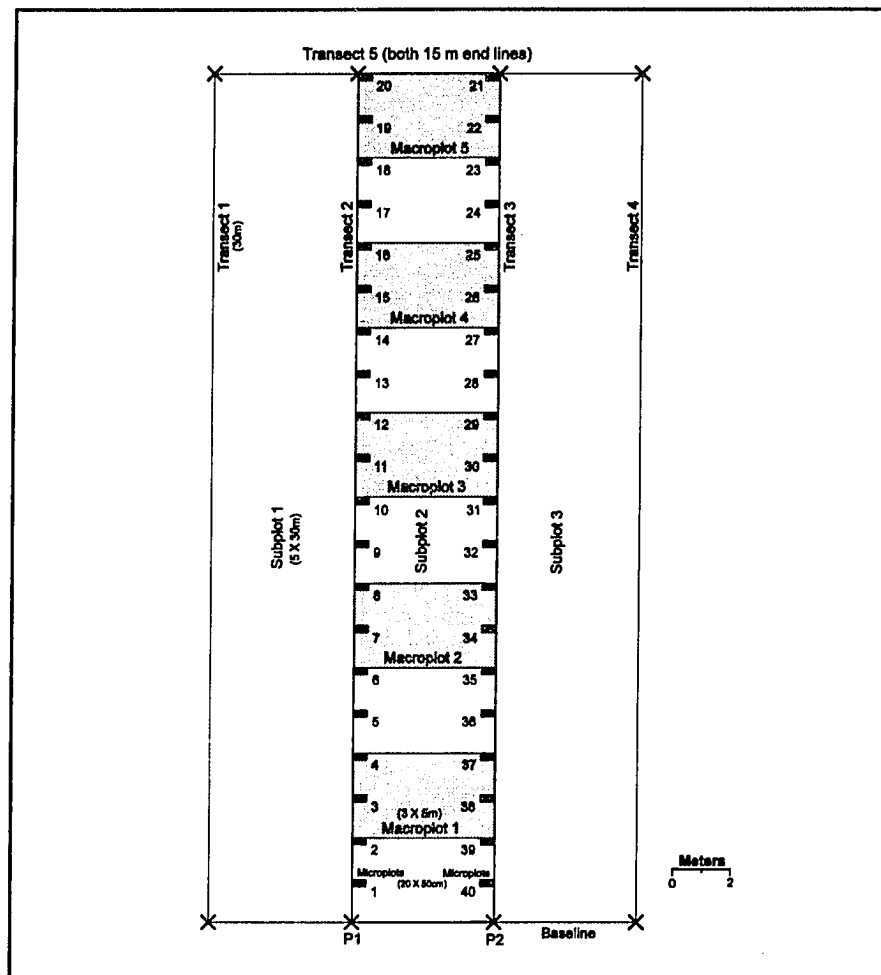
General plot design was compact to facilitate placement within homogeneous sites, in an area where topography and vegetation were variable. Rectangularly shaped quadrats were used for all density samples, since many important plant species had clumped distributions. This shape provides better estimates with lower variances when sampling clumped vegetation (Mueller-Dombois and Ellenberg 1974). I determined sampling adequacy for common species from species-area curves for minimal sample area, and by plotting running means for an "efficient" number of density quadrats (Mueller-Dombois and Ellenberg 1974).

Species identification follows Kearney and Peebles (1951). Non-flowering vegetative graminoids were identified using Barnard and Potter (1984). I collected voucher specimens of nearly all species encountered during sampling.

## 4.2 Field Methods

Site selection - Criteria I used in site selection were; 1) locations away from developed areas to avoid possible disturbance due to hikers, campground or road proximity, 2) necessity for areas with well-defined fire boundaries between subsites, 3) areas that were fairly uniformly burned (as opposed to patchy) for placement of burned plots, 4) sites that appeared to have been homogeneous and vegetatively alike before burning and 5) sites with similar slope, aspect, elevation and other topographical features between subsites. Three sites were then selected, one each on a south facing slope (S), southeast facing slope (E) and north facing slope (N).

Sampling layout - At each subsite, beginning at a random point, I ran a 60 m transect perpendicular to the slope, along which I established three random non overlapping plots. The plots were 15 x 30 m with their long axis parallel to the slope (Figure 8). Eight iron rebar posts (20-30 cm high) were placed at 0, 5, 10, and 15 m along the top and bottom of each plot. Each post had an aluminum tag attached, showing site (S1-3), plot (P1-3), transect (T1-4) and position, either top (T) or bottom (B). Five 30 m line intercept transects were laid out at each plot, four running lengthwise from top to bottom at 0, 5, 10 and 15 m, and one broken into two sections across the top and bottom of the plot. Tree, shrub and subshrub cover were measured along these transects. Nested quadrats within each plot were delineated with metal pins and flagging. Each plot was subdivided into three 5 x 30 m subplots for measuring tree and shrub density (number of



**Figure 8.** Sample plot design used in sampling cover, frequency, and density. Diagram shows baseline along which the three plots at each site were randomly positioned, and the location the two photo-points (P1 and P2) for most plots.

stems) and frequency (number of plots in which species occurred). Within the center plot I marked out ten 3 x 5 m macroplots with an alternating set of five used to sample subshrub density and frequency. Along the interior sides of the two central transects I used forty 0.1 m<sup>2</sup> herbaceous vegetation microplots (20 x 50 cm) to sample cover, frequency and density with a movable quadrat frame. The microplots were placed 1.5 m apart along a tape forming the

transect. One corner of each was permanently marked, allowing repeated measures of the same area. Opposite each plot and outside any other plot, I clipped and collected six random herbaceous and litter biomass 1 m<sup>2</sup> plots.

#### 4.3 Data Collection

Field methods. The data collected in the field consisted of cover, number of individuals, height, DBH of trees, photos, and biomass. The photos were taken at two points at each plot during each sample. I collected data at three sites (S, E, N) with six plots located at each site, three in an unburned subsite and three in a burned subsite, for a total of 18 plots for the study. Collection procedures for each of the plots are summarized below for the various components. Data were collected at approximately six month intervals for two years, with samples taken in the spring following the winter rains and again in the fall following the summer monsoon.

##### I. Herbaceous species microplots (40 per plot), 20 x 50 cm (0.1 m<sup>2</sup> each, 4 m<sup>2</sup> total).

a) Cover of each herbaceous species in a microplot was recorded using modified

Daubenmire cover classes (Daubenmire 1968b, Mueller-Dombois and Ellenberg 1974). All vegetation within the three-dimensional vertical column (0.1 m<sup>2</sup>) of the microplot boundary was recorded. Cover was based on the crown area of each plant, such that total cover could exceed 100%. Cover classes and midpoint values used to calculate averages were as follows;

T = 0-1% cover (midpoint value 0.5%)

1 = >1-5 (3)

4 = >50-75 (62.5)

2 = >5-25 (15)

5 = >75-95 (85)

3 = >25-50 (37.5)

6 = >95-100 (97.5)

b) Number of individuals of each species rooted in a microplot was counted. Each clump of species such as bunch-grasses were counted as one individual.

c) Coverage of bare ground, rock, and litter in each microplot was recorded using the modified cover classes. I defined cover of bare ground as exposed surface area without plant or litter cover.

II. Subshrub species macroplots (five per plot), 3 X 5 m (15 m<sup>2</sup> each, 75 m<sup>2</sup> total).

a) Number of individuals of each species in a macroplot was recorded.

b) Heights of all counted individuals were measured.

III. In tree and shrub species subplots (three per plot), 5 X 30 m (150 m<sup>2</sup> each, 450 m<sup>2</sup> total) the following information was recorded.

a) Number of individuals by species.

b) Heights of each individual by height class, given as follows; 1 = >25-50 cm, 2 = >50-100 cm, 3 = >100-200 cm, 4 = >200-400 cm.

c) A one time measure of each tree's actual height.

d) DBH of all trees greater than 1 cm DBH.

IV. Line intercept transects for subshrub, tree and shrub (150 m total) cover were established.

These measured the amount of distance the crown of each species intercepted a vertical plane above or below the line.

V. At six random six biomass plots (1 m<sup>2</sup> each) outside the vegetation plots, all herbaceous

growth and all litter fuels, except woody material greater than 1 cm in diameter (little material >1 cm was present), was clipped at ground level and collected.

VI. Photo points. Two photo points were established in each plot, usually at the origins of transects 2 and 3. Two color photos were taken at each point during each sample period, one looking down at a 1 m<sup>2</sup> area overlapping the first microplot position and the second an overview looking along the transect. Exact locations are given in Table 2 and shown in Figure 8.

Lab methods. Lab procedures involved separating herbaceous biomass samples by species and

**Table 2.** Descriptive characteristics of each site and plot (see plot diagram: Figure 8 for location of points).

UTM Coord.	Site		Plot (Pos) <sup>#</sup>	Slope %	Aspect	Photo	
	Elev.	Baseline <sup>*</sup>				Pts <sup>†</sup>	
<u>South - Unburned (S1)</u>			P1(A)	56	S2E	T2	T3
527.6 E	1525 m	S83W	P2(B)	71	S3W	T2	T3
3578.1 N			P3(A)	53	S32E	T2	T4
<u>South - Burned (S2)</u>			P1(B)	62	S2W	T2	T3
527.8 E	1520 m	N90E	P2(B)	62	S3W	T2	T3
3578.1 N			P3(A)	62	S3W	T1	T3
<u>East - Unburned (E1)</u>			P1(B)	67	S72E	T2	T3
528.2 E	1525 m	N20E	P2(B)	84	S60E	T2	T3
3578.1 N			P3(A)	67	S55E	T2	T3
<u>East - Burned (E2)</u>			P1(A)	67	S89E	T2	T3
528.0 E	1525 m	N10W	P2(B)	69	S79E	T2	T3
3577.3 N			P3(A)	71	N85E	T2	T1
<u>North - Unburned (N1)</u>			P1(B)	80	N22W	T2	T3
529.5 E	1465 m	S70W	P2(A)	76	N15W	T2	T3
3578.6 N			P3(B)	71	N6W	T2	T3
<u>North - Burned (N2)</u>			P1(A)	78	N4W	T2	T3
529.5 E	1475 m	N70E	P2(A)	76	N2W	T1	T3
3578.4 N			P3(B)	71	N2W	T2	T3

<sup>\*</sup> Baseline is the bearing of the baseline transect along which random plots were established.

<sup>#</sup> Position indicates whether a plot was located above or below the baseline.

<sup>†</sup> Point indicates at which transect origin along the baseline photos were taken.



species and then drying and weighing these and the litter fuel samples. All samples were dried at 75°C for two days and weighed to the nearest gram.

#### 4.4 Statistical analysis

Sørensen's index ( $IS_s$ ) was calculated and used for making comparisons of species occurrence among the six treatments, three sites with unburned (control) and burned areas (Mueller-Dombois and Ellenburg 1974). The equation for the index is:

$$\text{Sørensen's Index } IS_s = \frac{c}{\frac{1}{2}(A+B)}$$

where  $c$  is the number of common species between two treatments,  $A$  is the total number of species in treatment "A" and  $B$  is the total number of species in treatment "B".

The binomial frequency data were normalized with an arcsine (or angular) transformation using the following equation (Snedecor and Cochran 1967):

$$\text{Arcsin} = \sin^{-1} \sqrt{X}$$

The analysis was conducted to determine the existence of significant differences in cover, frequency, density and biomass (fuels) of individual species and groupings of species, using analysis of variance (ANOVA) with a two-factor design, site and fire, and six treatments. The first factor consisted of the three sites ( $df=2$ ); vegetation on south, southeast, and north facing slopes, while the second factor had two treatments ( $df=1$ ); burned and unburned areas. Significant site effects indicated differences among sites regardless of fire treatment while significant fire effects indicated a difference across all sites. Significant interaction effects (burn x site) occurred when differences among sites or burn treatments were not constant. I used the

regression approach to two-factor analysis of variance with equal sample sizes. When main effects were significant and without significant factor interaction present (0.05 level used for both) I examined site treatments further using orthogonal contrasts in the MGLH module of SYSTAT (Wilkinson 1990). Additional analysis of fire treatments was not needed because only two levels were present. When significant factor interaction effects were encountered "simple contrasts" of site differences were calculated within the two levels of fire (burned and unburned areas) using SYSTAT hypothesis testing procedures (Wilkinson 1990). Homogeneity of variances were screened using procedures outlined by Wilkinson (1990) for SYSTAT by examining scatter plots of studentized residuals versus estimated values and stem-and-leaf plots of studentized residuals for the presence of outliers.

Because only one burn was investigated, plots at each site were placed on both sides of the burn boundary to evaluate the effects of the fire. I recognize this does not conform to strict randomized placement of burn plots and unburned control plots with respect to one another and that individual plots were in actuality only pseudoreplicated (Hulbert 1984) but this is an unavoidable problem when investigating wildfires where pre-burn information is not obtainable. A necessary assumption in this sampling is that vegetation and fuels on either side of the burn boundary were similar before the fire. Wang (1986) argues that if significant differences between burned and unburned areas exist when such "*after-the-fact comparisons*" are made, two interpretations about the data may be made: 1) the differences pre-existed and are not related to the fire or, 2) the differences actually reflect fire effects. He feels comparisons based strictly on statistical inferences are invalid since this invalidates the statistical model. However, he further states that differences are probably real if the differences between burned and unburned areas are dramatic and far exceed the variation between replicate plots within an area. For the final

interpretation the investigator's judgement is required to support the conclusions. Thus, my presentation of the Molino Basin data will follow this model such that when I speak of differences between burned and unburned areas as being significant this is only to the extent that real differences exist but not to the cause. My approach is to observe which differences are significant with these results then interpret their meaning with regards to fire effects and postfire response based on my judgment about the comparisons.

Additionally, because my sampling involved remeasuring the same areas within a plot, analysis was performed to avoid statistical problems associated with repeated measures. Therefore analysis of variance (ANOVA) was performed for each of the four sample periods (spring 1984, fall 1984, spring 1985, fall 1985) to determine significant differences in each category that I call "sample periods" in the Results and Discussion section. Similarly, differences between the two years (1984 vs. 1985) for the two seasons (spring and fall) were calculated and analyzed. I refer to these interval measures (interval differences) as the "spring interval" and "fall interval". The latter allowed me to determine if significant changes in categories occurred between years while avoiding violating statistical assumptions if repeated measures were used.

My analysis focused on three areas; 1) description of species patterns and physical characteristics of the three sites, which provided baseline information important for the interpretation of the fire effects and postfire plant response, 2) comparison of differences between burned and unburned areas of individual species and broader life-form groupings of species, and 3) response of vegetation for the two intervals between the first and second year samples (i.e. the difference between the two spring and the two fall samples) as a way of judging what postfire changes were occurring over a short period of time. Three basic measures; cover, frequency, and density (plus biomass for some species) were used to quantify the vegetation and ascertain

changes. The use of multiple measures to determine fire effects allows the detection of effects or responses that may not be apparent in any single measure. For example, total cover may be reduced, indicating a reduction in a species, while density might not be affected, indicating no reduction. Taken together multiple measures provide a better overall look at fire effects and species response. They may show that a particular species is susceptible to fire but is either not killed and resprouts or rapidly reestablishes from seed banks.

## RESULTS and DISCUSSION

While sampling the unburned and burned areas at the three sites I recorded over 169 plant species, with about 100 being moderately common (Table 3). From these I selected a subset of the most common species for a detailed look at fire effects and vegetation response. Criteria used in selecting this subset of 21 "major" species (Table 4) was their presence in nine or more plots ( $\geq 50\%$  occurrence) with an absolute coverage of greater than 2% for plots in which a species was found. Three exceptions were made allowing inclusion of species of special interest. These were for *Haplopappus laricifolius*, *Aristida orcuttiana*, and *Heteropogon contortus*. All species were used in looking at broader aspects of fire effects and vegetation response and when summed life-form coverage and number of species by treatments were analyzed. Mean and standard deviations of all sample values by burned and unburned areas are listed in the appendices.

Analysis of fine-fuel biomass data was limited to 14 of the 21 major non-woody species because woody biomass was not collected. All herbaceous species were used in the analysis of summed-biomass data by life-form group. Mean and standard deviations of all biomass values collected in each burned and unburned area are listed in the appendices.

### 5.1 Number of Species

The number of species for the six treatments showed no significant differences between site location or burned and unburned areas. Shifts in number of species by life-form group showed a slight decrease in shrubs and subshrub species and an increase in herbaceous species in burned areas (Table 5). Inspection of Sørensen's index values ( $IS_s$ ) for all site combinations (Table 6) showed the greatest degree of similarity among plots at a particular

**Table 3.** Scientific and common names of the important plant species found at the Molino Basin study sites. Major species used in analysis are indicated by an asterisk (\*).

SPECIES NAME		COMMON NAME
<u>TREES</u>		
<i>Juniperus</i>	<i>deppcana</i>	alligator juniper
<i>Pinus</i>	<i>discolor</i>	border piñon (formerly Mexican piñon)
<i>Quercus</i>	<i>arizonica</i>	Arizona white oak
<i>Quercus</i>	<i>emoryi</i>	Emory oak / bellota *
<i>Quercus</i>	<i>oblongifolia</i>	Mexican blue oak *
<u>SHRUBS</u>		
<i>Arctostaphylos</i>	<i>pungens</i>	point-leaf manzanita *
<i>Crossosoma</i>	<i>bigelovii</i>	crossosoma
<i>Garrya</i>	<i>wrightii</i>	Wright silktassel *
<i>Rhamnus</i>	<i>crocea</i>	rhamnus
<i>Rhus</i>	<i>trilobata</i>	squawbush / skunkbush
<i>Vauquelinia</i>	<i>californica</i>	Arizona rosewood
<u>SUBSHRUBS</u>		
<i>Acacia</i>	<i>angustissima</i>	white-ball acacia
<i>Agave</i>	<i>schottii</i>	amole / shin-dagger *
<i>Agave</i>	<i>palmeri</i>	Palmer agave
<i>Asclepias</i>	<i>linaria</i>	milkweed
<i>Ayenia</i>	<i>pusilla</i>	
<i>Baccharis</i>	spp.	
<i>Bouvardia</i>	<i>glaberrima</i>	scarlet bouvardia
<i>Brickellia</i>	<i>californica</i>	
<i>Calliandra</i>	<i>erriophylla</i>	fairy-duster
<i>Carphochaete</i>	<i>bigelovii</i>	
<i>Dalea</i>	<i>pulchra</i>	indigo bush
<i>Dasylirion</i>	<i>wheeleri</i>	sotol *
<i>Desmodium</i>	<i>cinerascens</i>	tick-clover
<i>Echinocereus</i>	<i>triglochidiatus</i>	red hedgehog cactus
<i>Eriogonum</i>	<i>wrightii</i>	wild-buckwheat
<i>Erythrina</i>	<i>flabelliformis</i>	western coral bean
<i>Ferocactus</i>	<i>wislizeni</i>	barrel cactus
<i>Gossypium</i>	<i>thurberi</i>	wild cotton / algodoncillo
<i>Haplopappus</i>	<i>laricifolius</i>	turpentine bush
<i>Mammillaria</i>	spp.	pincushion / fishhook

Table 3 continued.

SPECIES NAME		COMMON NAME
<u>SUBSHRUBS continued</u>		
<i>Mimosa</i>	<i>bluncifera</i>	wait-a-minute / cat-claw
<i>Nolina</i>	<i>microcarpa</i>	* beargrass / sacahuista
<i>Opuntia</i>	<i>engelmannii</i>	prickly-pear
<i>Selloa</i>	<i>glutinosa</i>	
<i>Yucca</i>	<i>schottii</i>	Schott yucca
<u>PERENNIAL FORBS</u>		
<i>Agastache</i>	<i>breviflora</i>	
<i>Anemone</i>	<i>tuberosa</i>	wind-flower
<i>Arabis</i>	spp.	
<i>Artemisia</i>	<i>ludoviciana</i>	* sagebrush / groundsel
<i>Castilleja</i>	<i>laxa</i>	paint-brush
<i>Comandra</i>	<i>pallida</i>	bastard-toadflax
<i>Dalea</i>	<i>albiflora</i>	indigo bush
<i>Desmodium</i>	<i>angustifolium</i>	tick-clover
<i>Erigeron</i>	spp.	daisy
<i>Galium</i>	<i>microphyllum</i>	bedstraw
<i>Galium</i>	<i>rothrockii</i>	bedstraw
<i>Gilia</i>	<i>multiflora</i>	
<i>Gnaphalium</i>	<i>wrightii</i>	* coral-bells / alum root
<i>Heuchera</i>	<i>sanguinea</i>	
<i>Iva</i>	<i>ambrosiaefolia</i>	
<i>Lotus</i>	<i>rigidus</i>	* deer-vetch
<i>Penstemon</i>	<i>parryi</i>	Parry's penstemon
<i>Verbena</i>	<i>ciliata</i>	vervain / sand verbena
<u>ANNUAL FORBS</u>		
<i>Caucalis</i>	<i>microcarpa</i>	
<i>Cirsium</i>	<i>noemexicanum</i>	thistle
<i>Datura</i>	<i>meteloides</i>	jimson-weed
<i>Daucus</i>	<i>pusillus</i>	wild carrot
<i>Euphorbia</i>	<i>melanadenia</i>	
<i>Galactia</i>	<i>wrightii</i>	
<i>Ipomoea</i>	spp.	morning-glory
<i>Plantago</i>	<i>purshii</i>	indian wheat
<i>Solanum</i>	<i>douglasii</i>	
<i>Sphaeralcea</i>	<i>laxa</i>	globe-mallow

Table 3 continued.

Table 5 continued.

SPECIES NAME		COMMON NAME	
<u>PERENNIAL GRAMINIODS</u>			
<i>Andropogon</i>	<i>hirtiflorus</i>	blue-stem	
<i>Andropogon</i>	<i>cirratus</i>	*	Texas bluestem
<i>Aristida</i>	<i>barbata</i>		Harvard three-awn
<i>Aristida</i>	<i>ternipes</i>		spidergrass
<i>Aristida</i>	<i>orcuttiana</i>	*	beggertick grass
<i>Bothriochloa</i>	<i>barbinodis</i>		cane beardgrass
<i>Bouteloua</i>	<i>curtipendula</i>	*	side-oats grama
<i>Bouteloua</i>	<i>hirsuta</i>		hairy grama
<i>Bouteloua</i>	<i>chondrosioides</i>		spruce-top grama
<i>Eragrostis</i>	<i>intermedia</i>	*	plains lovegrass
<i>Eragrostis</i>	<i>lehmanniana</i>		Lehman lovegrass
<i>Heteropogon</i>	<i>contortus</i>	*	tangle-head
<i>Koeleria</i>	<i>cristata</i>		mountain Junegrass
<i>Leptochloa</i>	<i>dubia</i>		green spangletop
<i>Leptoloma</i>	<i>cognatum</i>		fall witch-grass
<i>Lycurus</i>	<i>phleoides</i>		wolftail
<i>Muhlenbergia</i>	<i>polycaulis</i>		cliff muhly
<i>Muhlenbergia</i>	<i>emersleyi</i>	*	bull grass
<i>Rhynchelythrum</i>	<i>roseum</i>		Natal grass
<i>Sitanion</i>	<i>hystrix</i>		squirrel tail wild-rye
<i>Trachypogon</i>	<i>secundus</i>	*	crinkle-awn
<i>Trichachne</i>	<i>californica</i>		California cottontop
<u>ANNUAL GRAMINIODS</u>			
<i>Aristida</i>	<i>adscensionis</i>	*	six-weeks three-awn
<i>Bouteloua</i>	<i>aristidoides</i>		six-weeks three-awn
<i>Bromus</i>	<i>rubens</i>		foxtail chess
<i>Bulbostylis</i>	<i>capillaris</i>		
<i>Enneapogon</i>	<i>desvauxii</i>		spike pappus-grass
<i>Eragrostis</i>	<i>cilianensis</i>		stink grass
<i>Festuca (Vulpia)</i>	<i>octoflora</i>		six-weeks fescue
<i>Muhlenbergia</i>	<i>fragilis</i>		
<i>Panicum</i>	<i>scribnerianum</i>		panicum
<i>Poa</i>	<i>biglovii</i>		
<i>Seteria</i>	<i>viridis</i>		green bristle grass



Table 3 continued.

SPECIES NAME		COMMON NAME
<b>NON-FLOWERING PLANTS</b>		
<i>Bommeria</i>	<i>hispida</i>	copper fern
<i>Cheilanthes</i>	<i>wootoni</i>	beaded lip-fern
<i>Notholaena</i>	<i>aurea</i>	golden cloak-fern
<i>Notholaena</i>	<i>sinuata</i>	wavy cloak-fern
<i>Pellaea</i>	<i>truncata</i>	spiny cliff-brake
<i>Selaginella</i>	<i>rupicola</i>	salaginella

site and treatment followed by plots for the two treatments at a particular site. However, they do show a high degree of similarity between the unburned plots on the south and east slopes.

Departures of the similarity index values between these two sample periods was calculated (Table 7). Between the spring 1984 and fall 1985 samples, average similarity generally decreased within a site and treatment while similarities between treatments at a site increased or only decreased slightly. Within sites and treatments the average similarity decreased (-5.53) while the average similarity within a site but between treatments remained nearly constant (-0.13) with it decreasing on the south slope (-4.9) and increasing on the east and north slopes (1.3 and 3.2 respectively). These data indicate that there was a degree of change in the unburned "control" plots over time and that the vegetation composition of the burned plots was becoming slightly more similar to the unburned plots during the course of the study. The change in the unburned plots may have been a response of the vegetation to increased moisture and a lower average temperature during the study period which was associated with the very strong El Niño event of 1982/83. I would expect an opposite effect during a period of warm dry weather following a cool wet period.

Most species were present in all treatments with few eliminated by fire, though abundance varied considerably. A slight increase in the number of species occurred in burned plots as annuals invaded, an apparent result of disturbance and reduced competition from

perennials. Similar results were reported by Dwyer and Pieper (1967) for semi-desert grassland in southern New Mexico and by Ahlstrand (1979b) for succulent desert vegetation in Carlsbad Caverns and Guadalupe National Parks in the Chihuahuan desert. Ahlstrand (1979b) found nearly 100% of the species to be shared between burned and unburned areas when species of low (<2%) frequency or cover were not considered. Bock et al. (1976), working in semi-desert grasslands in southeastern Arizona, report an 80% species similarity between burned and unburned plots six months postfire and a 90% similarity by 1½ yr. In *Quercus coccifera* garrique in southern France (Trabaud and Lepart 1981) and Mediterranean maquis (*Quercus ilex*) in Italy (Gratani and Amadori 1991) the floristic composition remained stable with respect to the impact

**Table 4.** Major species used in analysis organized by life-form; tree, shrub, etc.

SPECIES NAME	COMMON NAME
<i>Quercus emoryi</i>	Emoryi oak / bellota
<i>Quercus oblongifolia</i>	Mexican blue oak
<i>Arctostaphylos pungens</i>	point-leaf manzanita
<i>Garrya wrightii</i>	Wright siltkassel
<i>Agave schottii</i>	amole / shin dagger
<i>Dasyllirion wheeleri</i>	sotal
<i>Nolina microcarpa</i>	beargrass / sacahuista
<i>Artemisia ludoviciana</i>	sagebrush / groundsel
<i>Gnaphalium wrightii</i>	----
<i>Haplopappus laricifolius</i>	turpentine bush
<i>Lotus rigidus</i>	deer-vetch
<i>Andropogon cirratus</i>	Texas bluestem
<i>Aristida orcuttiana</i>	beggertick grass
<i>Bouteloua curtipendula</i>	side-oats grama
<i>Eragrostis intermedia</i>	plains lovegrass
<i>Heteropogon contortus</i>	tangle-head
<i>Muhlenbergia emersleyi</i>	bull grass
<i>Trachypogon secundus</i>	crinkle-awn
<i>Aristida adscensionis</i>	six-weeks three-awn
<i>Cheilanthes wootoni</i>	beaded lip-fern
<i>Selaginella rupincola</i>	salaginella

of the fire with this stability due to most taxa present prior to the burn able to resprout post-burn. My observations indicated that no species was eliminated by the fire as some individuals of even the most fire intolerant species such as *Agave schottii* and *Selaginella rupincola* survived in burned areas. The effect of the fire was to produce a redistribution of how common or rare the various woodland species were. I found this effect least pronounced on the south slope with a high proportion of resprouting species, primarily graminoid, and more obvious on the north slope where the fire had a greater impact because of a large number of non-sprouting species that were reduced.

With sampling beginning one year postfire the full extent of the initial increase in annuals

**Table 5.** Number of species found in each plot during the four sample periods. Sites are south (S), east (E), and north (N) slopes.

Treatment	Site	Plot	Number of Species			
			Spr 84	Fall 84	Spr 85	Fall 85
Unburned	S	1	37	40	43	33
		2	39	40	42	39
		3	32	30	28	28
Burned	S	1	37	34	37	39
		2	43	37	47	41
		3	36	34	41	41
Unburned	E	1	31	34	33	31
		2	34	32	29	32
		3	29	26	32	28
Burned	E	1	39	35	43	43
		2	35	29	32	39
		3	33	31	34	34
Unburned	N	1	29	27	34	32
		2	27	31	30	31
		3	22	27	26	30
Burned	N	1	21	24	31	32
		2	35	34	37	37
		3	26	30	27	35

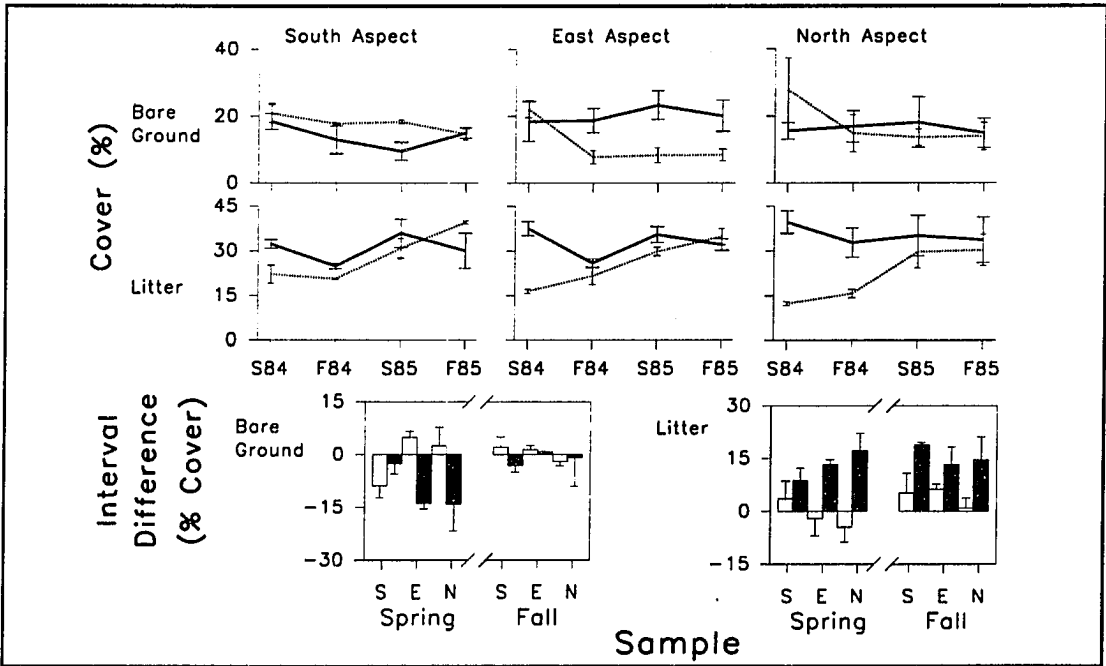
**Table 6.** Cross-tabulation of Sørensen's index of similarity values for all plot combinations. Values for the spring 1984 sample are given below the diagonal (lower left) and Fall 1985 values above the diagonal (upper right). Both vertical and horizontal plot names correspond.

Plot			S1	S2	S3	S4	S5	S6	E7	E8	E9	E10	E11	E12	N13	N14	N15	N16	N17	N18
South	UB	1 S1		73.2	59.0	58.3	48.6	62.2	59.4	52.3	55.7	50.0	47.2	38.8	49.2	46.9	41.3	40.0	42.9	41.2
		2 S2	73.7		54.5	62.3	53.2	60.8	60.9	57.1	51.5	51.9	49.4	52.8	40.0	40.6	38.2	34.3	42.7	43.8
		3 S3	69.6	62.0		41.8	34.8	46.4	71.2	63.3	64.3	50.7	47.8	51.6	50.0	44.1	44.8	43.3	40.0	38.1
	B	1 S4	70.3	63.2	52.2		65.0	57.5	48.6	36.6	41.8	48.8	48.7	46.6	36.6	34.3	37.7	47.9	31.6	40.5
		2 S5	62.5	56.1	45.3	72.5		68.3	38.9	38.4	31.9	42.9	42.5	37.3	27.4	27.8	36.6	32.9	25.6	31.6
		3 S6	63.0	56.0	44.1	76.7	75.9		52.8	46.6	43.5	50.0	50.0	45.3	24.7	30.6	31.0	30.1	33.3	34.2
East	UB	1 E7	64.7	60.0	79.4	55.9	43.2	44.8		63.5	67.8	54.1	60.0	55.4	47.6	41.9	45.9	44.4	41.2	36.4
		2 E8	47.9	57.5	66.7	39.4	39.0	37.1	73.8		60.0	56.0	59.2	60.6	50.0	38.1	38.7	37.5	40.6	38.8
		3 E9	54.5	58.8	62.3	42.4	38.9	33.8	73.3	66.7		53.5	53.7	51.6	50.0	47.5	41.4	40.0	43.1	34.9
	B	1 E10	50.0	51.3	53.5	50.0	51.2	50.7	57.1	52.1	52.9		65.9	57.1	37.3	37.8	32.9	37.3	37.5	38.5
		2 E11	47.2	54.1	53.7	44.4	46.2	45.1	57.6	58.0	56.3	73.0		65.8	45.1	42.9	49.3	47.9	52.6	48.6
		3 E12	42.9	47.2	55.4	42.9	52.6	46.4	56.3	53.7	48.4	63.9	70.6		39.4	36.9	37.5	42.4	39.4	37.7
North	UB	1 N13	39.4	41.2	45.9	30.3	33.3	24.6	46.7	54.0	41.4	38.2	37.5	35.5		73.0	61.3	62.5	60.9	56.7
		2 N14	43.8	48.5	47.5	40.6	34.3	28.6	48.3	39.3	39.3	42.4	35.5	40.0	53.6		59.0	50.8	67.6	57.6
		3 N15	44.1	45.9	48.1	33.9	43.1	24.1	52.8	42.9	39.2	42.6	42.1	40.0	66.7	61.2		71.0	56.7	67.7
	B	1 N16	41.4	40.0	41.5	41.4	43.8	28.1	42.3	40.0	32.0	40.0	42.9	44.4	56.0	50.0	60.5		55.1	65.7
		2 N17	50.0	45.9	53.7	47.2	43.6	36.6	54.5	52.2	46.9	48.6	48.6	52.9	56.3	61.3	56.1	64.3		55.6
		3 N18	44.4	46.2	48.3	31.7	40.6	29.0	49.1	43.3	36.4	49.2	49.2	54.2	50.9	60.4	70.8	63.8	65.6	

**Table 7.** Departure of Sørensen's index values between the spring 1984 and fall 1985 sample indicating whether species composition increased or decreased during the study period. Average departure was -2.14. Plot identification follow Table 6.

Plot	S1																
S2	-0.5	S2															
S3	-10.6	-7.5	S3														
S4	-12.0	-0.9	-10.4	S4													
S5	-13.9	-2.9	-10.5	-7.5	S5												
S6	-0.8	4.8	2.3	-19.2	-7.6	S6											
E7	-5.3	0.9	-8.2	-7.3	-4.3	8.0	E7										
E8	4.4	-0.4	-3.4	-2.8	-0.6	9.5	-10.3	E8									
E9	1.2	-7.3	2.0	-0.6	-7.0	9.7	-5.5	-6.7	E9								
E10	0.0	0.6	-2.8	-1.2	-8.3	-0.7	-3.0	3.9	0.6	E10							
E11	0.0	-4.7	-5.9	4.3	-3.7	4.9	2.4	1.2	-2.6	-7.1	E11						
E12	-4.1	5.6	-3.8	3.7	-15.3	-1.1	-0.9	6.9	3.2	-6.8	-4.8	E12					
N13	9.8	-1.2	4.1	6.3	-5.9	0.1	0.9	-4.0	8.6	-0.9	7.6	3.9	N13				
N14	3.1	-7.9	-3.4	-6.3	-6.5	2.0	-6.4	-1.2	8.2	-4.6	7.4	-3.1	19.4	N14			
N15	-2.8	-7.7	-3.3	3.8	-6.5	6.9	-6.9	-4.2	2.2	-9.7	7.2	-2.5	-5.4	-2.2	N15		
N16	-1.4	-5.7	1.8	6.5	-10.9	2.0	2.1	-2.5	8.0	-2.7	5.0	-2.0	6.5	0.8	10.5	N16	
N17	-7.1	-3.2	-13.7	-15.6	-18.0	-3.3	-13.3	-11.6	-3.8	-11.1	4.0	-13.5	4.6	6.3	0.6	-9.2	N17
N18	-3.2	-2.4	-10.2	8.8	-9.0	5.2	-12.7	-4.5	-1.5	-10.7	-0.6	-16.5	5.8	-2.8	-3.1	1.9	-10.0

was missed. While inspecting site locations immediately following the fire (summer of 1983) I observed the appearance of many annuals which had nearly disappeared by the second year (1984). These annuals, called 'pyrophyte endemics' by Hanes (1977) using the term 'pyrophyte' coined by Kuhnholz-Lordat (1938) or 'therophytes' by Trabaud (1987b), are probably responding to reduced competition from perennials and the increased nutrient availability following fire. Their appearance immediately following the fire indicates the presence of a soil seed bank that is maintained between fires. It is unknown whether their germination is a response solely to fire or just due to the occurrence of a major disturbance. These species usually disappeared by the second or third year postfire. Similar annuals are common in California chaparral (Muller et al.



**Figure 9.** Percent surface area covered by bare ground and litter during the four sample periods (S84=spring 1984, F84=fall 1984, etc.) on burned and unburned areas at the three sites (S=south facing slope, E=East slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass differences plots are for burned areas and open bars for unburned.

1968; Parsons 1976; Hanes 1977; Keeley and Keeley 1988; Dunne et al. 1991), in Australian heathlands (Specht et al. 1958; Bell et al. 1984), Mediterranean garrique (Trabaud and Lepart 1980; 1981), Israel (Naveh 1974), and in South African fynbos (Kruger 1977, 1983; Kruger and Bigalke 1984).

## 5.2 Bare Ground and Litter

**Bare Ground.** During my initial sampling in the spring of 1984 bare ground was greater in all burned areas (21-28%) relative to unburned areas (15-19%) (Figure 9) although the differences were not significant (Table 8). Bare ground remained relatively constant in unburned plots for all sample periods while decreasing in burned plots. The greatest decrease in burned plots took place on the east and north slopes. The major proportion of this decrease occurred between the first and second sample, the period of summer rain. A significant difference was also found in the amount of change between the two spring samples with simple contrasts showing differences between unburned plots on the south slope and those on the east and north which

**Table 8.** Probability levels from 2-WAY ANOVA using cover values from physical data. Data from three sites (S) and two fire (F) treatments show levels of differences in percent cover within each of the four sampling periods and change in percent cover for two sampling intervals. Significant differences ( $P < 0.05$ ) are indicated by asterisk (\*).

Category	Sample Period				Sample Interval	
	Spring 84	Fall 84	Spring 85	Fall 85	Spring	Fall
	Probability Level					
<u>Bare Ground</u>						
S	0.925	0.774	0.959	0.985	0.941	0.803
F	0.167	0.399	0.290	0.134	0.018 *	0.606
S X F	0.597	0.159	0.032 *	0.197	0.023 *	0.689
<u>Litter</u>						
S	0.843	0.836	0.971	0.833	0.983	0.614
F	0.001 *	0.001 *	0.161	0.460	0.001 *	0.007 *
S X F	0.009 *	0.038 *	0.997	0.415	0.173	0.676

decreased more. In the south slope burn plots, bare ground decreased 6% (a 29% relative decrease) between the first and last sampling while on the east this was 13% (59%) and 15% (50%) on the north. The greater change on the north and east slopes may be a result of the colonization of open areas where the fire had reduced woody species. This decrease of bare ground on the east and north slopes was slowed by the need for new plants to become established from seed. In contrast, the south slope had a sizable preburn herbaceous component and so was not as severely affected due to its rapid recovery. By the final sample bare ground in all burn treatments was similar to unburned areas and on the east slope about half again as much (8% vs 20%). These findings are consistent to those reported following a cool prescribed burn in open oak woodland. Bock and Bock (1986a) report more bare ground on burned than unburned plots 1 yr postfire with differences dampening by the second year. They felt these differences would disappear by the third season. Bock et al. (1976) state that bare ground decreased rapidly on burned plots in semi-desert grassland so that by 1½ yr postfire it was similar to unburned plots. Rapid recovery in sagebrush communities is also reported from central Utah (West and Hassan 1985). Bare ground was 77% on burned and 13% on unburned plots at 1 yr and 31% and 25% respectively at 3 yr.

The only significant difference among the two intervals was the amount of change between burned areas for the spring interval. Although there was interaction, examination of the means indicated a decrease in bare ground occurred at burned sites.

Litter. Litter cover during the spring 1984 sampling was less on burned (12-22%) than unburned (32-40%) areas (Figure 9). Seasonal trends in unburned plots were apparent, with decreases between spring and fall samples and increases between fall and spring. This was most



noticeable on the south slope. Decomposition appeared to be most rapid during the warm moist summer months while in the cooler drier winter months plant die back increased litter accumulations. This was a response also observed in other grassland/savanna ecosystems (Singh 1993). The ANOVA results showed no site differences (Table 8).

Between the first and last sampling litter cover increased in burned areas by an average of 18% (an 82% relative increase on the south slope, 100% on the east, and 150% on the north). By the last sample litter cover in burned plots was greater than unburned on the south (40 vs 30%) and east slopes (35 vs 32%) and only slightly less on the north (29 vs 32%). Differences between burned and unburned sites were significant (Table 8) for the 1984 samples but were affected by interaction which was apparently a result of a stronger impact on the north and east slopes. Linear contrasts of both unburned and burned areas for the spring sample showed litter differences between the south slope and the north slope to be significant, while the east slope was not significantly different from either which indicated intermediate levels of cover. A similar pattern was obvious in unburned areas for the fall 1984 sample while in burned areas none of the three sites showed differences. The increase in litter cover was likely caused by rapid growth of herbs after burning and a larger proportion of the litter composed of herbs rather than dead woody material. This occurred more rapidly on the south slope with its high proportion of resprouting herbs relative to the north slope where the increase was delayed because of the need for new plants to become established in areas previously occupied by shrubs. The herbaceous response may be attributed to a short-term increase in available plant nutrients after burning (Anderson 1982; Ohr and Bragg 1985; Knapp, and Seastedt 1986), greater than average rainfall during the study, and release from woody plant competition. Bock et al. (1976) report less litter cover on burned than unburned at six months postburn but about equal at 1½ years.

Significant differences in the change in litter cover between burned and unburned areas occurred for both sample intervals (Table 8). Cover in burned areas changed more than at unburned with consistent and relatively large increases occurring (Figure 9). This increase parallels the decrease in bare ground observed during the same time span.

### 5.3 Summed Biomass Data

The four categories I used in the analysis of summed biomass data were "live biomass" (predominantly live shoot biomass), "dead biomass" (predominantly dead shoot biomass), "litter biomass", and "total biomass" (Figure 10). Dead biomass consisted of dead plant parts still attached and part of a plant that could be identified to the species to which it belonged. Litter biomass consisted of unconsolidated plant material that generally could not be identified as to which species it had originated. Total biomass was the sum of live, standing dead, and litter biomass. The "total biomass" category comprises the main fuel component important for fire spread in the woodland.

Live biomass. Significant differences in live biomass were found between burned and unburned areas but not among sites (Table 9). Inspection of the means (Appendix 3) generally showed more live biomass on burned than unburned plots, particularly on the south and east sites. This greater live biomass may have been the result of increased nutrient availability producing a positive growth response. Live biomass was lowest in the spring and the greatest in the fall a result of fall sampling following the summer growing season when graminoids, a major component of the vegetation on the south and east sites, grew most actively (Figure 10). A similar response was also seen by Singh (1993) in a dry savanna that had a strong summer

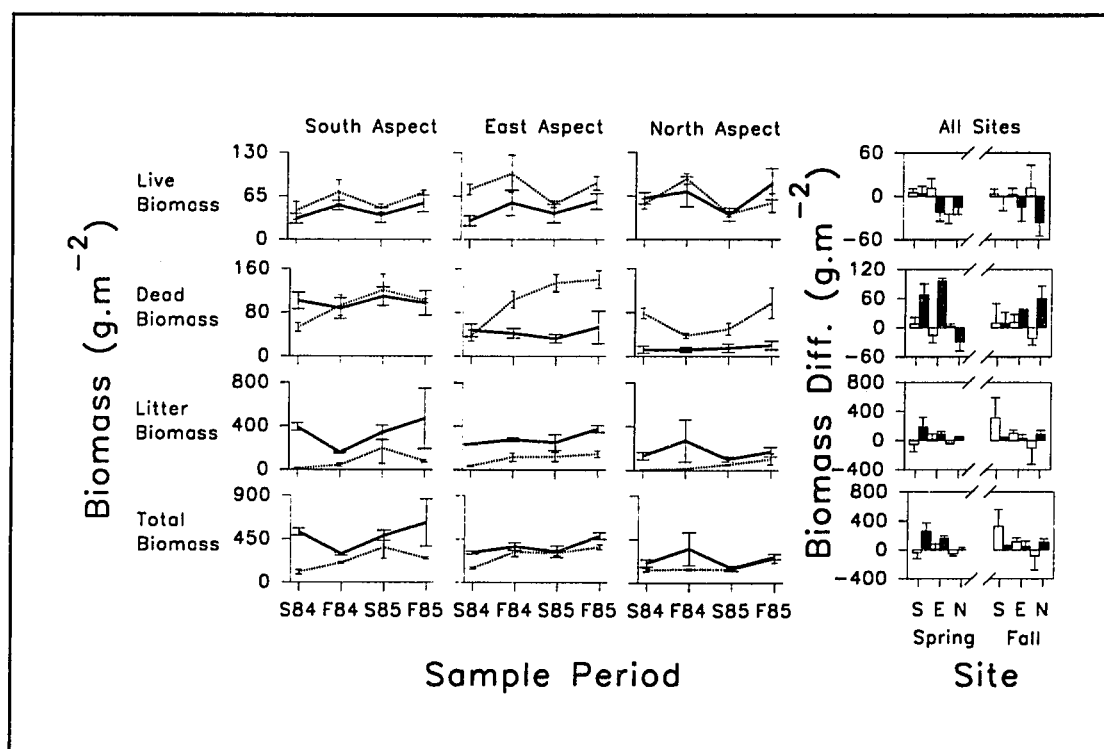
moisture component. No differences between intervals were significant, indicating nearly equivalent growth for the two seasons.

Dead biomass. Dead biomass accumulations were greatest on the south slope and smallest on the north (Figure 10). Significant differences between sites were found for the first three sample periods with the fall 1985 sample showing a strong but not significant difference (Table 9). Orthogonal contrasts for the two 1984 samples showed biomass to be less on the north and east aspects than on the south. Linear contrasts for the spring 1985 sample showed similar results for unburned areas while in burned areas the north slope was significantly different from the south and east which were not different from one another. Dead biomass was less in burned areas from the two sites with greater dominance of graminoid perennials, the south and east slopes, with 53% of the biomass in unburned plots on the south slope, 80% on the east for the spring 1984 sample. In contrast it was much greater in the burned plots on the north slope, with 635% of the biomass in the unburned pots. I believe this was a result of the rapid increase of herbaceous species in the burned plots relative to the unburned. There was also a significant increase in dead biomass in burned areas for the spring interval but not in the unburned. Linear contrasts showed that the increase on the north slope was different from the south and east which did not differ. By the last sample (fall 1985) dead biomass was equivalent between burned and unburned plots on the south slope, while it had increased by 2.6, and 4.8 times respectively on the east and north slopes. The equivalency of dead biomass on the south slope is probably a result of the rapid recovery of the perennial graminoids that dominated the area prior to the burn whereas on the east and north slopes graminoid species increased after woody species were reduced following the burn.

**Table 9.** Probability levels from 2-WAY ANOVA for biomass summed into component categories. Live biomass is the sum of all living herbaceous biomass, total dead biomass is the sum of litter and standing dead biomass, litter biomass is all fine fuel biomass lying on the ground surface, total standing biomass is the sum of live and standing dead biomass, and total biomass is the sum of all biomass collected. Data show differences in biomass for each of the four sampling periods and the change in biomass for two sampling intervals in the three site (S) and two burned areas (F). Significant differences ( $P < 0.05$ ) are indicated by asterisks (\*).

Category	Sample Period				Sample Interval	
	Spr. 84	Fall 84	Spr. 85	Fall 85	Spring	Fall
Probability Levels						
<b><u>Live biomass</u></b>						
S	0.099	0.541	0.650	0.811	0.120	0.792
F	0.035 *	0.094	0.279	0.678	0.331	0.174
S X F	0.022 *	0.756	0.770	0.150	0.144	0.528
<b><u>Total Dead Biomass</u></b>						
S	0.001 *	0.426	0.003 *	0.224	0.266	0.532
F	0.001 *	0.042 *	0.289	0.075	0.009 *	0.827
S X F	0.001 *	0.663	0.609	0.226	0.239	0.219
<b><u>Litter Biomass</u></b>						
S	0.001 *	0.504	0.063	0.449	0.739	0.492
F	0.001 *	0.019 *	0.099	0.035 *	0.065	0.687
S X F	0.001 *	0.678	0.783	0.419	0.504	0.337
<b><u>Total Standing Biomass</u></b>						
S	0.497	0.119	0.005 *	0.306	0.007 *	0.937
F	0.148	0.008 *	0.007 *	0.016 *	0.047 *	0.919
S X F	0.028 *	0.223	0.105	0.239	0.081	0.977
<b><u>Total Biomass</u></b>						
S	0.001 *	0.352	0.002 *	0.206	0.162	0.444
F	0.001 *	0.072	0.333	0.070	0.012 *	0.662
S X F	0.001 *	0.556	0.594	0.255	0.261	0.240

Litter Biomass. Site differences in litter biomass were only significant for the first sample (Table 9). No contrasts were made because of significant interaction although inspection of means (Appendix 3) indicate a higher litter biomass on the south slope in unburned treatments relative to the north. Litter on the south and east sites was composed of a mixture of herbaceous species (predominantly graminoids) and dead woody plant material while on the north it was predominantly woody. In burned plots litter biomass was usually largest on the east site and least on the north with these trends continuing for all four sample periods (Figure 10). Fluctuations were also observed by season in unburned plots, apparently due to differing rates of



**Figure 10.** Biomass sums of live, total dead, litter, and total of all biomass collected during the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

decomposition and accumulation. The largest litter accumulations were found in the fall following the warm, moist summer monsoon growing season with smaller accumulations in the spring.

Litter biomass differed significantly between treatments with greater amounts in unburned plots for spring and fall 1984, and fall 1985 sample periods. Litter in unburned plots varied between  $131.1 \text{ g}\cdot\text{m}^{-2}$  and  $391.5 \text{ g}\cdot\text{m}^{-2}$  for the first sample period and at burned treatments from  $4.3 \text{ g}\cdot\text{m}^{-2}$  and  $35.2 \text{ g}\cdot\text{m}^{-2}$ . This was 97% less on the south slope, and 85% and 97% less respectively on the east and north with most dead biomass consisting of standing dead material as opposed to litter accumulations on the ground surface. These large differences show that the bulk of litter fuels were consumed during burning.

Litter accumulated rapidly in burned areas during the study. By the final sample accumulations were  $83 \text{ g}\cdot\text{m}^{-2}$  on the south slope,  $61 \text{ g}\cdot\text{m}^{-2}$  east, and  $40 \text{ g}\cdot\text{m}^{-2}$  north representing an increase of 7.1, 4.1, and 23.7 times respectively.

Total Biomass. Total litter and herbaceous biomass (summation of "live" and "total dead" biomass in Figure 10) recovered rapidly at all sites. Accumulations of fuels were heavy enough to carry a second fire in May 1985 when a portion of the 1983 burn, south of the north slope site, reburned. Highly flammable herbaceous fuels were more contiguous on the east and north slopes following the 1983 burn than before it. This was a result of the removal of woody and decadent vegetation along with mat forming *Selaginella* by the fire that then allowed establishment and spread of herbaceous species. I believe the establishment of a continuous herbaceous layer is important in the maintenance of a high frequency of low intensity fires in

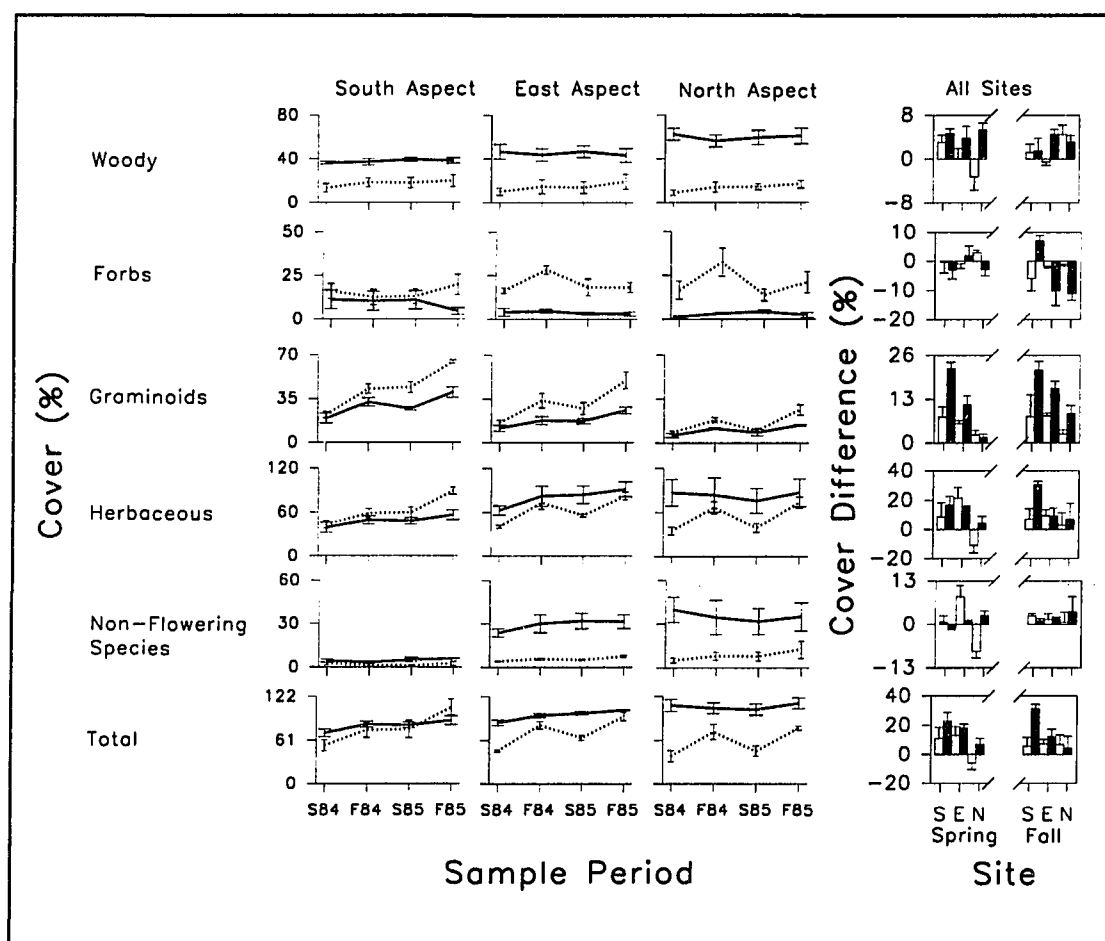
contrast to a lower frequency of higher intensity fires that would occur when fuel continuity is broken as when shrubs with intervening openings dominate a site.

Total biomass as a fuel estimate showed a consistent decrease from south to the north slope (Figure 10). It averaged  $4.82 \text{ mt}\cdot\text{ha}^{-1}$  on the south slope,  $3.73 \text{ mt}\cdot\text{ha}^{-1}$  on the east, and  $2.46 \text{ mt}\cdot\text{ha}^{-1}$  on the north. My estimates for burned areas in the spring 1984 was  $1.07 \text{ mt}\cdot\text{ha}^{-1}$  on the south,  $3.19 \text{ mt}\cdot\text{ha}^{-1}$  on the east, and  $1.36 \text{ mt}\cdot\text{ha}^{-1}$  on the north slope. These increased to  $2.53 \text{ mt}\cdot\text{ha}^{-1}$ ,  $3.70 \text{ mt}\cdot\text{ha}^{-1}$ , and  $2.54 \text{ mt}\cdot\text{ha}^{-1}$  respectively by the fall 1985 sample. Haworth (1992) and McPherson (1992) report herbaceous fuels of  $8\text{-}9 \text{ mt}\cdot\text{ha}^{-1}$  under oak canopies and  $16 \text{ mt}\cdot\text{ha}^{-1}$  in openings in Arizona, while in woodlands in Texas  $1.54 \text{ mt}\cdot\text{ha}^{-1}$  is reported from grassland openings and  $2.34$  to  $5.70 \text{ mt}\cdot\text{ha}^{-1}$  under oaks (Fonteyn et al. 1988). These correspond to  $5.6 \text{ mt}\cdot\text{ha}^{-1}$  for heavy grassland fuels and  $33 - 112 \text{ mt}\cdot\text{ha}^{-1}$  for California chaparral (Wells et al. 1979). For the spring 1984 sample I found that total biomass showed significant differences between sites and between burned and unburned areas. Because of a significant interaction effect linear contrasts showed that in unburned areas all sites were significantly different from one another while at burned sites no significant differences were apparent. By the fall 1984 sample none of the sites or comparisons of burned and unburned areas had significant differences. The only significant interval difference occurred between the spring samples. These two comparisons indicate to me the rapid recovery of the herbaceous species.

## 5.4 Cover, Frequency, Density, and Biomass -

### by Life-form Groups and Individual Species

Data on cover, frequency, and density were collected on all species encountered but only analyzed for the major species. Data on cover were also summed across all species at a plot into life-form groups (Table 10). These groups refer to general plant form, such as tree,



**Figure 11.** Crown cover summed for major groups of species during the four sample periods (S84=Spring 1984, F84=Fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=East slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.



**Table 10.** Probability levels from 2-WAY ANOVA for cover of all species grouped into major life form categories. Data from three sites (S) and two fire (F) factors show levels for differences in percent cover within each of the four sampling periods and change in percent cover for the two sampling intervals. Significant differences ( $P < 0.05$ ) are indicated by an asterisk (\*).

Category	Sample Period				Sample Interval	
	Spring 84	Fall 84	Spring 85	Fall 85	Spring	Fall
	Probability Levels					
<i>Trees</i>						
S	0.657	0.875	0.770	0.775	0.439	0.690
F	0.007	0.016	0.013	0.008	0.484	0.157
S X F	0.664	0.492	0.746	0.600	0.619	0.490
<i>Shrub</i>						
S	0.001	0.002	0.003	0.002	0.492	0.021 *
F	0.001	0.001	0.001	0.001	0.485	0.709
S X F	0.006	0.032	0.033	0.060	0.369	0.164
<i>Subshrub</i>						
S	0.272	0.232	0.108	0.440	0.658	0.864
F	0.001	0.001	0.001	0.023	0.007	0.072
S X F	0.247	0.740	0.360	0.904	0.202	0.162
<i>Woody</i>						
S	0.066	0.338	0.240	0.224	0.292	0.278
F	0.001 *	0.001 *	0.001 *	0.001 *	0.006 *	0.295
S X F	0.012 *	9.105	0.081	0.099	0.167	0.123
<i>Forbs</i>						
S	0.444	0.373	0.718	0.895	0.722	0.077
F	0.003 *	0.001 *	0.011 *	0.001 *	0.406	0.444
S X F	0.363	0.026 *	0.239	0.850	0.320	0.004 *
<i>Perennial Forbs</i>						
S	0.689	0.260	0.810	0.929	0.633	0.293
F	0.003 *	0.001	0.016	0.001	0.346	0.402
S X F	0.198	0.017	0.171	0.807	0.191	0.003 *
<i>Annual Forbs</i>						
S	0.051	0.010 *	0.037 *	0.592	0.245	0.304
F	0.033 *	0.038 *	0.081	0.016	0.578	0.523
S X F	0.521	0.043	0.724	0.399	0.339	0.624
<i>Graminoids</i>						
S	0.001 *	0.001 *	0.001 *	0.001 *	0.001 *	0.041 *
F	0.138	0.002 *	0.002 *	0.001 *	0.002 *	0.004 *
S X F	0.899	0.443	0.070	0.261	0.008 *	0.477

Table 10 continued.

Category	Sample Period				Sample Interval	
	Spring 84	Fall 84	Spring 85	Fall 85	Spring	Fall
Probability Levels						
<b>Perennial Graminoids</b>						
S	0.001	0.001	0.001	0.001	0.001	0.050 *
F	0.248	0.050	0.004	0.001	0.002	0.003 *
S X F	0.919	0.360	0.083	0.126	0.011	0.419
<b>Annual Graminoids</b>						
S	0.339	0.383	0.325	0.163	0.191	0.364
F	0.056	0.063	0.028	0.247	0.708	0.044 *
S X F	0.883	0.848	0.395	0.570	0.303	0.687
<b>Herbaceous</b>						
S	0.988	0.580	0.071	0.107	0.015 *	0.045 *
F	0.318	0.092	0.954	0.001 *	0.204	0.075
S X F	0.170	0.929	0.093	0.094	0.639	0.049 *
<b>Non-Flowering Plants</b>						
S	0.001 *	0.012 *	0.005 *	0.006 *	0.006 *	0.870
F	0.001 *	0.002 *	0.001 *	0.002 *	0.724	0.612
S X F	0.004 *	0.089	0.048 *	0.123	0.001 *	0.463
<b>Ferns</b>						
S	0.004 *	0.052	0.038 *	0.055	0.105	0.913
F	0.003 *	0.040 *	0.010 *	0.309	0.167	0.181
S X F	0.003 *	0.045 *	0.064	0.745	0.019 *	0.096
<b>Total</b>						
S	0.208	0.356	0.575	0.846	0.018 *	0.125
F	0.001 *	0.012 *	0.001 *	0.154	0.047 *	0.059
S X F	0.004 *	0.252	0.009 *	0.007 *	0.734	0.081

shrub, herb, or forb, etc. Using groups presented an overall picture of the vegetation dynamics in woodland that included species not analyzed separately but which taken together represent a substantial portion of the total vegetation cover. Biomass was collected on all individual herbaceous species and also only analyzed for those listed as major species. No significant differences in biomass were found for the following four species, *Heteropogon contortus*, *Muhlenbergia emersleyi*, *Trachypogon secundus*, and *Aristida adscensionis*, so this component of the analysis was not described in the individual treatment of species below.

My review of the results often showed significant cover decreases in burned areas compared to unburned but not for frequency or density. This usually indicated a species was partially or completely topkilled but resprouted soon after the burn. Inspection of these measures as a group often provided a clearer picture on how a species responded to fire than any single measure alone.

Distribution of the major species in the study area was generally similar to that reported by Whittaker and Niering (1965) for elevations between 1220 - 1525 m with several exceptions. I found *Quercus oblongifolia*, *Nolina microcarpa*, and *Muhlenbergia emersleyi* to be more common on the south facing slope than they report, possibly due to the fact that the site was at a slightly higher elevation. Their coverage data were not comparable since it was an average of several aspects while mine was for three specific aspects. However, the overall magnitude of coverage percentages for the different species was similar. I only found *Selaginella rupincola* to be of much greater cover than they report.

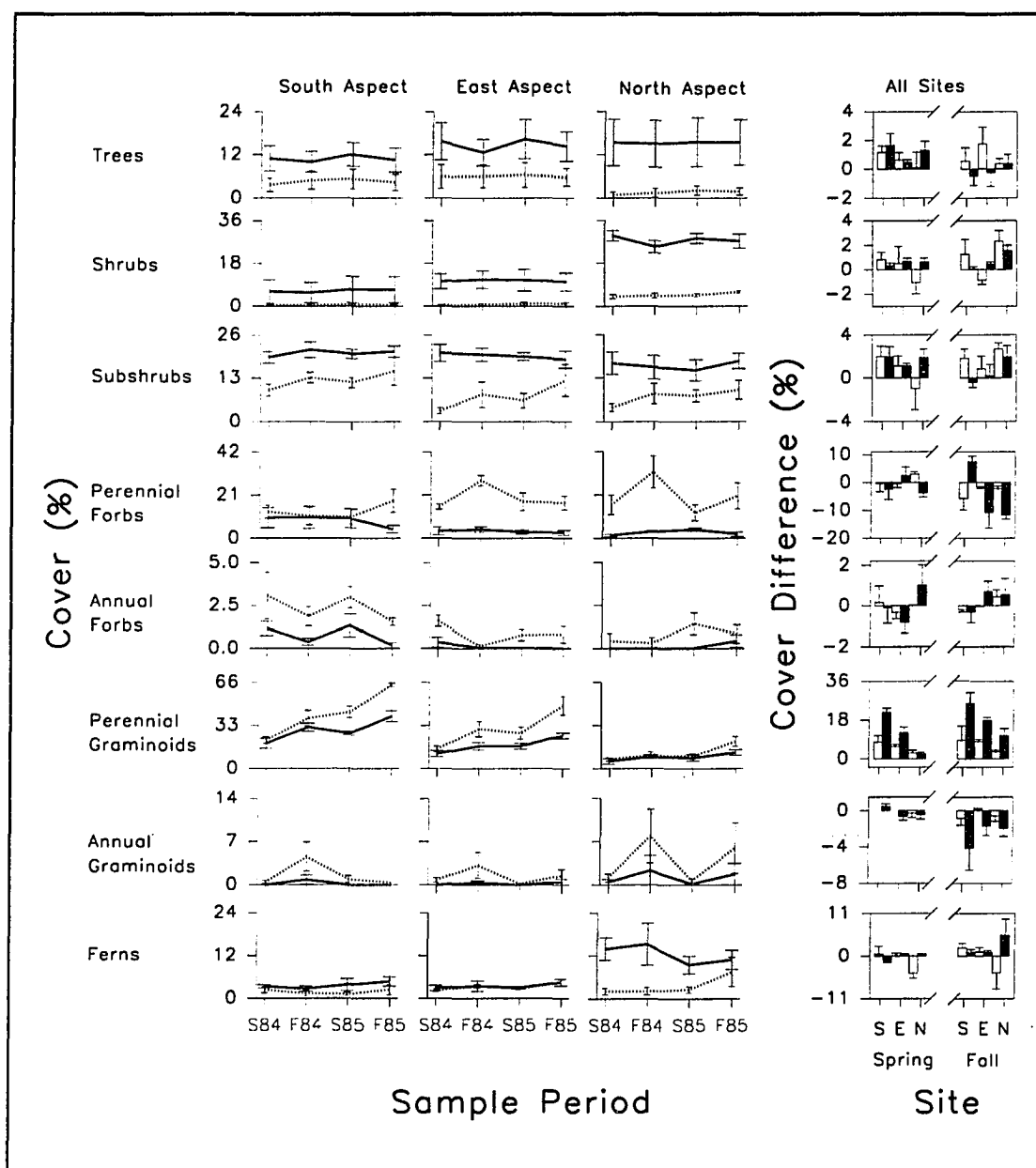
Woody Species - Woody plant cover (trees, shrubs and subshrubs) was similar between sites within burned (10-20%) and unburned (40-60%) areas (Figure 11) but species composition differed greatly between the three aspects. Although cover did not differ significantly between sites it did differ between burned and unburned areas with less cover in areas burned by the 1983 fire. The greatest difference between burned and unburned areas was on the north slope, and least on the south. Cover was 53% on the north slope (or 85% less woody species cover in burned plots compared to unburned plots) while on the east and south slopes respectively this was 38% (81% relative) and 24% (65% relative). As noted by Ahlstrand (1982), woody species, with particular exceptions, showed little mortality with most species responding to burning by

resprouting. By two years postfire, recovery of trees and shrubs had been minimal while subshrubs generally responded quickly with some species, such as *Calliandra eriophylla*, rapidly regaining their preburn cover.

**Trees** - In addition to the two dominant oak species I identified three other tree species in the study plots; *Q. arizonica*, *Juniperus deppeana*, and *Pinus discolor* (formerly called *Pinus cembroides* which was split into several species). Overall tree cover was not significantly different between the three sites (Figure 12) though it was lowest on the south slope and about equivalent between the east and north slopes. However, there was significantly less tree cover in the burned than in the unburned areas during all four sample periods. The difference in tree cover was greatest on the north slope, with 14.5% absolute (a 94% relative reduction in tree cover), while on the east slope it was 9.8% (62%) , and 7.2% (66%) on the south.

Basal area and reduction in basal area due to the fire caused mortality or topkill of the five tree species varied by site and plot (Figure 13). *Q. oblongifolia* dominated on the south and east slopes with relatively minor reduction in basal area resulting from the fire. *Q. emoryi* dominated on the north slope but also had substantial basal area on the east slope. It suffered the largest reductions in basal area in burned plots. *Q. arizonica*, *Juniperus deppeana*, and *Pinus discolor* were all of minor importance and only found on the north slope within the plots.

I believe the lesser fire impact on trees on the south slope may be a result of several factors. First, because fuels at this site were primarily graminoid and the fire may have burned through the area quickly with reduced impact. Second, there were fewer ladder fuels because shrub density was lower. Third, *Q. oblongifolia* was the dominant tree and was more resistant to fire than *Q. emoryi* (Caprio and Zwolinski 1992). Additionally, because this slope probably had

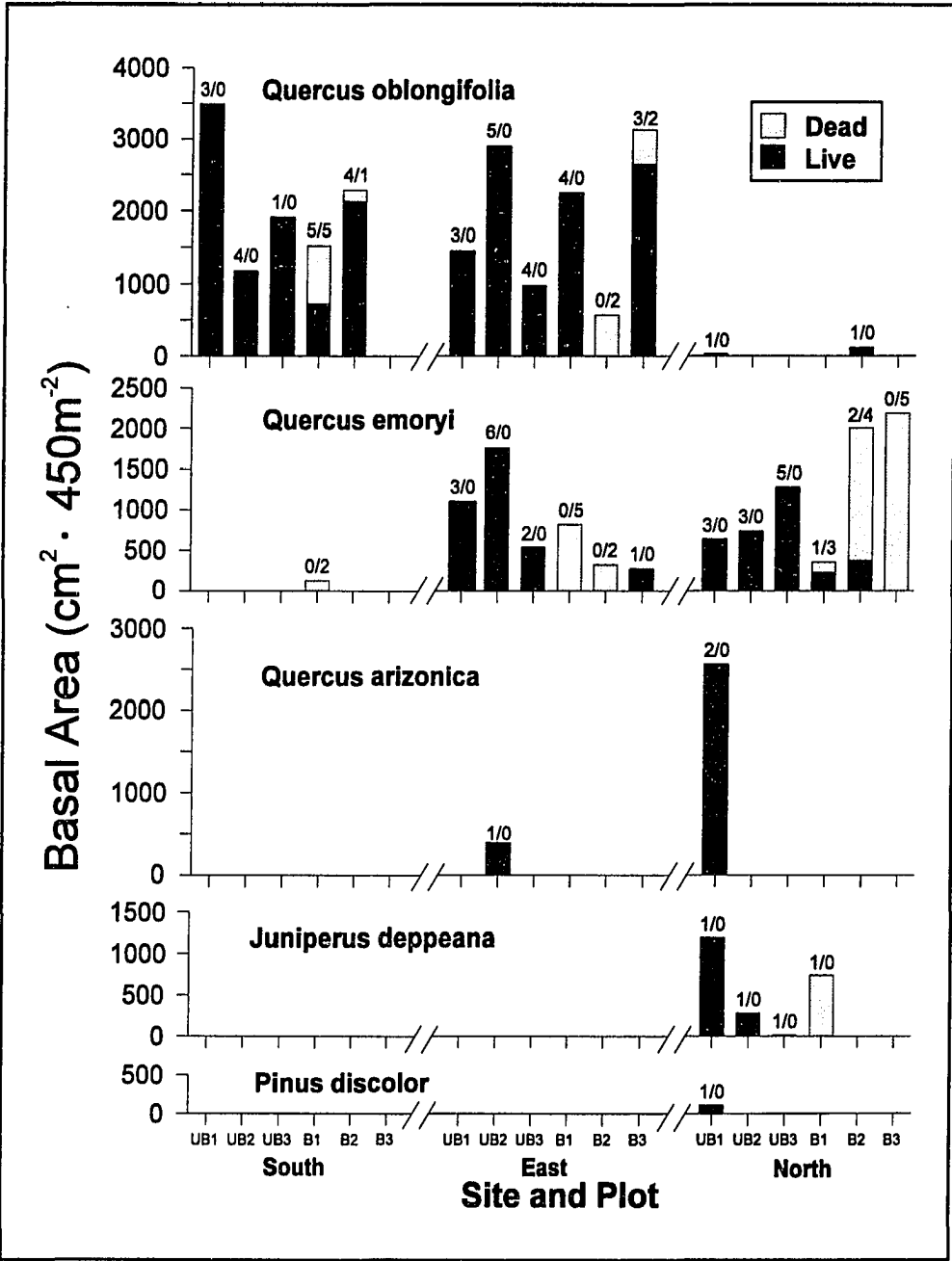


**Figure 12.** Crown cover of different life-form groups summed for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

a high past fire frequency these trees have likely survived fires in the past and thus acquired resistance characteristics (such as elevated crowns) or growing positions (such as in areas sheltered by rocks).

Of the three less common tree species, *J. deppeana* was moderately tolerant with limited sprouting ability from trunk and branches, although I feel it would probably be severely reduced or eliminated with repeated burns, while no *P. discolor* were found to have survived in burned areas. This intolerance of fire may be one explanation for their limited distribution in many areas of southeastern Arizona where a high fire frequency exists. Carmichael et al. (1978) also found *P. discolor* to be intolerant of fire and *J. deppeana* to have some ability to sprout from the root crown. *Q. arizonica* was so uncommon that I was unable to make a judgement but Babb (1992) and Barton (1993) feel it is more resistant to fire than *Q. emoryi*. However, when comparing the size class distribution of *Q. arizonica* to *Q. emoryi*, Sanchini (1981) found a greater number of large *Q. arizonica* which I feel could be accounted for by this greater resistance and thus it shares some characteristics with *Q. oblongifolia*. Additionally, like the two dominant oak species in the study area *Q. arizonica* is listed as being adapted to fire via root crown sprouting by Carmichael et al. (1978), Babb (1992) and Barton (1993).

Recruitment patterns of evergreen oaks in the Southwest has been poorly studied. Sanchini (1981) found weak masting in *Q. arizonica* to *Q. emoryi* with seedling recruitment of *Q. arizonica* paralleling seed production while recruitment of *Q. emoryi* is relatively constant. Borelli (1990) surveyed recruitment patterns at seven sites around southeastern Arizona and found very limited recruitment of oaks a pattern also reported by Phillips (1912). Recruitment was greatest in the Huachuca Mountains and lowest in the Santa Catalina Mountains (Molino Basin). Low recruitment is also reported for oak woodlands in California (White 1966) but *Q.*



**Figure 13.** Basal area distribution by tree species in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope). Reduction in basal area through crown kill or tree death at burned plots is shown as light shading. Above each bar the number of live trees (left of slash) with a crown or sprouting and the number of trees dying (right of slash) is indicated.

*douglasii*, related to Arizona oaks, is strongly influenced by fire. Bartolome et al. (1987), McClaran and Bartolome (1989), Mensing (1992) report regeneration following fire although Allen-Diaz and Bartolome (1992) found there was no association between fire and seedling recruitment and survival. Regeneration appears to be through the reestablishment of individuals by resprouting after crown kill by fire. In California current recruitment in oak woodlands appears to be insufficient to replace existing stands (Bolsinger 1988; Mensing 1992). Regeneration in the past via sprouting was associated with the occurrence of fires with a concurrent decrease as fire frequency decreased (McClaran 1986). A peak in recruitment was found as fire frequency decreased and was followed by long-term survival. This led to increased stand densities and other changes in stand structure relative to the pre-European settlement period (Mensing 1992). Other factors important in these changes appear to be shifts in land use practices such as the introduction of livestock grazing and competition from annuals (Vankat and Major 1978; Mensing 1992).

*Quercus emoryi* - Emory oak was an important cover component on the east and north slopes with 9.1% and 3.6% cover respectively in unburned areas (Figure 13). On the east slope it made up 58% of the tree cover, sharing dominance with *Q. oblongifolia*, while on the north slope it was 23% and shared with *Juniperus deppeana*, *Q. arizonica*, and *Pinus discolor*. Significant site differences existed for cover during all sample periods and for frequency during the last three periods (Table 11). While cover was lower on the north slope than the east slope basal area was similar indicating fewer larger trees on this site. Density was significantly different for the first three samples being lowest on the south slope and greatest on the north (Table 12). Linear



**Table 11.** Probability levels from 2-WAY ANOVA of cover of for major species. Data show differences in cover (%) within each of four sampling periods and change for two sampling intervals for the three site (S) and two fire (F) treatments. Significant differences ( $P < 0.05$ ) are indicated by an asterisk (\*).

Species	Sample Period				Sample Interval	
	Spring 84	Fall 85	Spring 85	Fall 85	Spring	Fall
Probability Levels						
<i>Quercus emoryi</i>						
S	0.042 *	0.047 *	0.032 *	0.023 *	0.395	0.023 *
F	0.007 *	0.005 *	0.007 *	0.005 *	0.911	0.078
S X F	0.042 *	0.039 *	0.029 *	0.040 *	0.385	0.142
<i>Quercus oblongifolia</i>						
S	0.021 *	0.020 *	0.020 *	0.016 *	0.071	0.541
F	0.177	0.345	0.291	0.229	0.412	0.493
S X F	0.269	0.451	0.383	0.322	0.855	0.843
<i>Arctostaphylos pungens</i>						
S	0.994	0.887	0.933	0.962	0.422	0.643
F	0.035 *	0.048 *	0.047 *	0.047 *	0.326	0.281
S X F	0.886	0.734	0.843	0.839	0.665	0.384
<i>Garrya wrightii</i>						
S	0.001 *	0.001 *	0.001 *	0.001 *	0.550	0.008
F	0.001 *	0.001 *	0.001 *	0.001 *	0.005 *	0.289
S X F	0.001 *	0.001 *	0.001 *	0.001 *	0.102	0.442
<i>Agave schottii</i>						
S	0.001 *	0.001 *	0.001 *	0.002 *	0.810	0.572
F	0.001 *	0.001 *	0.001 *	0.001 *	0.057	0.556
S X F	0.001 *	0.001 *	0.001 *	0.004 *	0.357	0.656
<i>Dasyllirion wheeleri</i>						
S	0.002 *	0.013 *	0.009 *	0.030 *	0.386	0.402
F	0.001 *	0.001 *	0.001 *	0.002 *	0.191	0.504
S X F	0.027 *	0.048 *	0.036 *	0.168	0.533	0.954
<i>Haplopappus laricifolius</i>						
S	0.137	0.200	0.305	0.576	0.097	0.260
F	0.007 *	0.003 *	0.008 *	0.006 *	0.360	0.610
S X F	0.172	0.127	0.202	0.304	0.099	0.254
<i>Nolina microcarpa</i>						
S	0.001 *	0.003 *	0.008 *	0.001 *	0.029 *	0.108
F	0.001 *	0.004 *	0.006 *	0.001 *	0.049 *	0.951
S X F	0.002 *	0.008 *	0.022 *	0.001 *	0.115	0.082

Table 11 continued.

Species	Sample Period				Sample Interval	
	Spring 84	Fall 84	Spring 85	Fall 85	Spring	Fall
Probability Levels						
<i>Artemisia ludoviciana</i>						
S	0.552	0.966	0.955	0.633	0.539	0.458
F	0.761	0.144	0.201	0.003 *	0.091	0.022 *
S X F	0.364	0.229	0.283	0.751	0.453	0.051
<i>Gnaphalium wrightii</i>						
S	0.014 *	0.019 *	0.260	0.418	0.011 *	0.015 *
F	0.001 *	0.001 *	0.011 *	0.005 *	0.001 *	0.001 *
S X F	0.013 *	0.026 *	0.351	0.389	0.008 *	0.022 *
<i>Lotus rigidus</i>						
S	0.198	0.042 *	0.025 *	0.022 *	0.570	0.711
F	0.429	0.514	0.396	0.073	0.139	0.027 *
S X F	0.164	0.660	0.776	0.026 *	0.105	0.007 *
<i>Andropogon cirratus</i>						
S	0.048 *	0.296	0.026 *	0.008 *	0.123	0.001 *
F	0.014 *	0.201	0.107	0.658	0.872	0.212
S X F	0.253	0.207	0.130	0.333	0.266	0.972
<i>Aristida orcuttiana</i>						
S	0.002 *	0.042 *	0.004 *	0.061	0.065	0.795
F	0.389	0.931	0.780	0.944	0.151	0.862
S X F	0.316	0.027 *	0.076	0.729	0.009 *	0.139
<i>Bouteloua curtipendula</i>						
S	0.002 *	0.002 *	0.004 *	0.002 *	0.033 *	0.018 *
F	0.029 *	0.104	0.028 *	0.029 *	0.084	0.026 *
S X F	0.081	0.029 *	0.064	0.067	0.157	0.390
<i>Eragrostis intermedia</i>						
S	0.174	0.018 *	0.002 *	0.029 *	0.001 *	0.327
F	0.001 *	0.002 *	0.001 *	0.002 *	0.001 *	0.044 *
S X F	0.288	0.027 *	0.001 *	0.050 *	0.001 *	0.447
<i>Heteropogon contortus</i>						
S	0.007 *	0.031 *	0.024 *	0.005 *	0.473	0.086
F	0.068	0.191	0.687	0.044 *	0.223	0.098
S X F	0.106	0.072	0.159	0.159	0.278	0.256
<i>Muhlenbergia emersleyi</i>						
S	0.018 *	0.010 *	0.008 *	0.018 *	0.025 *	0.725
F	0.281	0.937	0.545	0.675	0.672	0.489
S X F	0.031 *	0.001 *	0.007 *	0.001 *	0.010 *	0.122

Table 11 continued.

Species	Sample Period				Sample Interval	
	Spring 84	Fall 84	Spring 85	Fall 85	Spring	Fall
Probability Levels						
<i>Trachypogon secundus</i>						
S	0.120	0.008 *	0.005 *	0.025 *	0.013 *	0.427
F	0.142	0.159	0.166	0.544	0.867	0.086
S X F	0.545	0.544	0.593	0.758	0.920	0.396
<i>Aristida adscensionis</i>						
S	0.999	0.045 *	0.999	0.060	0.999	0.139
F	0.999	0.869	0.999	0.796	0.999	0.157
S X F	0.999	0.448	0.999	0.964	0.999	0.054
<i>Cheilanthes wootoni</i>						
S	0.339	0.098	0.067	0.118	0.021 *	0.528
F	0.055	0.444	0.122	0.540	0.210	0.936
S X F	0.614	0.181	0.758	0.579	0.391	0.270
<i>Selaginella rupincola</i>						
S	0.001 *	0.003 *	0.003 *	0.005 *	0.007 *	0.073
F	0.001 *	0.001 *	0.001 *	0.001 *	0.575	0.015 *
S X F	0.001 *	0.019 *	0.015 *	0.029 *	0.001 *	0.008 *

**Table 12.** Probability levels from 2-WAY ANOVA of density for major species. Data from three sites (S) and two fire (F) factors show differences within each of the four sampling periods and change in density for two sampling intervals. Significant differences ( $P < 0.05$ ) are indicated by an asterisk (\*).

Species	Sample Period				Sample Interval	
	Spring 84	Fall 84	Spring 85	Fall 85	Spring	Fall
Probability Levels						
<i>Quercus emoryi</i>						
S	0.041 *	0.009 *	0.012 *	0.006 *	0.052	1.000
F	0.010 *	0.044 *	0.202	0.091	0.287	0.472
S X F	0.110	0.287	0.341	0.246	0.076	0.590
<i>Quercus oblongifolia</i>						
S	0.034 *	0.084	0.049 *	0.014 *	0.275	0.393
F	0.733	0.744	0.869	0.268	0.408	0.068
S X F	0.354	0.993	0.875	0.540	0.499	0.068
<i>Arctostaphylos pungens</i>						
S	0.838	0.847	0.876	0.987	0.733	0.294
F	0.151	0.126	0.152	0.167	0.209	0.803
S X F	0.661	0.480	0.606	0.576	0.527	0.972
<i>Garrya wrightii</i>						
S	0.001 *	0.001 *	0.001 *	0.001 *	0.928	0.170
F	0.001 *	0.001 *	0.009 *	0.001 *	0.689	0.002 *
S X F	0.001 *	0.001 *	0.003 *	0.001 *	0.684	0.002 *
<i>Agave schottii</i>						
S	0.060	0.015 *	0.003 *	0.012 *	0.011 *	0.347
F	0.014 *	0.002 *	0.001 *	0.001 *	0.401	0.259
S X F	0.154	0.023 *	0.004 *	0.026 *	0.022 *	0.621
<i>Dasyllirion wheeleri</i>						
S	0.001 *	0.004 *	0.002 *	0.013 *	0.826	0.011 *
F	0.020 *	0.026 *	0.024 *	0.045	0.337	0.067
S X F	0.420	0.352	0.307	0.564	0.117	0.296
<i>Haplopappus laricifolius</i>						
S	0.137	0.180	0.122	0.063	0.967	0.286
F	0.016 *	0.003 *	0.005 *	0.005 *	0.049 *	0.394
S X F	0.243	0.130	0.121	0.120	0.056	0.999
<i>Nolina microcarpa</i>						
S	0.004 *	0.006 *	0.012 *	0.003 *	0.003 *	0.173
F	0.172	0.427	0.435	0.153	0.041 *	0.179
S X F	0.113	0.086	0.466	0.140	0.010 *	0.085

Table 12 continued.

Species	Sample Period				Sample Interval	
	Spr. 84	Fall 84	Spr. 85	Fall 85	Spring	Fall
Probability Levels						
<i>Artemisia ludoviciana</i>						
S	0.528	0.531	0.979	0.604	0.352	0.831
F	0.323	0.379	0.318	0.237	0.431	0.588
S X F	0.340	0.140	0.279	0.743	0.144	0.189
<i>Gnaphalium wrightii</i>						
S	0.001 *	0.029 *	0.317	0.299	0.001 *	0.216
F	0.001 *	0.001 *	0.222	0.005 *	0.001 *	0.404
S X F	0.001 *	0.051	0.128	0.280	0.001 *	0.356
<i>Lotus rigidus</i>						
S	0.363	0.206	0.092	0.055	0.847	0.874
F	0.504	0.373	0.600	0.363	0.738	0.037 *
S X F	0.634	0.756	0.526	0.255	0.766	0.037 *
<i>Andropogon cirratus</i>						
S	0.095	0.199	0.041 *	0.038 *	0.234	0.028 *
F	0.013 *	0.082	0.095	0.246	0.014 *	0.064
S X F	0.205	0.117	0.260	0.165	0.690	0.763
<i>Aristida orcuttiana</i>						
S	0.001 *	0.015 *	0.004 *	0.315	0.442	0.568
F	0.999	0.818	0.618	0.380	0.493	0.370
S X F	0.215	0.191	0.032 *	0.387	0.081	0.504
<i>Bouteloua curtipendula</i>						
S	0.001 *	0.001 *	0.020 *	0.004 *	0.834	0.145
F	0.004 *	0.406	0.329	0.097	0.214	0.050 *
S X F	0.033 *	0.090	0.301	0.215	0.146	0.247
<i>Eragrostis intermedia</i>						
S	0.416	0.021 *	0.091	0.072	0.727	0.196
F	0.005 *	0.020 *	0.003 *	0.006 *	0.865	0.687
S X F	0.691	0.071	0.045 *	0.161	0.368	0.362
<i>Heteropogon contortus</i>						
S	0.004 *	0.049 *	0.038 *	0.006 *	0.911	0.669
F	0.297	0.193	0.917	0.415	0.152	0.133
S X F	0.022 *	0.085	0.594	0.624	0.138	0.007 *
<i>Muhlenbergia emersleyi</i>						
S	0.129	0.055	0.014 *	0.003 *	0.016 *	0.660
F	0.927	0.664	0.239	0.701	0.029 *	0.767
S X F	0.002 *	0.002 *	0.004 *	0.001 *	0.397	0.646

Table 12 continued.

Species	Sample Period				Sample Interval	
	Spr. 84	Fall 84	Spr. 85	Fall 85	Spring	Fall
Probability Levels						
<i>Trachypogon secundus</i>						
S	0.178	0.110	0.026 *	0.226	0.858	0.119
F	0.203	0.140	0.051	0.194	0.663	0.248
S X F	0.635	0.552	0.236	0.460	0.445	0.543
<i>Aristida adscensionis</i>						
S	0.999	0.276	0.999	0.419	0.999	0.164
F	0.999	0.585	0.999	0.848	0.999	0.212
S X F	0.999	0.762	0.999	0.509	0.999	0.965
<i>Cheilanthes wootoni</i>						
S	0.017 *	0.580	0.010 *	0.033 *	0.003 *	0.235
F	0.038 *	0.508	0.776	0.754	0.088	0.999
S X F	0.069	0.361	0.060	0.098	0.521	0.880
<i>Selaginella rupincola</i>						
S	0.001 *	0.001 *	0.001 *	0.001 *	0.224	0.019 *
F	0.001 *	0.001 *	0.001 *	0.001 *	0.128	0.721
S X F	0.006 *	0.022 *	0.008 *	0.020 *	0.627	0.326

**Table 13.** Probability levels from 2-WAY ANOVA of frequency for major species. Data from three sites (S) and two burned areas (F) and show differences within each of the four sampling periods and change in frequency for two sampling intervals. Significant differences ( $P < 0.05$ ) are indicated by an asterisk (\*).

Species	Sample Period				Sample Interval	
	Spr. 84	Fall 84	Spr. 85	Fall 85	Spring	Fall
Probability Levels						
<i>Quercus emoryi</i>						
S	0.058	0.002 *	0.001 *	0.004 *	0.025 *	0.566
F	0.011 *	0.098	0.569	0.323	0.025 *	0.290
S X F	0.065	0.457	0.476	0.743	0.052	0.608
<i>Quercus oblongifolia</i>						
S	0.125	0.082	0.079	0.047 *	0.329	0.605
F	0.806	0.811	0.885	0.977	0.817	0.174
S X F	0.781	0.800	0.689	0.719	0.627	0.605
<i>Arctostaphylos pungens</i>						
S	0.553	0.304	0.437	0.619	0.418	0.098
F	0.047 *	0.031 *	0.032 *	0.012 *	0.345	0.319
S X F	0.881	0.561	0.561	0.857	0.441	0.102
<i>Garrya wrightii</i>						
S	0.008 *	0.001 *	0.001 *	0.001 *	0.504	0.999
F	0.340	0.559	0.364	0.192	0.849	0.183
S X F	0.726	0.459	0.972	0.953	0.703	0.178
<i>Agave schottii</i>						
S	0.001 *	0.001 *	0.001 *	0.001 *	0.397	0.151
F	0.024 *	0.003 *	0.008 *	0.003 *	0.357	0.837
S X F	0.001 *	0.001 *	0.009 *	0.001 *	0.397	0.038 *
<i>Dasyllirion wheeleri</i>						
S	0.041 *	0.002 *	0.002 *	0.026 *	0.044 *	0.680
F	0.051	0.001 *	0.020 *	0.026 *	0.337	0.361
S X F	0.746	0.134	0.210	0.437	0.204	0.687
<i>Haplopappus laricifolius</i>						
S	0.295	0.228	0.279	0.504	0.960	0.253
F	0.001 *	0.001 *	0.001 *	0.001 *	0.969	0.547
S X F	0.179	0.110	0.080	0.040 *	0.403	0.585
<i>Nolina microcarpa</i>						
S	0.005 *	0.014 *	0.002 *	0.001 *	0.920	0.798
F	0.069	0.367	0.298	0.093	0.107	0.825
S X F	0.027 *	0.171 *	0.249	0.196	0.029 *	0.394

Table 13 continued.

Species	Sample Period				Sample Interval	
	Spr. 84	Fall 84	Spr. 85	Fall 85	Spring	Fall
Probability Levels						
<i>Artemisia ludoviciana</i>						
S	0.596	0.288	0.355	0.449	0.326	0.922
F	0.140	0.025 *	0.101	0.069	0.327	0.948
S X F	0.604	0.348	0.333	0.827	0.131	0.111
<i>Gnaphalium wrightii</i>						
S	0.002 *	0.002 *	0.573	0.037 *	0.052	0.001 *
F	0.001 *	0.001 *	0.001 *	0.001 *	0.016 *	0.030 *
S X F	0.001 *	0.027 *	0.038 *	0.065	0.001 *	0.030 *
<i>Lotus rigidus</i>						
S	0.080	0.002 *	0.001 *	0.001 *	0.013 *	0.738
F	0.645	0.539	0.158	0.042 *	0.177	0.121
S X F	0.473	0.382	0.729	0.056	0.088	0.007 *
<i>Andropogon cirratus</i>						
S	0.141	0.018 *	0.037 *	0.029 *	0.241	0.552
F	0.006 *	0.044 *	0.175	0.161	0.032 *	0.191
S X F	0.833	0.367	0.564	0.136	0.229	0.671
<i>Aristida orcuttiana</i>						
S	0.001 *	0.001 *	0.001 *	0.002 *	0.989	0.749
F	0.318	0.194	0.311	0.901	0.406	0.103
S X F	0.004 *	0.014 *	0.389	0.268	0.593	0.041 *
<i>Bouteloua curtipendula</i>						
S	0.003 *	0.002 *	0.005 *	0.003 *	0.521	0.417
F	0.082	0.286	0.047 *	0.083	0.605	0.154
S X F	0.162	0.010 *	0.044 *	0.066	0.346	0.180
<i>Eragrostis intermedia</i>						
S	0.059	0.009 *	0.031 *	0.004 *	0.728	0.401
F	0.001 *	0.001 *	0.001 *	0.001 *	0.297	0.862
S X F	0.946	0.226	0.136 *	0.022 *	0.190 *	0.453
<i>Heteropogon contortus</i>						
S	0.001 *	0.001 *	0.001 *	0.001 *	0.877	0.145
F	0.602	0.963	0.211	0.928	0.010 *	0.881
S X F	0.168	0.031 *	0.056	0.882	0.126	0.050 *
<i>Muhlenbergia emersleyi</i>						
S	0.127	0.008 *	0.041 *	0.004 *	0.126	0.237
F	0.874	0.754	0.995	0.285	0.746	0.218
S X F	0.001 *	0.005 *	0.004 *	0.003 *	0.502	0.770



Table 13 continued.

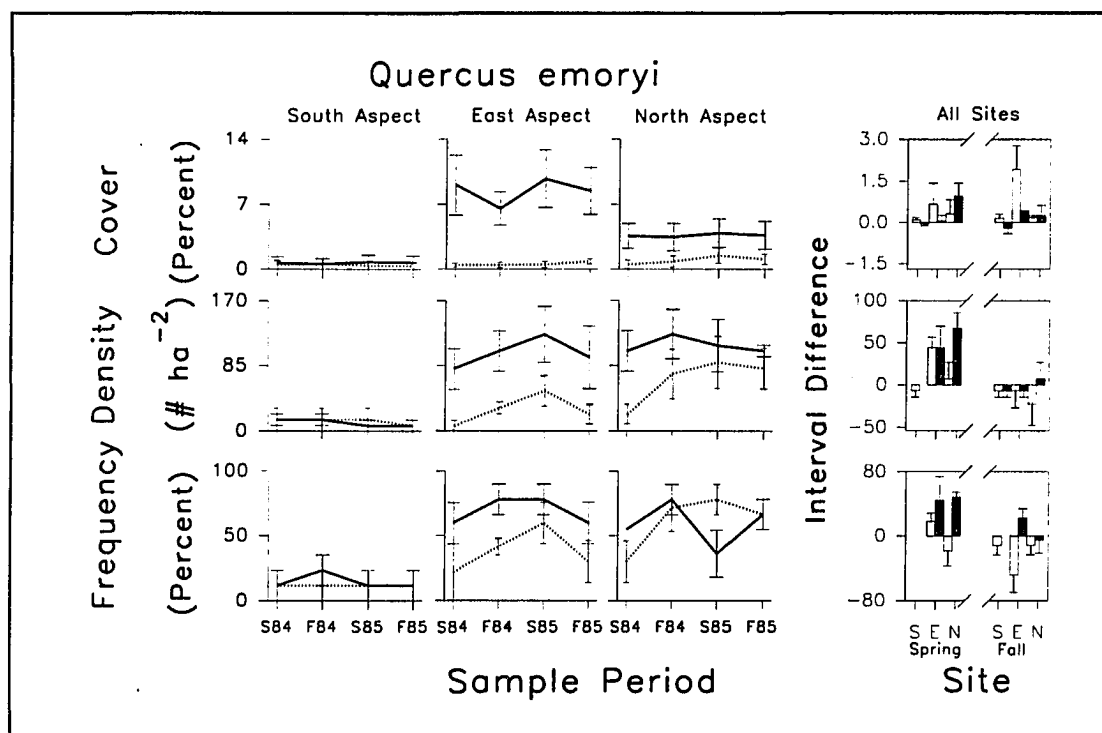
Species	Sample Period				Sample Interval	
	Spr. 84	Fall 84	Spr. 85	Fall 85	Spring	Fall
Probability Levels						
<i>Trachypogon secundus</i>						
S	0.001 *	0.001 *	0.001 *	0.004 *	0.005 *	0.980
F	0.175	0.081	0.181	0.227	0.851	0.711
S X F	0.604	0.328	0.540	0.462	0.737	0.804
<i>Aristida adscensionis</i>						
S	0.999	0.633	0.999	0.220	0.999	0.092
F	0.999	0.130	0.999	0.386	0.999	0.178
S X F	0.999	0.885	0.999	0.801	0.999	0.440
<i>Cheilanthes wootoni</i>						
S	0.009 *	0.160	0.144	0.178	0.057	0.561
F	0.098	0.908	0.843	0.955	0.450	0.895
S X F	0.170	0.471	0.566	0.457	0.810	0.631
<i>Selaginella rupincola</i>						
S	0.001 *	0.001 *	0.001 *	0.001 *	0.465	0.015 *
F	0.001 *	0.001 *	0.001 *	0.001 *	0.047 *	0.526
S X F	0.028 *	0.052	0.040 *	0.048 *	0.291	0.257

contrasts showed *Q. emoryi* frequency and density to be significantly less on the south slope than on either the east or north which were not different.

Significant differences between burned and unburned areas existed for cover (Table 11) during all periods while density and frequency differences were only found for the first period (Table 12 and 13). Cover was less on burned than on unburned areas but with a significant interaction term. Linear contrasts showed that cover in the unburned area on the east slope was different from the south or north slopes while cover in burned areas did not differ among sites (31%, 95% and 86% respectively). Less cover was found in burned areas compared to unburned on the south, east and north slopes. No interval changes were significant apparently because of slow recovery. Lack of frequency and density differences after the first sample period was probably a result of resprouting. Both characteristics increased and changed more in burned than unburned areas as resprouting and recovery occurred. Contrasts of site interval changes showed less change on the south slope than on either the east or north slopes.

Crown scorch and death of above ground stems (topkill) occurred in many of the Emory oaks but most individuals showed recovery by producing multiple sprouts from the base. Varying results have been reported for fire effects on *Q. emoryi* and may be related to differences in fire intensity and other site features. Bock and Bock (1986a) state a cool prescribed burn had no impact on *Q. emoryi* whereas the burn in Molino Basin did have an impact suggesting the fire was severe. Hibbert et al. (1974) working in interior chaparral tentatively list the species as tolerant showing an ability to refoliate while they and Carmichael et al. (1978) report it being adapted to fire though sprouting. Phillips (1912) felt most stands of this species originated from sprouts developing after fire.

*Quercus oblongifolia* - Cover of Mexican blue oak was important on the south and east slopes, 10.3% and 6.3% respectively, in unburned areas which represented 94% of the tree cover on the south and 40% on the east slope (Figure 15). It was codominant at the east site with *Q. emoryi*. Location of *Q. oblongifolia* on the dry south slope is partially explained by its drought resistance (Johnson et al. 1962). Significant site differences existed in *Q. oblongifolia* cover during all samples while significant site differences for density and frequency did not exist with one exception (frequency fall 1985). No significant changes in cover (Table 11), frequency (Table 13) or density (Table 12) for the two sample intervals occurred. Contrasts of site



**Figure 14.** Cover, density, and frequency of *Quercus emoryi* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

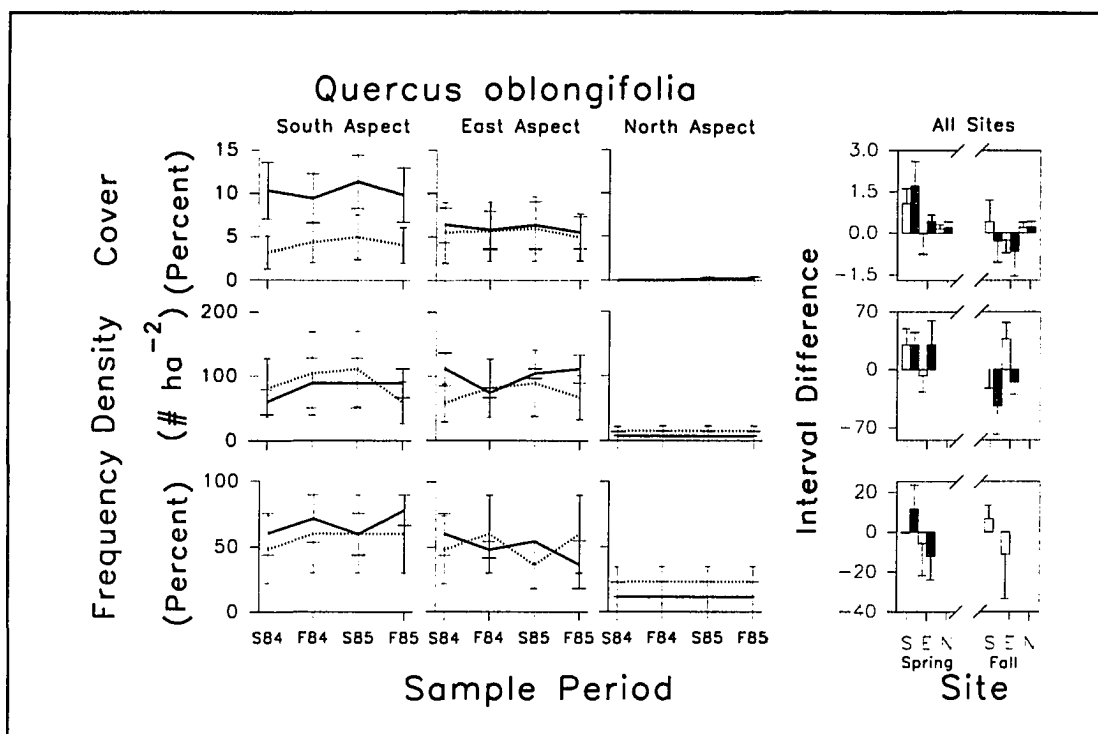
**Table 14.** Mean and standard deviation of number of sprouts per tree in burned and unburned areas on the south (S), east (E) and north (N) slopes for the two predominant oak species in the study area.

Site	<i>Quercus emoryi</i>		<i>Quercus oblongifolia</i>	
	Unburned	Burned	Unburned	Burned
	Number of Sprouts (SD)			
S	0.00	15.33 (26.56)	0.11 (0.19)	5.02 (4.50)
E	0.00	37.83 (35.53)	0.28 (0.31)	10.77 (2.73)
N	0.87 (1.50)	19.98 (12.31)	0.00	2.67 (4.62)

differences showed cover on the north slope to be significantly less than on the south or east sites which were not significantly different. In contrast, frequency was greater on the south slope than on either the east or north slopes.

I detected no significant effect due to the burn on cover (Table 11), frequency (Table 13) or density (Table 12), although average cover values on the south and east slopes were less in burned than in unburned areas. These results suggest this oak species is relatively fire resistant. In comparison to *Q. emoryi* less crown scorch and top-kill occurred and it was a moderately good sprouter when top-killed (sprouting will be treated more fully in the next section). Lack of any significant differences between burned and unburned areas may be because of fire resistance and sprouting ability. On the south slope this species was observed to be frequently located on microsites surrounded by large rocks which appear to give some protection from fire, an observation also made in California for coast live oaks (Snow 1980).

*Oak Sprouting* - Basal sprouting of the two main oak species was more prominent in burned than in unburned areas (Table 14). Few unburned individuals showed sprouting activity while nearly all trees surviving the fire developed sprouts (a topkilled tree sprouting from the root-crown was considered a survivor). *Q. emoryi* trees with sprouts averaged 94% on burned



**Figure 15.** Cover, density, and frequency of *Quercus oblongifolia* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=East slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

and 8% on unburned sites. For *Q. oblongifolia* this was 95% and 16% respectively. Number of sprouts per tree was significantly greater in burned areas than in unburned (ANOVA;  $F=7.587, df=1, P=0.011$ ) but did not differ among sites ( $F=1.369, df=2, P=0.274$ ). Although the number of sprouts did not differ significantly when the two species were compared ( $F=3.136, df=1, P=0.089$ ) *Q. emoryi* appeared to have a stronger response. No interaction effects were significant in the ANOVA tests. Of the trees surviving fire, *Q. emoryi* had a greater average number of sprouts per tree (15.3 to 37.8 by plot) than did *Q. oblongifolia* (2.7 to 10.8). Up to 141 sprouts per tree were counted for the former and up to 41 for the latter species. This could be

better quantified with a larger sample size since the number of trees examined was limited by the small plot size which resulted in a large amount of noise in the data. The number of sprouts a tree produced also appeared associated with the amount of crown-kill but here again a larger sample size was needed to fully quantify this observation. Trees failing to sprout in my study often had delayed mortality (1-two years postfire) even after complete trunk girdling had occurred similar to postfire mortality in several oak species in California (Plumb 1980a) and Florida (Rebertus et al. 1989).

By the final sample period in the fall of 1985 (2½ years postfire) sprout height of the tallest sprout per tree for *Q. emoryi* averaged 180 cm in the burned treatments with individuals reaching a maximum of 310 cm. Similarly, Phillips (1912) reports growth of 1-4 ft (30-122 cm) the first season postfire for *Q. emoryi*. For *Q. oblongifolia* the average height was 152 cm with a maximum of 254 cm. After a fire in Guadalupe Mountains National Park, stem killed oaks resprouted vigorously, reaching 60-90 cm (2-3 ft) in height in two months and grew 25-38 cm (10-15 in) per year for three years (Kittams 1972). In Mediterranean oaks rapid sprout growth is observed immediately postfire, reaching a cover asymptote in 4-5 years (Trabaud 1981; Gratani and Amadori 1991). In French mediterranean oak woodland Trabaud (1981) found sprouts reached an average height of 11 cm one month after the fire and 55 cm by eleven months post-burn. Sprouting vigor and biomass may also be related to individual preburn (or precutting) plant size measured as stump area (Meyer 1988; Canadell et al. 1991).

The capacity of oaks in the West to sprout has been described by many investigators but no detailed analysis of Madrean woodland oaks has been carried out. Wagle (1981) found a high percentage of oaks in Madrean woodlands develop sprouts following fire, as did Phillips (1912) who found 5-25 sprouts/tree. Most sprouts originate from the root collar (Phillips 1912; Hibbert

et al. 1974; Carmichael et al. 1978). *Q. gambelii* (Gambel oak), a deciduous oak species also found in the Southwest, develops a massive system of underground lignotubers, rhizomes and roots (Tiedemann et al. 1987). Lignotubers made up the largest proportion of this system (72%) and had large numbers of adventitious buds that sprout prolifically after stems are top-killed by fire. In southwestern Colorado sprouting ability of *Q. gambelii* was dependent on nonstructural root carbohydrate concentrations (Harrington 1989). Burns during summer carbohydrate depression contributed to oak reduction. A similar case has been made for differences in seasonal fire effects in *Q. coccifera* garrigue in southern France (Trabaud 1991). These varying sprouting and growth responses are partially a result of carbohydrate reserves accumulating differentially in various parts of a plant over a year (Berg and Plumb 1972; Boo and Pettit 1975; Garrison 1972; Wilson et al. 1975). It is unknown whether similar seasonal differences in fire would have the same effects on *Q. emoryi* and *Q. oblongifolia*.

The differential sprouting ability of oaks has been examined in a number of studies. Sampling by Whittaker and Niering following a 1963 burn above Molino Basin showed *Q. oblongifolia* was a vigorous sprouter after stem kill (Niering and Lowe 1984). Johnson et al. (1962) found 47% of the *Q. emoryi* sprouting on a burned site and 21% in a nearby unburned area, although they indicate the results were affected by drought mortality. In the same study they report that *Q. arizonica*, a species closely related to *Q. oblongifolia*, which did not appear affected by the drought, to have 30% of the trees develop sprouts after burning while 2% sprouted on unburned areas. A more detailed analysis of these two oak species in Molino Basin shows that sprouting is more important for the survival of *Q. emoryi* than for *Q. oblongifolia* which is more fire resistant. This suggests a trade off between sprouting ability and the ability to resist fire (Caprio and Zwolinski 1992), a response also suggested for other oak species (and oaks vs. pines)

in southeastern Arizona (Barton 1993) and among several California oaks (Haggerty 1991).

In other studies of evergreen oaks in southeastern Arizona, Meyer (1988) found *Q. emoryi* produced more coppice sprouts than *Q. arizonica* (a species closely related to *Q. oblongifolia*) with a similar response reported to follow fire (Babb 1992). Variable resistance and sprouting response to fire are also found in woodland oaks in California (Plumb 1980a; McClaran 1986; Haggerty 1991). The question remains as to whether this ability is inherent in all Southwestern evergreen oak woodlands. Some indications are that it is not. My personal observations in 1991 of two burned areas (Laguna Meadow Fire in March 1980 and the Blue Creek Fire in March 11-25 1989 in the Chisos Mountains, Big Bend National Park, Texas) classified as oak woodlands suggest sprouting may not be a consistent response in all Southwestern woodlands. Sprouting of oaks within these two burned areas was not observed. This suggests either a difference in effects and species response to fire in this eastern area of Madrean woodland or the season of the burn was affecting sprouting differently. The results obtained from one area of Madrean oak woodland may not be broadly applicable to all areas of the woodland where species compositions may differ considerably.

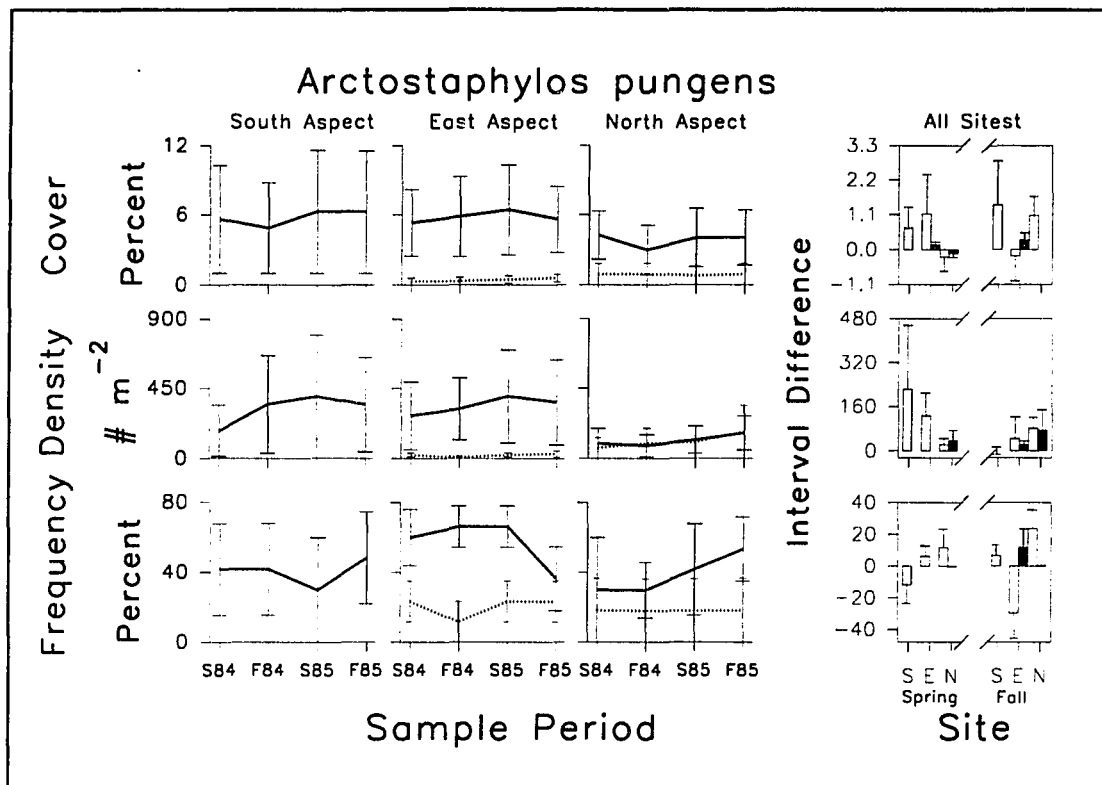
**Shrubs** - Shrub cover (Figure 12) varied significantly between sites and between burned and unburned areas for all four sample periods although it was confounded by interaction for the first three samples (Table 10). Linear contrasts indicated this was due to significant differences in shrub cover in unburned areas between the north slope versus the east and south slopes which were not different while in burned areas no differences were significant, most likely a result of shrub reduction by the fire that equalized cover at all sites. For the fall 1985 sample, shrub cover in unburned plots on the north slope was significantly greater than on either the south or east



slope. Cover ranged from 5 to 11% on the south and east slopes, and 25 to 30% on the north slope for all sample periods. Shrub cover was significantly less in all burned areas compared to the unburned, differing by 25.5% (an 86% reduction in shrub cover) on the north slope, 10.0% (96%) on the east, and 5.8% (93%) on the south. I also found a significant difference in the amount of change in shrub cover for the fall sample interval (Table 10). Contrasts showed the difference to be between the east and north slope sites with cover decreasing slightly on the east slope while increasing on the south and north. In Chihuahuan Desert mountain shrub vegetation Ahlstrand (1982) noted 37% less cover of woody species three years postfire and 23% less at 6 to 7 years postfire while Bunting and Wright (1977) found shrub cover decreased from 17.35% to 9.93%, but with vigorous sprouting occurring, two years postfire in desert mountain scrub near Big Bend National Park, Texas.

*Arctostaphylos pungens* - Point-leaf manzanita is an important constituent of both interior and California chaparral (Pase and Brown 1982; Cooper 1922). At higher elevation in interior chaparral *A. pringlei* is also common (Brown 1982) while at higher elevations in California it is replaced by *A. glandulosa* (Vogl and Schorr 1972). I found that *A. pungens* in Molino Basin did not differ significantly among sites in cover (Table 11), frequency (Table 13), or density (Table 12) during any sample period or interval. Although cover was similar in unburned plots at all sites the importance of this species varied from site-to-site (Figure 16). It was the most common of the shrub species on the south slope but was overshadowed by *Garrya wrightii* on the north slope. It made up 91% of the shrub cover on the south slope, 51% on the east, and 19% on the north. Actual cover values ranged from 4% and 6%.

This species was reduced by burning and was slow to recover. Cover and frequency were



**Figure 16.** Cover, density, and frequency of *Arctostaphylos pungens* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

significantly less in all burned areas compared to unburned for all sample periods while no significant changes occurred between the two intervals, indicating slow recovery (Table 11 and 13). Comparison of burned and unburned plots at the three sites during the first sample period showed a 100% decrease in cover on the south slope, 94% on the east, and 79% on the north. In contrast, density was not significantly different (Table 12) although density values were consistently lower in burned areas compared to unburned particularly on the south and east slopes (Appendix 9). This may be a result of the growth habit of the species with a few large individuals

in unburned areas while burned areas had a similar number but of much smaller individuals that were either surviving portions of larger clumps or newly germinated seedlings.

Burning killed *A. pungens* with no postfire sprouting occurring, unlike *A. glandulosa* which sprouts well following fire (Pase and Brown 1982; Vogl and Schorr 1972). Re-establishment of *A. pungens* from seed was observed during the fall 1984 with seedlings reaching heights of 35-40 cm by the fall of 1985. I only observed seedling establishment in areas previously occupied by adult plants. Similar findings have been reported by many other researchers. Hibbert et. al. (1974) working in interior chaparral and Niering and Lowe (1984) in Madrean oak woodland found this species susceptible to decrease following fire. It remained greatly reduced for six years in interior chaparral (Pase and Pond 1964). In manzanita chaparral in California this species is also highly susceptible to fire kill (Lathrop and Martin 1982; Biswell and Schorr 1958). Repeated burning of this species at intervals short enough to prevent accumulations of sufficient seed reserves in the soil could lead to its elimination from a site. Experimental burns in California were successful at reducing adult plants of this species and of subsequent seedling establishment and soil seed reserves with repeated burning (Biswell and Schorr 1958). Thus, the presence or absence of this species could be an indicator of recent fire frequency. Manzanita in Molino Basin appears to be at its lower moisture limit and thus controlled by both fire and rainfall (Niering and Lowe 1984). Mortality was observed after the dry spring of 1985 and exceptionally dry winter/spring of 1989.

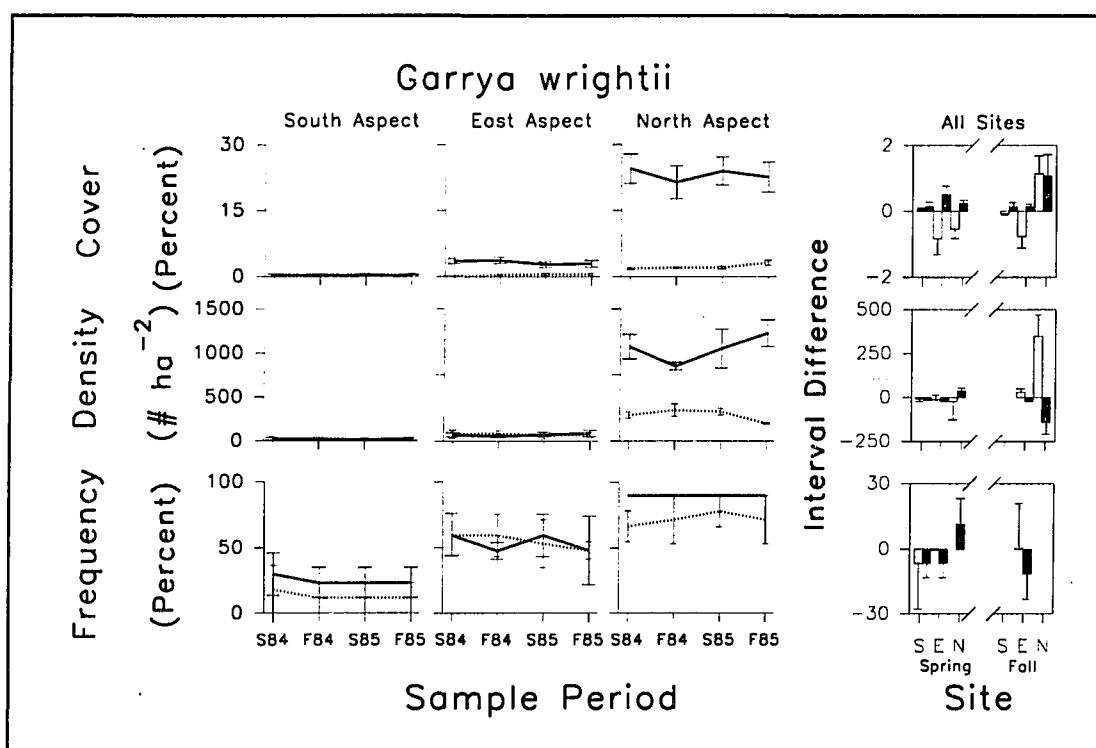
Although some *Arctostaphylos* species can sprout and form lignotubers (Vogl and Schorr 1972; James 1984), most are referred to as non-sprouters and obligate seeders, being totally dependent on a seed bank for re-establishment, without the ability to rejuvenate from basal sprouts or to recruit new seedlings except after fire (Montygiard-Loyba and Keeley 1987; Keeley

1987). Heat resistant seed from many *Arctostaphylos* species in both California and interior chaparral is produced throughout a plants' life and lies dormant in the soil until stimulated by fire to germinate (Glendening and Pase 1964; Pase 1965; Carmicheal et al. 1978; Montygierd-Loyba and Keeley 1987; Keeley 1987). Charate is reported to be important in cueing germination of some species with refractory seeds (dormant seeds that may be stimulated to germinate by intense heat shock,  $>100^{\circ}\text{C}$  but  $<150^{\circ}\text{C}$ , or charate) in the genera, such as *A. glandulosa*, *A. canescens*, and *A. patula*, found in California chaparral (Keeley 1987, 1991). *A. pungens* in Molino Basin showed no postfire sprouting ability but between fires did spread vegetatively to form clonal clumps or genet. Vegetative regeneration appears to occur around genet perimeters through layering, creating what appears to be a discrete age/size structure from the center to clump edge. These coalesce into new aggregates as they mature. As the genets age central areas often become senescent and die. The postfire establishment within the bounds of the prefire aggregate suggests that aggregates may continue to occupy a site from fire-to-fire, long after the original colonizer is gone.

*Garrya wrightii* - Silktassel was most prominent on the north facing slope and least prominent on the south facing slope (Figure 17). During the initial sample on unburned sites cover averaged 0.3%, 3.6%, and 24.5% at the south, east, and north sites respectively. On the south slope it made up 4% of the shrub cover, while on the east and north this was 34% and 83% respectively. Significant site differences were found for cover, frequency and density. Frequency was greater on the north than on the south or east slopes. Cover and density were similar but had significant interaction effects (Table 11 and 12). Linear contrasts showed cover on the north slope to be significantly different from the south or east slopes in unburned areas but not in

burned areas where cover had been reduced. Density was somewhat similar but with some differences appearing in the burned areas which was probably a result of resprouting.

Cover in burned areas was significantly less than in unburned (Table 11). Differences between burned and unburned treatments were 52% on the south slope 99% on the east, and 93% on the north. Significant changes in cover in burned areas were also found for the first interval (Table 11) with cover in burned plots increasing, indicating recovery, while cover in unburned plots decreased slightly. No fire effects or interval differences were significant for frequency (Table 13). Rapid postfire sprouting probably limits frequency differences. Significant density



**Figure 17.** Cover, density, and frequency of *Garrya wrightii* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

differences were observed but confounded by interaction effects (Table 12). Linear contrasts showed the north slope to be significantly different with greater density than the south or east slopes in unburned areas.

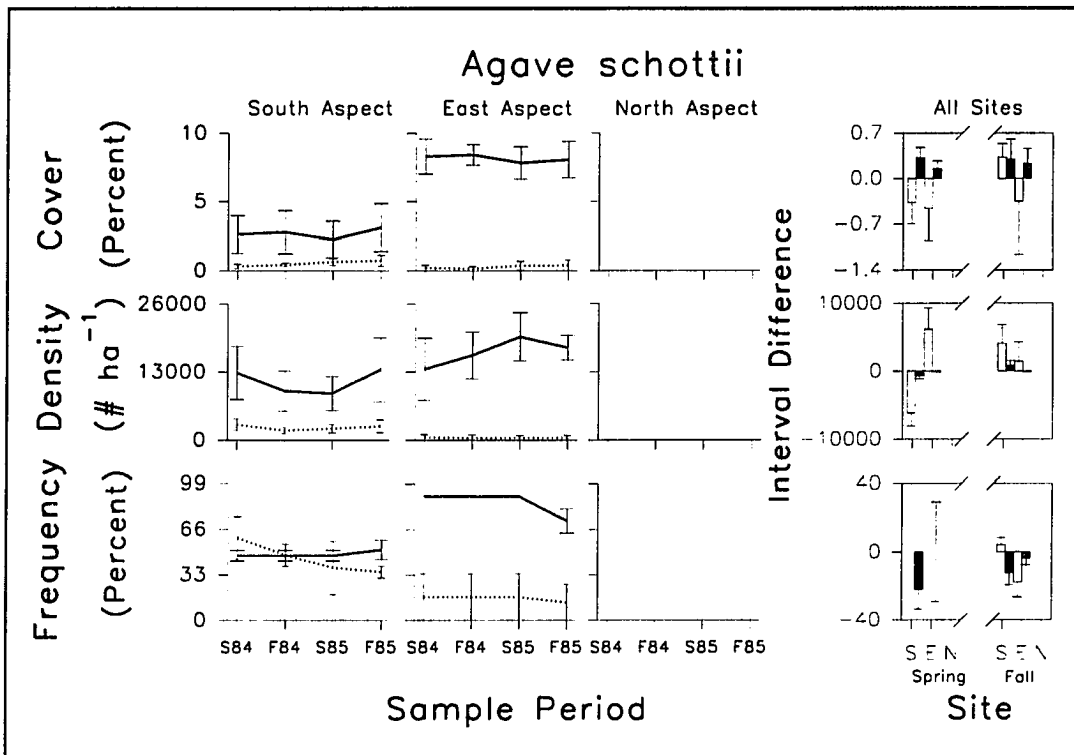
Resprouting occurred from enlarged lignotuber-like structures soon after burning. Sprouts grew rapidly the first year postfire, reaching heights up to about 50 cm, with growth slowing the second year postfire. *G. wrightii* is noted to be moderately fire tolerant and to resprout vigorously (Pond and Cable 1962; Hibbert et. al. 1974; Carmichael et al. 1978; and Wagle 1981). Sprouting from lignotubers as found in this species is a common regeneration strategy, particularly in Mediterranean-type ecosystems with frequent fires (20-50 year intervals). Lignotuber development, which requires a substantial energy outlay but allows rapid photosynthetic tissue replacement, essentially eliminates the establishment period of regeneration while also holding a site well suited for survival (James 1984). Few *G. wrightii* seedlings were observed in burned areas. Most were on the unburned north facing slope. This suggests postfire sprouting, as opposed to seed regeneration, is more important for re-establishment following fire, although Keeley (1987, 1991) found *G. flavescens* seeds in California chaparral to be stimulated to germinate by charate.

**Subshrubs** - Subshrub cover was nearly equivalent at all sites (Figure 12) without significant differences (Table 10) although species composition varied considerably among the sites. I did observed significant differences between burned and unburned plots during all sample periods with less cover in burned areas. On the north slope the difference was 13.0% (76% less cover in the burn), on the east slope 17.4% (84%), and 9.9% (51%) on the south. Additionally, a significant difference in the change of the spring interval differences occurred between burned

and unburned areas with greater increases in burned plots. In Chihuahuan Desert mountain shrub vegetation Ahlstrand (1982) recorded 69% less subshrub (rosette shrub and stem succulents) cover in burned areas at three years postburn and 67% less at 6 to 7 years postburn.

*Agave schottii* - "Amole" or "shin-dagger" was found only on the south (2.6% cover) and east slope sites (8.3%) where it was an important subshrub (Figure 18). In some areas in Molino Basin that were unsampled, cover was greater than 50%; approaching 100% in some aggregates. During the spring 1984 sample it made up 14% and 40% of the subshrub cover respectively at the two unburned sites where it occurred. Significant site differences existed for cover (Table 11), frequency (Table 13) and density (Table 12) but were confounded by interaction. Linear contrasts showed cover to be significantly different in unburned areas among each site for all samples whereas burned sites did not differ. Frequency also showed significant differences among all unburned sites in addition to differences between the south slope versus the east and north slopes which were not different. Density in unburned areas was significant less on the north slope compared to the south and east slopes. It did not differ among sites in burned areas. No interval changes were detected.

Significant fire treatment differences were detected for cover (Table 11), frequency (Table 13), and density (Table 12) with all less in burn areas. In the burned south slope plots cover was 88% less than in the unburned plots, while at the east site there was 97% less. Burning conditions on the south slope were probably less severe with fewer shrubs and oak litter fuel than at the east site which may account for the reduced kill. After a 1963 fire *A. schottii* was reduced in the upper parts of Molino Basin (Niering and Lowe 1984). A related species of agave, *A. lecheguilla*, found in Guadalupe Mountains National Park was also reduced by fire (Kittams



**Figure 18.** Cover, density, and frequency of *Agave schottii* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. *A. schottii* was not recorded on the north slope. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

1972, Ahlstrand 1982). In contrast, *A. lecheguilla* in desert mountain scrub near Big Bend National Park, Texas, showed a drastic reduction in cover (2.41% to 0.03%) but limited mortality following an August 1973 burn (Bunting and Wright 1977).

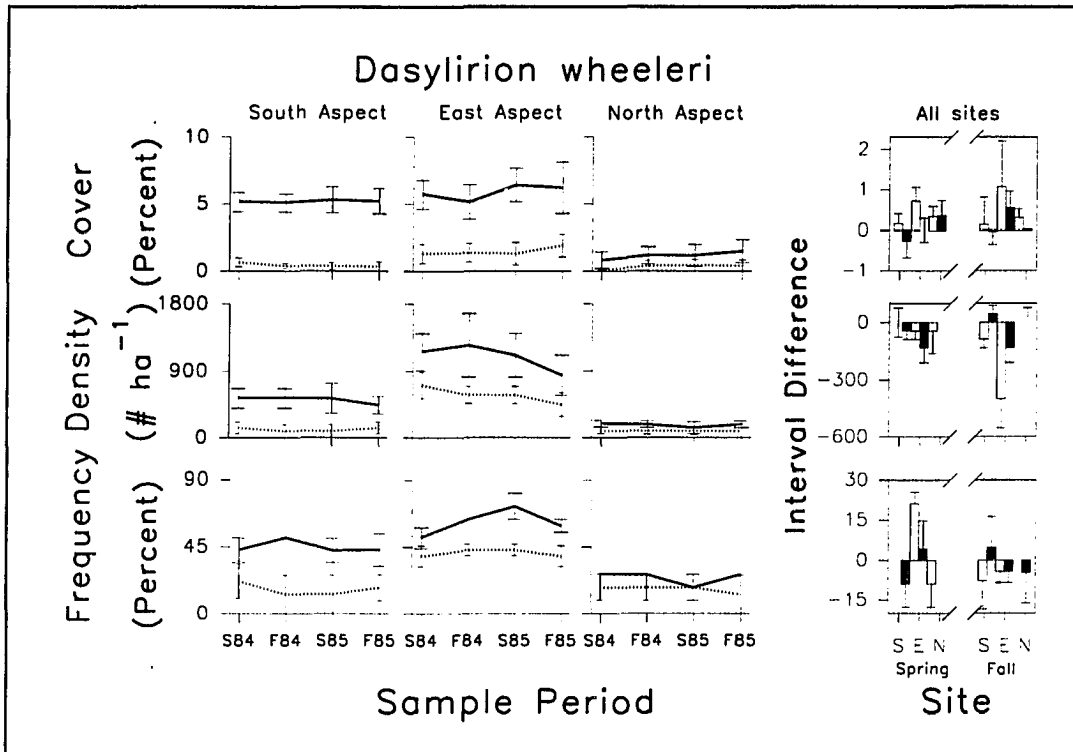
*A. schottii* was susceptible to fire damage with few individuals surviving. Very limited protection of the growing meristem is provided due to its low growing position and being surrounded by tightly appressed leaves. No regeneration from seed was observed in the field but vegetative sprouting was seen. In general, Southwestern agaves, including amole, are



semelparous species relying on production of ramets for regeneration (Schaffer and Schaffer 1977). This may account for the clumped growth form. Death of individuals after flowering appears to create substantial fuel loads within vegetative clumps. The often dense coverage of amole in unburned portions of the basin, coupled with its slow recovery, suggest fire had not occurred recently in much of the study area.

*Dasyllirion wheeleri* - Distribution of total varied by site, being most common on the south and east facing slopes, with 5.1% and 5.7% cover respectively for the spring 1984 sample (Figure 19). This cover amounted to 27%, 28%, and 5% of the subshrub cover on the south, east and north slope in unburned plots respectively. Significant site differences were found for cover, frequency and density (Table 11). Because cover was confounded by interaction I made comparisons of sites using linear contrasts. They showed significantly less cover in unburned areas on the north slope compared to the south and east slopes with no burned site differences. Density and frequency contrasts showed significant differences during all samples with the difference being greater on the east slope compared to the south or north.

I found significant differences between burned and unburned areas during all sample periods but not for intervals. Total cover was less in all burned sites with differences being 87%, 77%, and 94% on the south, east and north slopes, respectively (Table 11). Density differences were significant for the fall 1984 and spring 1985 samples with lower densities in burned areas relative to unburned areas (Table 12). Significant frequency differences were also found between burned and unburned plots for the last three periods (Table 13), with the first nearly significant ( $P=0.051$ ). This indicated death of individuals and was supported by the decline in density



**Figure 19.** Cover, density, and frequency of *Dasyllirion wheeleri* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

(Figure 19). Additionally, the lack of interval changes indicated no recovery during the period of study.

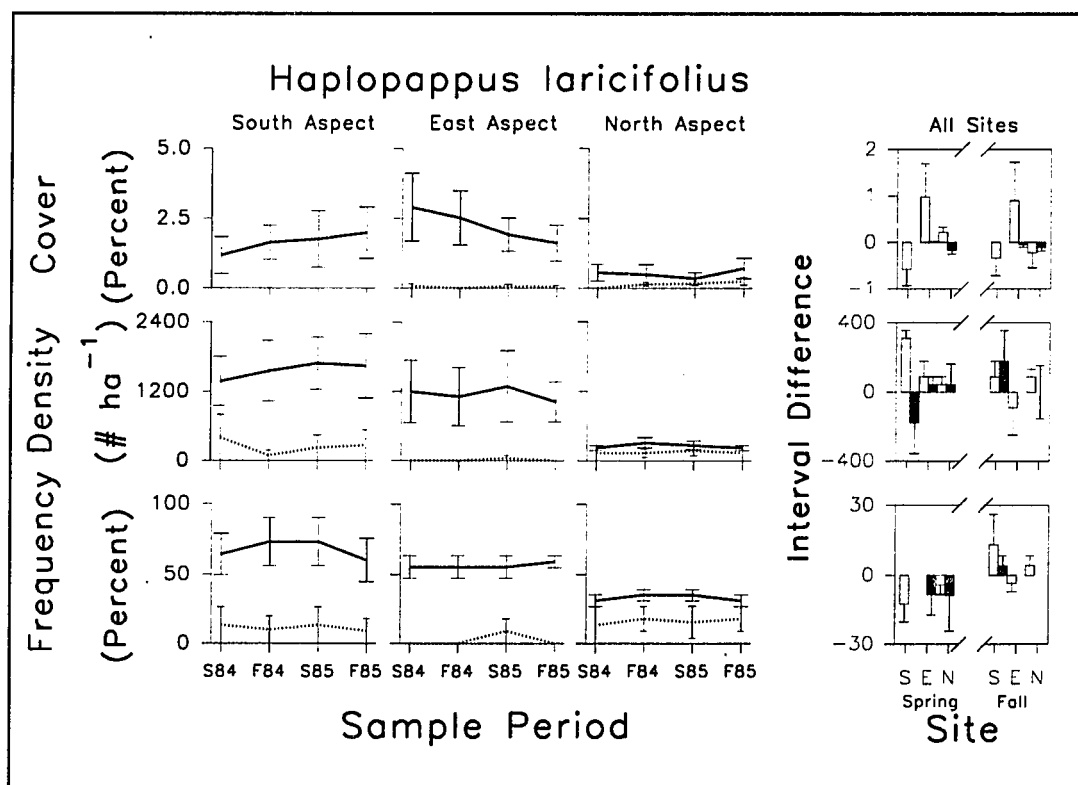
Sotal was intolerant of fire with moderate to severe burning conditions killing individuals. It appears to have no adaptations for surviving fire (Carmichael et al. 1978). Niering and Lowe (1984) report decreases following woodland burns in the Catalina Mountains. In semi-desert grassland this species has been noted as being intolerant of fire by Phillips (1992) and by Wright (1980) who found 97% mortality following severe burns but very low mortality after light

to moderate burns. White (1965) also reports high mortality which he attributed to accumulations of dead leaves around stems though lightly damaged plants recovered within two years. A similar response was reported for *Dasylirion leiophyllum* ("smooth sotol") found in woodlands and desert mountain scrub of the Chihuahuan Desert, with the sheath of leaves surrounding the stem making the plant susceptible to fire kill (Kittams 1972, Bunting and Wright 1977; Ahlstrand 1978b, 1982). I observed that the leaf bases surrounding the stem axis of smaller *D. wheeleri* usually do not burn and formed a spherical mass within the accumulations of dead leaves that may provide some fire resistance by protecting the growing meristem and stem of the plant. Older individuals which are taller appear to lose this dense mass of leaf bases around their base and thus may be more susceptible to death caused by heating of the stem when accumulations of dead leaves do burn.

***Haplopappus laricifolius*** - Although turpentine bush did not fit the strict criteria for analysis it was included because of its commonness in many areas where oak woodland borders semi-desert grassland. Cover at unburned sites during the spring 1984 sample varied from 0.6% on the north slope to 2.9% on the east (Figure 20). It made up 6%, 14%, and 3% of the unburned subshrub cover at the south, east and north slopes respectively. No significant site differences were detected during any sample period or interval for cover (Table 11), frequency (Table 13) or density (Table 12). *H. laricifolius* was significantly reduced by burning with differences in cover, frequency and density found between burned and unburned areas during all samples. In burned plots during the spring 1984 sample this species was absent (no cover) on the south and north slope and had only 0.08% cover (97% less than on unburned) on the east slope. No interval differences were significant, indicating little or no recovery for 2½ yr postfire. However, I

observed a few small seedlings around one surviving adult plant on the south slope, suggesting some regeneration can occur soon after burning.

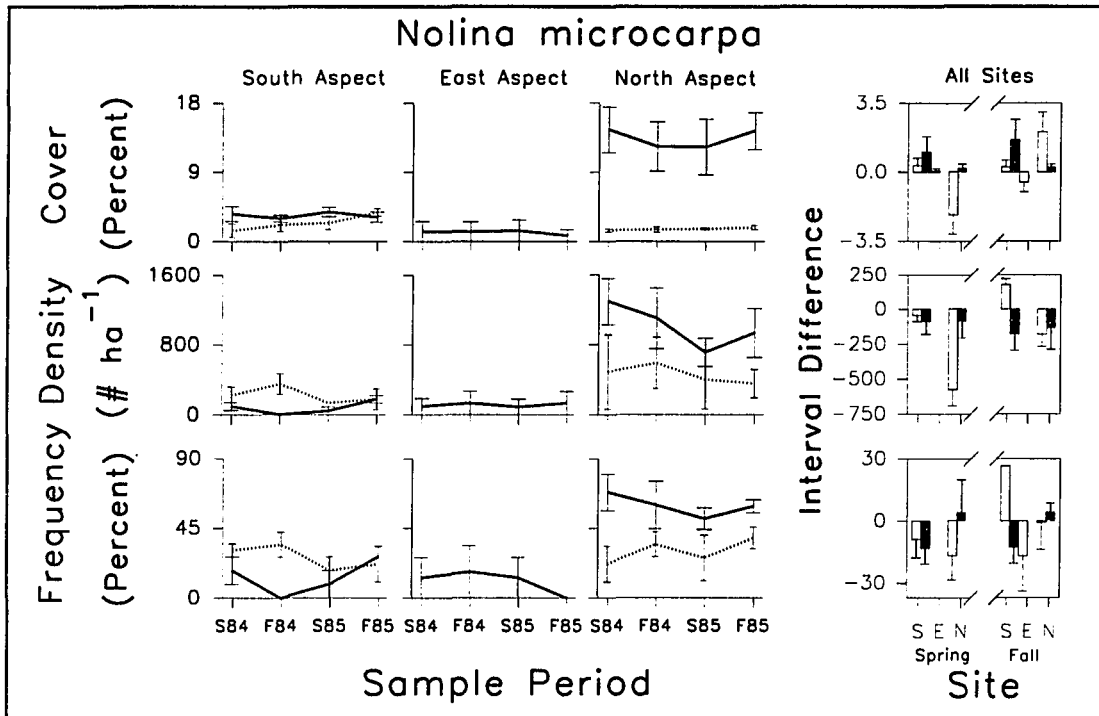
Decreases due to fire were reported by White (1965) and Niering and Lowe (1984) with White stating 90% reductions occurred after hot fires and 20% after light. A great deal of research in semi-desert grassland on a similar species (*H. tenuisectus*) has also shown it to be very intolerant of fire (Thornber 1907, Humphrey 1949, 1960, 1974, Humphrey and Everson 1951, Reynolds and Bohning 1956, Tschirley and Martin 1961, Cable 1967, 1972, White 1969, Wright 1980; Bock and Bock 1992a). *H. tenuisectus* may not recover to pre-burn levels for 10-



**Figure 20.** Cover, density, and frequency of *Haplopappus laricifolius* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

20 yr after burning has caused 95-100% mortality. Many areas in Molino Basin unburned by the 1983 fire have relatively high coverage of *H. laricifolius*, which like *Agave schottii*, suggests a fairly long interval since the last fire because these species are so dramatically reduced by fire.

*Nolina microcarpa* - Beargrass or sacahuista occurred at all sites with significant differences in cover, frequency and density found among sites during each sample which showed it to be a more important species on the north slope relative to the south or east slopes (Figure 21). Significant interaction terms existed for cover for all samples periods and for frequency for the 1984 samples (Table 11 and 13). Linear contrasts of the cover data showed it was significantly greater on the north slope than on the south or east. During the first sample cover on the north slope was 14.4% of the total plant cover or 83% of the subshrub cover. The east site had the lowest cover with 1.3% of the total (6% of the subshrubs). Low coverage on the south aspect may be a result of more xeric conditions or greater fire frequency. Significant changes in cover occurred between the two spring samples with contrasts showing differences between south and north aspects. Cover generally increased on the south slope while decreasing on the north. Contrasts of frequency data for the 1985 samples, showed it to be significantly higher on the north slope than the others during the spring 1985 sample with all sites different from one another during the fall 1985 sample. Linear contrasts showed essentially the same results for the 1984 samples. Frequency was highest at the north slope (59%) and least on the east slope (13%). Density was also significantly greater on the north slope than either the south or east (Table 12). Density changes were significant for both the spring and fall intervals with a decrease for the



**Figure 21.** Cover, density, and frequency of *Nolina microcarpa* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

spring interval and increase for the fall interval.

In burned plots cover and density were significantly lower compared to unburned plots (Table 11 and 12). The difference in cover was 60% less on the south, 100% on the east, and 90% at the north site. However, few plants were completely dead with most quickly sprouting. No significant differences in frequency were observed between burned and unburned plots (Table 13). Most individuals resprouted around the outer portions of an enlarged caudex following burning with little mortality occurring as reported by Carmichael et al. (1978). Like sotol this species develops large accumulations of leaves around its base (the largest fuel load measured

occurred when a 1 m<sup>2</sup> quadrat fell on a beargrass plant) but was not as severely impacted by fire probably because the growing meristems were near or below ground level and less susceptible to heat damage unlike the elevated total meristem. Niering and Lowe (1984), White (1965) and Wagle (1981) also report decreases or suppression. Johnson et al. (1962) working in open oak woodland in the Santa Rita Mountains south of Tucson found 10% of the beargrass dead with 65% showing little or no damage two years postfire. In a related species, sacahuista (*Nolina* spp.), inhabiting desert mountain scrub of the Chihuahuan Desert approximately 50% reductions were reported (Kittams 1972; Ahlstrand 1982). I also observed a significant change between the spring samples (spring interval) with burned plots showing an increase compared to unburned plots for cover and density. This was probably a result of resprouting and growth.

Herbaceous - Total cover of herbaceous species varied significantly among sites with cover on the south slope greater than on the east or north slopes (Table 10). The latter two sites only differed for the 1985 samples with cover greater on the east slope (Figure 11). A noticeable seasonal change in cover was also apparent, particularly in burned plots. All sites showed consistent increases in cover during the summer with decreases at east and north sites during the winter. This pattern was produced by seasonal growth of herbaceous species which occurred principally in the summer. In addition, the influence of summer annuals was also important in the winter decrease on the east and north slopes as they die in the fall.

Herbaceous species as a whole exhibited an immediate postfire response with cover rapidly reestablished that indicated individuals were either recovering or establishing quickly following the fire. By the spring 1984 sample, cover differences between burned and unburned areas were not significantly different, although cover was generally greater in unburned areas,

except for the fall 1985 sample. However, cover increased substantially more in burned plots than unburned during the study. The average percent change for unburned versus burned plots was, 143% vs 208%, 146% vs 204%, and 100% vs 210% for the south, east, and north slopes respectively. The general, rapid response in burned areas may be due to the combined influence of both fire, resulting in nutrient release (Ohr and Bragg 1985) and decreased competition, and to greater than normal rainfall during the study. Other studies have also reported increases in herbaceous species but the length of time for recovery was longer (Bock et al. 1976; Bock and Bock 1986a, 1992b). An additional reason for the response on the east and north slopes may have been the removal of *Selaginella* which dominated these sites, forming thick mats, and resulted in competition with other herbaceous species for resources. With its removal other herbaceous species responded to the expanded resource availability.

Cover of graminoids was more important than forbs except on the burned north slope where a large annual forb component was found. Death of many dominant perennial species on this slope was followed by rapid increases in annuals, many of which were forbs. In hot spots where *Arctostaphylos pungens* burned intensely, forbs were the primary colonizers, whereas where *Selaginella* was removed the annual grass *Aristida adscensionis* was the dominant colonizer.

The differing fire severity impacts on the vegetation at the three sites resulted in varying postfire responses of annual and perennial herbaceous species at these sites. During the period of sampling annuals were more important on the north slope where the fire effects were more severe, resulting in reduction of several dominant perennial species. These annuals were able to establish in the more highly disturbed areas where they persisted for much of the study. On the south slope perennial species, predominantly graminoid, reestablished rapidly following the fire



with annuals only being important immediately following the fire. Moreno and Oechel (1991) make a distinction between fire annuals, where fire intensity (severity) has little effect, and opportunistic annuals, where fire intensity has a direct effect on the postfire response of these species.

Combined biomass data for herbaceous species are presented in the above section on 'Summed Biomass Data'. They were placed into three categories; live biomass, dead biomass, and total standing biomass (Appendix 3 and 4).

**Forbs** - Total forb cover did not vary significantly between sites but did vary between burned and unburned areas on the east and north aspects (Table 10) with cover greatest in burned plots (Figure 11). Cover also increased on the south slope but to a lesser extent.

Comparison of annual and perennial forb species (Figure 12) showed perennials to be more important with about 17.69% of the cover in burned areas and 4.88% in unburned areas (mean of all sites and samples). Annuals were most prominent during spring samples while perennials dominated fall samples. I observed many annuals, particularly forbs, that appeared to be "fire following species". They occurred only during the first summer wet season (1983) following the fire but were uncommon or absent thereafter, findings similar to those reported by Bock and Bock (1986a, 1992a) after a prescribed fire in Madrean oak woodland.

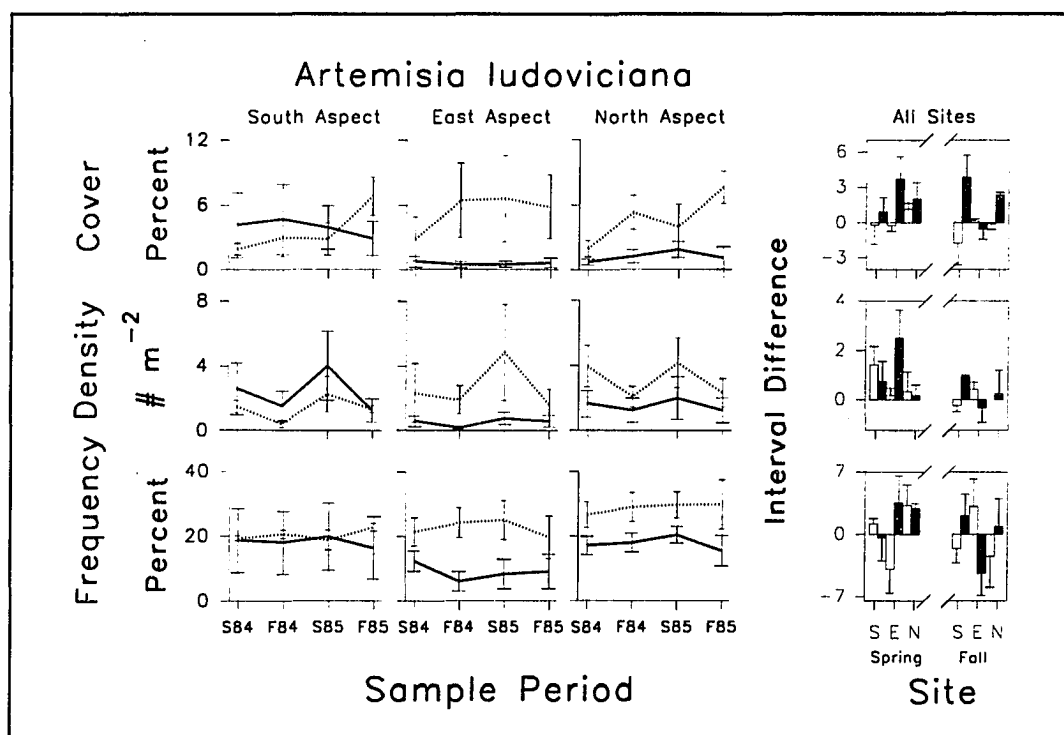
No site differences were significant for perennials, but strong fire effects and a positive postfire response were apparent for all sample periods (Table 10). Comparison of perennial cover at burned and unburned plots for the first sample showed 2.9% more cover in burned than in unburned south slope plots (this amounts to 29% more perennial cover at burned relative to unburned) while on the east and north slopes, differences were 11.9% (341%) and 14.8%

(1112%) respectively.

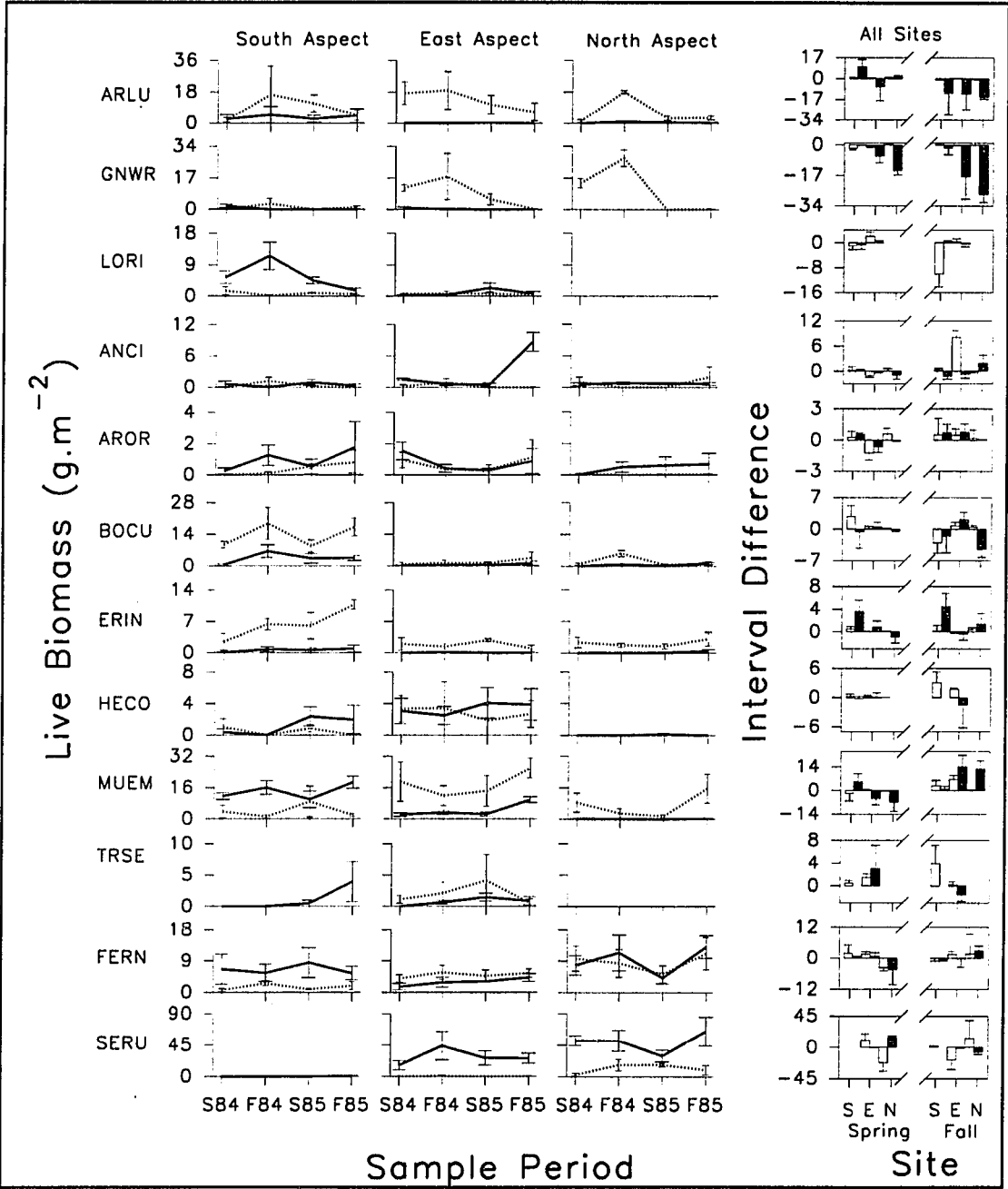
Annual forbs showed significant cover differences among sites and between burned and unburned areas (Table 10). Contrasts of locations showed cover on the south slope to be significantly less than on the north for all sample periods while less on the east slope for only the second and third sample periods (fall 1984 and spring 1985). For the first postfire sample cover of annuals was greater in burned plots with differences on the south slope being 1.9% (166% greater), on the east slope 1.2% (344%), while on the on the north slope no annuals were found in unburned plots.

Results from semi-desert grassland, with many species in common with oak woodland, are comparable (Wright 1980; Bock and Bock 1978) although Schmutz et al. (1985) report little effect by fire on forbs. Forbs have also been found to respond similarly in interior chaparral (Pase and Brown 1982) and Great Basin sagebrush communities (Wright et al. 1979; Barney and Frischknecht 1974). Their response to burning is often more vigorous and rapid than graminoids. Annual forbs such as *Ipomoea*, *Bidens*, *Solidago*, and *Chenopodium* showed very vigorous growth the first summer following the burn (1983), often dominating an area, but their importance declined rapidly by the time I began sampling in 1984. Overall they were only a minor constituent of the forb species. In Chihuahuan Desert mountain shrub vegetation Ahlstrand (1982) found 21% less cover in burned areas three years postburn and 50% greater cover at 6 to 7 years postburn. In contrast, Bunting and Wright (1977) report an increase in forbs and half-shrubs two years following a 1973 fire in desert mountain scrub near Big Bend National Park, Texas that seldom burns. Precipitation for the two years following the burn was greater than normal.

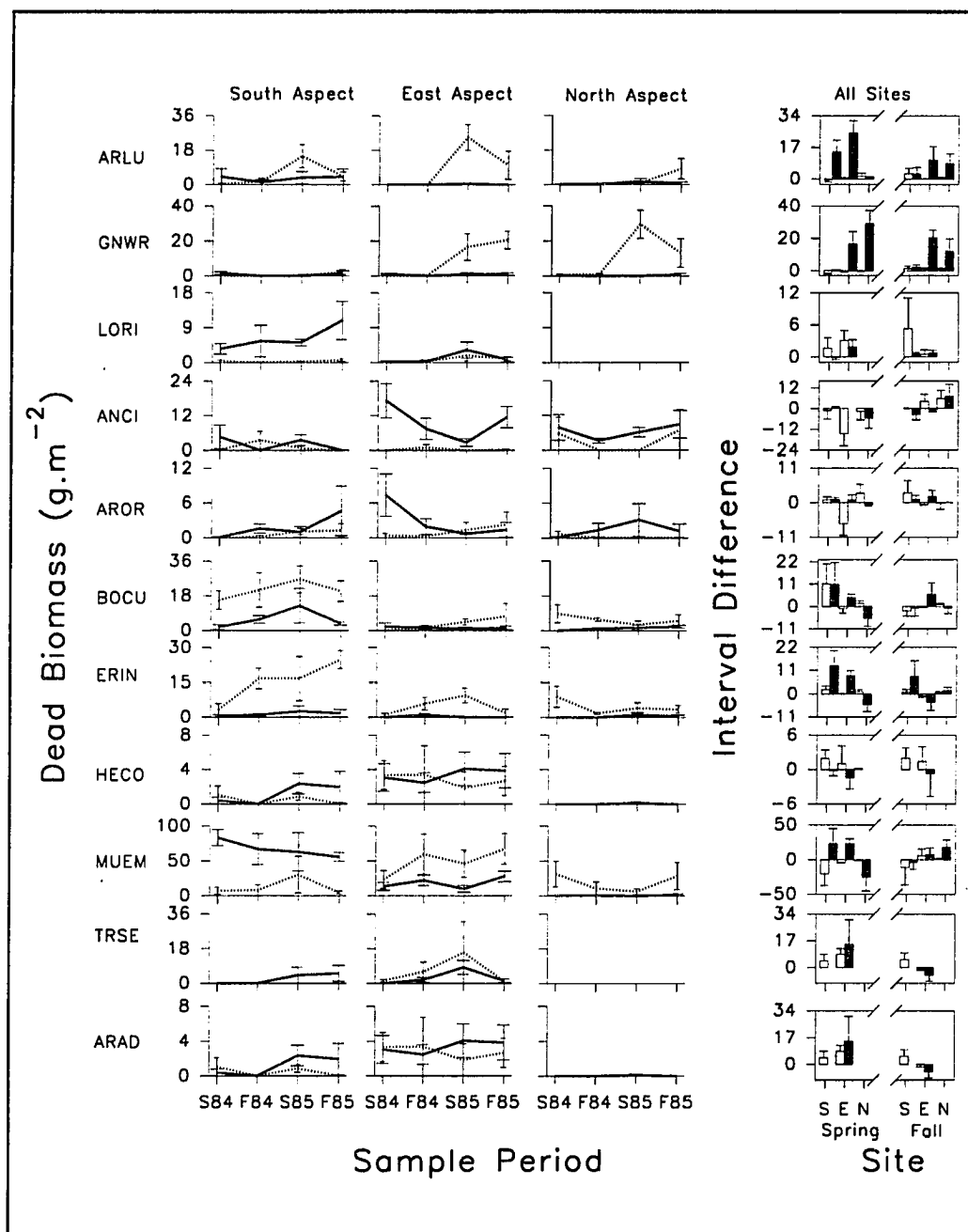
***Artemisia ludoviciana*** - This non-woody species of sagebrush was common on all sites (Figure 22) and showed no differences in cover (Table 11), frequency (Table 13) or density (Table 12) between sites. However, this species resprouted following the burn and responded positively to the postfire environment. By the fall of 1985 cover was greater in burned than in unburned areas (236% more on the south, 940% on the east, and 713% on the north slopes). Cover also changed between the two fall samples, increasing more in burned than unburned areas. In unburned plots during the first sample, *A. ludoviciana* made up 21% to 50%



**Figure 22.** Cover, density, and frequency of *Artemisia ludoviciana* for the four sample periods (S84=Spring 1984, F84=Fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=East slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.



**Figure 23** Live biomass of the major herbaceous species for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.



**Figure 24.** Dead biomass of the major herbaceous species for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

**Table 15.** Probability levels from 2-WAY ANOVA on live biomass for major species. Data from three sites (S) and two burned areas (F) and show differences within each of the four sampling periods and change in live biomass ( $\text{g}\cdot\text{m}^{-2}$ ) for two sampling intervals. Significant differences ( $P<0.05$ ) are indicated by an asterisk (\*).

Species	Sample Period				Sample Interval	
	Spr. 84	Fall 84	Spr. 85	Fall 85	Spring	Fall
Probability Levels						
<i>Artemisia ludoviciana</i>						
S	0.039 *	0.987	0.253	0.628	0.340	0.976
F	0.025 *	0.036 *	0.014 *	0.208	0.776	0.113
S X F	0.018 *	0.900	0.421	0.596	0.326	0.986
<i>Gnaphalium wrightii</i>						
S	0.001 *	0.122	0.067	0.249	0.020 *	0.112
F	0.001 *	0.004 *	0.082	0.063	0.002 *	0.006 *
S X F	0.001 *	0.125	0.065	0.276	0.004 *	0.115
<i>Lotus rigidus</i>						
S	0.004 *	0.006 *	0.010 *	0.088	0.175	0.026 *
F	0.140	0.017 *	0.012 *	0.237	0.448	0.044 *
S X F	0.066	0.005 *	0.077	0.520	0.455	0.013 *
<i>Andropogon cirratus</i>						
S	0.526	0.526	0.539	0.006 *	0.352	0.012 *
F	0.226	0.226	0.025 *	0.013 *	0.806	0.012 *
S X F	0.249	0.249	0.935	0.001 *	0.313	0.002 *
<i>Aristida orcuttiana</i>						
S	0.004 *	0.467	0.716	0.632	0.034 *	0.811
F	0.352	0.061	0.516	0.575	0.862	0.871
S X F	0.623	0.315	0.591	0.820	0.445	0.964
<i>Bouteloua curtipendula</i>						
S	0.001 *	0.007 *	0.003 *	0.001 *	0.811	0.174
F	0.001 *	0.039 *	0.081	0.008 *	0.443	0.689
S X F	0.001 *	0.234	0.198	0.013 *	0.578	0.243
<i>Eragrostis intermedia</i>						
S	0.963	0.001 *	0.149	0.001 *	0.102	0.213
F	0.029*	0.001 *	0.009 *	0.001 *	0.267	0.162
S X F	0.980	0.008 *	0.303	0.001 *	0.208	0.264
<i>Heteropogon contortus</i>						
S	0.146	0.282	0.269	0.161	0.939	0.718
F	0.529	0.434	0.943	0.258	0.731	0.242
S X F	0.682	0.537	0.780	0.350	0.959	0.693

Table 15 continued.

Species	Sample Period				Sample Interval	
	Spr. 84	Fall 84	Spr. 85	Fall 85	Spring	Fall
Probability Levels						
<i>Muhlenbergia emersleyi</i>						
S	0.450	0.053	0.195	0.061	0.389	0.130
F	0.169	0.617	0.325	0.151	0.605	0.081
S X F	0.067	0.003 *	0.401	0.001 *	0.198	0.209
<i>Trachypogon secundus</i>						
S	0.077	0.135	0.235	0.368	0.390	0.194
F	0.099	0.418	0.615	0.223	0.808	0.120
S X F	0.077	0.513	0.627	0.302	0.832	0.398
<i>Aristida adscensionis</i>						
S	0.999	0.999	0.999	0.228	0.999	0.228
F	0.999	0.999	0.999	0.108	0.999	0.108
S X F	0.999	0.999	0.999	0.228	0.999	0.228
<u>FERNS</u>						
S	0.089	0.137	0.923	0.014 *	0.147	0.765
F	0.783	0.684	0.385	0.517	0.655	0.900
S X F	0.239	0.550	0.112	0.646	0.988	0.925
<i>Selaginella rupincola</i>						
S	0.001 *	0.024 *	0.004 *	0.006 *	0.402	0.585
F	0.001 *	0.012 *	0.012 *	0.004 *	0.123	0.893
S X F	0.001 *	0.148	0.088	0.039 *	0.007 *	0.332

of the perennial forb cover while at burned plots this was 12% to 19%. By the fall 1985 sample it constituted 34% to 37% of the perennial forb cover in burned plots while remaining basically unchanged in unburned areas. Frequency was generally higher in burned areas although only significant for the fall 1984 sample. Although cover of this species increased in burned areas only a slight increase in frequency was observed, indicating plants increased in size without new establishment. This was supported by lack of significant density effects. Lack of these effects was probably due to limited mortality of established individuals during the fire. This species responded positively to the fire with increased growth of established individuals and indicated

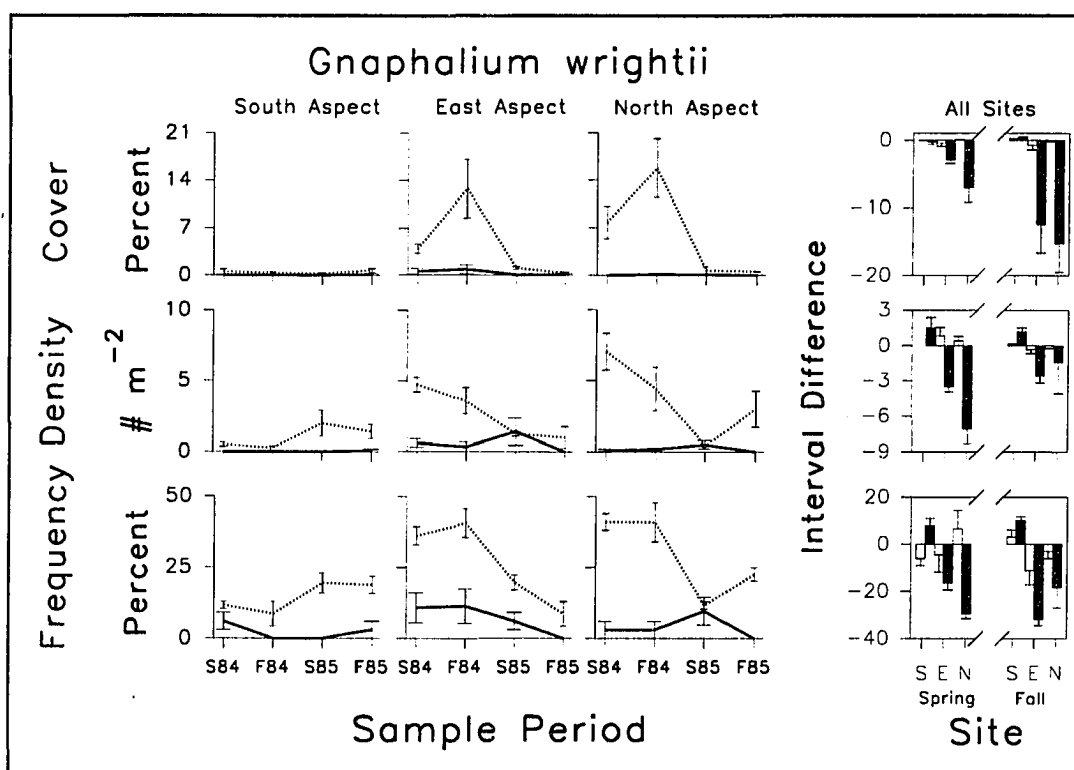
plants tended to survive fire by resprouting from below ground plant parts. It may be well adapted to this strategy since it is an herbaceous species that dies back to the root crown each winter, resprouting the following year.

Live biomass of *A. ludoviciana* was significantly greater in burned plots compared to unburned plots (Table 15) during the first three samples periods, showing a pattern similar to cover (Figure 23). Dead biomass showed no significant site differences (Table 16) and was generally less than live biomass during 1984 and greater during 1985 (Figure 24). Dead biomass was also significantly greater in burned than in unburned areas for the spring 1985 sample. Additionally, significant increases in dead biomass were also recorded for the first spring interval for both site and fire treatments. Linear contrasts showed increases in dead biomass on the south and east slopes in burned areas but not on the north slope nor at any site in unburned areas. This evidence indicates a postfire peak in growth occurred for this species in burned areas during the summer of 1984 and was followed by a rapid decline, accounting for the increase in dead biomass in 1985. This species responded rapidly and positively to the postfire environment by resprouting and apparently taking advantage of reduced competition and increased nutrients but established few new individuals.

***Gnaphalium wrightii*** - This species (cud-weed) was most important on the north slope and appeared to have a similar role and niche as *A. ludoviciana* on the south slope (figure 25). Cover differed significantly between sites during the two 1984 samples and for both the spring and fall intervals indicating a shift in this species over time (Table 11). Linear contrasts, used because of a significant interaction term, showed no differences among sites in unburned areas but striking differences among all sites in burned areas during the fall 1984 sample. The strength



of these differences in burned areas declined over the two years of sampling such that by the fall 1985 sample none of the sites were different. This pattern appears to be a result of the decline of this species with time postfire (see section below on fire response). Density also showed site differences for the two 1984 samples and for the spring interval (Table 12). Frequency was also significantly different for site treatments for the two 1984 and the fall 1985 sample but had significant interaction effects (Table 13). Linear contrasts for both showed no differences among unburned sites and a pattern similar to cover for burned areas. Sites had significantly different



**Figure 25.** Cover, density, and frequency of *Gnaphalium wrightii* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

**Table 16.** Probability levels from 2-WAY ANOVA on dead biomass for major species. Data from three sites (S) and two fire (F) treatments show differences within each of the four sampling periods and change in dead biomass for two sampling intervals. Significant differences ( $P < 0.05$ ) are indicated by an asterisk (\*).

Species	Sample Period				Sample Interval	
	Spring 84	Fall 84	Spring 85	Fall 85	Spring	Fall
Probability Levels						
<i>Artemisia ludoviciana</i>						
S	0.351	0.208	0.038 *	0.973	0.038 *	0.849
F	0.387	0.940	0.004 *	0.105	0.002 *	0.105
S X F	0.463	0.938	0.026 *	0.482	0.022 *	0.446
<i>Gnaphalium wrightii</i>						
S	0.654	0.005 *	0.023 *	0.119	0.024 *	0.111
F	0.055	0.003 *	0.001 *	0.006 *	0.001 *	0.007 *
S X F	0.085	0.004 *	0.023 *	0.100	0.041 *	0.095
<i>Lotus rigidus</i>						
S	0.009 *	0.221	0.045 *	0.035 *	0.180	0.453
F	0.035 *	0.197	0.032 *	0.069	0.358	0.454
S X F	0.029 *	0.209	0.099	0.040 *	0.785	0.507
<i>Andropogon cirratus</i>						
S	0.344	0.764	0.368	0.136	0.367	0.179
F	0.037 *	0.646	0.002 *	0.174	0.315	0.483
S X F	0.193	0.175	0.285	0.312	0.175	0.729
<i>Aristida orcuttiana</i>						
S	0.050 *	0.877	0.908	0.566	0.132	0.591
F	0.106	0.047 *	0.482	0.497	0.432	0.891
S X F	0.051	0.980	0.359	0.624	0.051	0.564
<i>Bouteloua curtipendula</i>						
S	0.055	0.018 *	0.005 *	0.084	0.154	0.432
F	0.012 *	0.052	0.135	0.016 *	0.894	0.476
S X F	0.049 *	0.163	0.421	0.200	0.623	0.496
<i>Eragrostis intermedia</i>						
S	0.213	0.008 *	0.281	0.001 *	0.050 *	0.196
F	0.030 *	0.001 *	0.028 *	0.001 *	0.143	0.537
S X F	0.195	0.017 *	0.463	0.001 *	0.065	0.372
<i>Heteropogon contortus</i>						
S	0.025 *	0.108	0.095	0.070	0.784	0.891
F	0.729	0.803	0.223	0.339	0.266	0.439
S X F	0.953	0.938	0.688	0.751	0.747	0.853

Table 16 continued.

Table 10 continued.

Species	Sample Period				Sample Interval	
	Spring 84	Fall 84	Spring 85	Fall 85	Spring	Fall
	Probability Levels					
<i>Muhlenbergia emersleyi</i>						
S	0.034 *	0.087	0.084	0.074	0.309	0.415
F	0.203	0.780	0.821	0.640	0.215	0.433
S X F	0.001 *	0.028 *	0.189	0.008 *	0.080	0.847
<i>Trachypogon secundus</i>						
S	0.047 *	0.155	0.212	0.484	0.233	0.136
F	0.070	0.440	0.841	0.250	0.896	0.129
S X F	0.047 *	0.546	0.694	0.296	0.740	0.526
<i>Aristida adscensionis</i>						
S	0.397	0.246	0.999	0.007 *	0.397	0.377
F	0.337	0.084	0.999	0.016 *	0.337	0.478
S X F	0.397	0.246	0.999	0.007 *	0.397	0.377

amounts of dead biomass during the fall 1984 and both 1985 samples and live biomass during the spring 1984 sample. It was significantly greater in burned areas on the east and north slopes compared to the south slope. Changes in live and dead biomass by site were significant for the first interval but confounded by interaction. Between 1984 and 1985 dead biomass increased greatly in burned areas on the east and north slope with only slight changes on the south slope with a live biomass showing a sharp decrease for the same period.

Cover and frequency were higher in burned compared to unburned areas during all sample periods (Table 11 and 13). Cover was low at unburned sites, ranging from 0 to 0.5% (1% of the relative perennial forb cover on the south slope, 15% on east, and none on north) during the first period while in burned plots it varied from 0.5% to 7.8% (4%, 26%, and 48% relative on the south, east and north sites). It increased initially in burned areas on the east and north slopes but

declined sharply in 1985, decreasing from peaks of 12.7% and 15.8% to 0.3% and 0.5% respectively. These peaks compared to peaks of 0.9% and 0.1% in unburned plots. Interval differences were also significant with a sharp decrease for each interval in burned areas but not in unburned. Frequency in burned areas was 12 to 41% for the spring 1984 sample and 3 to 11% in unburned areas. Contrasts for the last period showed the east slope to be significantly less than the others which were not different from one another. Interval changes were significant for burn differences during both intervals and for site differences during the fall interval only. Frequency in burned plots generally decreased during both intervals while increasing at the unburned. Density was significantly higher in burned plots for the two 1984 samples and the fall 1985 sample. Contrasts showed it to be greater on the north and east slopes. Differences in live biomass between burned and unburned plots were significant for the first two periods (Table 15), with greater biomass in burned plots (Figure 23). It peaked during the fall of 1984 and declined during 1985. For the last three sample periods (fall 1984 to fall 1985) there was significantly more dead biomass in burned than unburned areas (Figure 24). Biomass remained relatively stable over time in unburned plots while data from burned plots indicated a dramatic increase with major shifts in the proportions of live and dead biomass during the same period.

This species responded quickly to burning with increases the first 18 months after the fire followed by a rapid decline the second year. The response was most pronounced on the north and east slopes where the disturbance by the fire was the greater because of the lower number of resprouting graminoids than on the south slope. *G. wrightii* appeared to be a short-lived perennial (biennial) taking advantage of a fire-caused disturbance. It produced a large seed crop during the fall of 1984 and then declined but continued to occur as a relatively unimportant species. Germination of refractory seeds was enhanced by charate in a related California

chaparral species, *G. californica* (Keeley and Keeley 1987; Keeley 1991). Another species on the study area with a similar strategy of rapid postfire increase but with an even more rapid response was *Verbena ciliata*. Its cover and frequency were relatively high during the spring 1984 sample but declined greatly thereafter. The large seed crop of this species attracted many seed eating birds who concentrated in burned woodland during the spring of 1984. I have noted its presence following other burns in southeastern Arizona also. These plant species appear to have life history attributes which allows them to establish seed banks that persist until the next disturbance.

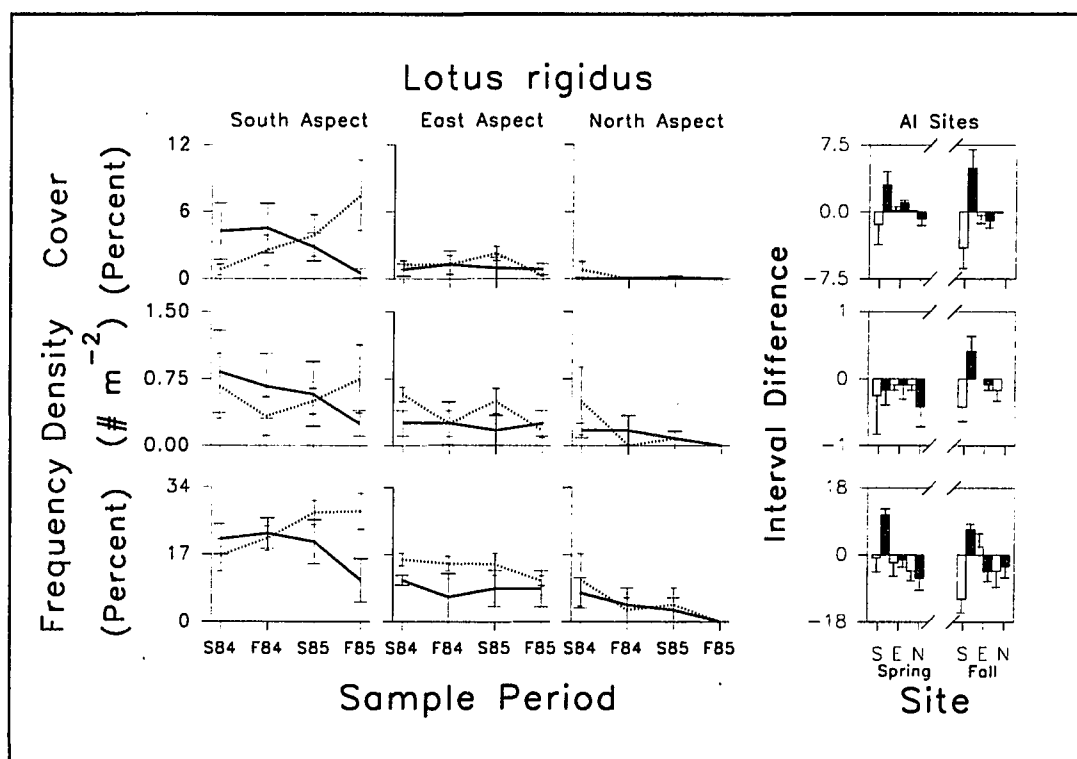
*Lotus rigidus* - Cover of deer-vetch was greatest on the south slope where it made up 42% of the perennial forbs during the first sample (Figure 26). On the east slope cover was 22% while on the north 4%. Significant site differences were found for cover (Table 11), frequency (Table 13) and biomass (Table 15) during most sample periods while density did not differ (Table 12). Contrasts for cover, frequency, density and biomass revealed that cover on the south slope to be greater than on the east or north slopes.

I detected no significant differences in cover or density between burned and unburned areas (Table 11 and 13), although frequency was greater at burned sites for the last period indicating some establishment may be occurring (Table 12). In contrast, live biomass was generally greater in unburned than in burned plots with this difference significant for the fall 1984 and spring 1985 samples (Table 15). Dead biomass was similar with differences occurring during the two spring samples (Table 16). Change in biomass was significant for live biomass during the fall interval at both sites and between burned and unburned areas, although confounded by an interaction. Linear contrasts indicated that significant decreases in live biomass occurred in

unburned areas on the south slope but not on the east or north slopes.

Fire had little effect on deer-vetch although there was some indication of a slow increase in biomass in burned areas. In California chaparral *Lotus scoparius*, a shrubby species, increased beyond preburn levels by the third year following a prescribed fire (Dunne et al. 1991). *Lotus* species can be nitrogen fixers and may be an important source of nitrogen on some rangelands (Vlamis et al. 1958; Mooney and Miller 1985).

**Graminoids** - The data on total graminoid cover showed strong differences between all



**Figure 26.** Cover, density, and frequency of *Lotus rigidus* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned..

sites (Table 10). The largest amount of cover was found on the south slope and least on the north (Figure 11). Interval data revealed significantly different amounts of change occurring at each site between the two spring samples with only the south versus the north sites significantly different for the fall interval. The change in cover was greatest on the south slope and least on the north. Graminoid cover values on the south slope were similar to those found by Wentworth (1981) in the Mule Mountains.

Graminoid cover was greatest and increased the most in burned areas on the south slope (Figure 11) although it increased in all plots during the period of study (Table 10). This increase was more pronounced with perennial species than with annual species (Figure 12). The increases at unburned sites were 108%, 119% and 122% respectively for the south, east and north slopes, while at burned sites they were 196%, 221% and 197%. The rapid recovery was also observed by Bock and Bock (1992a) who state, "*By two years following the fire, native grass cover on burned plots was nearly indistinguishable from that of the unburned native grassland. However, individual species differences did occur. The individuality of inter-specific responses suggests that broad generalizations about fire effects in grasslands may lead to over-simplification of the natural patterns (see Glenn-Lewin et al. 1990)*". In Chihuahuan Desert mountain shrub vegetation Ahlstrand (1982) found 2% more cover in burned areas three years postburn and 51% more at 6 to 7 years postburn. In contrast, Bunting and Wright (1977) found a decrease in total grass cover from 11.6% to 3.21 % in desert mountain scrub vegetation near Big Bend National Park, Texas that burns infrequently.

Seasonal fluctuations in cover were also apparent with most increases observed during the summer and decreases or only slight increases in the winter. This might be a result of the above normal rainfall during the period of study with warm season grasses, primarily C<sub>3</sub> species

(Wentworth 1985), responding favorably. The difference in total amount of perennial graminoid cover between burned and unburned areas also increased with time. Comparison of the first and last sample showed differences to be 2.3% (12% greater) and 24.1% (60%) on the south slope unburned and burned plots respectively, 3.5% (31%) and 23.1% (91%) on the east, and 1.5% (27%) and 8.6% (70%) on the north. All differences between burned and unburned areas were significant for all four sample periods.

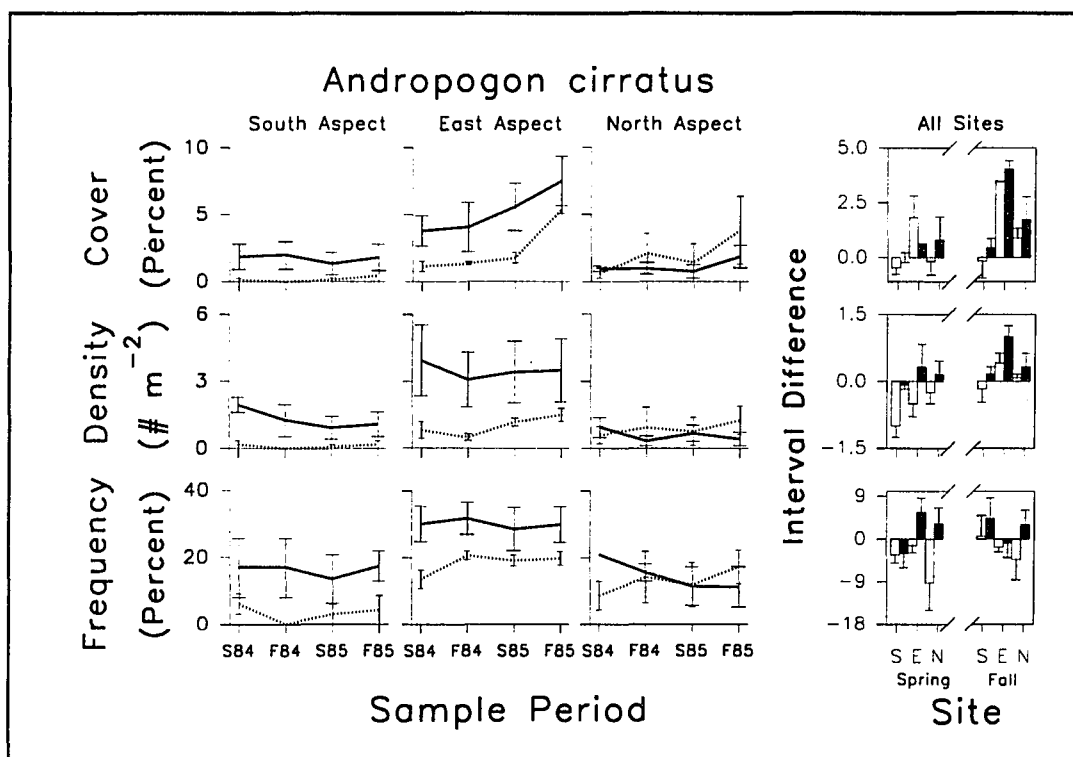
Annual graminoid cover was low in unburned areas (Figure 12) with values also on the same scale as found by Wentworth (1981) in the Mule Mountains. The only significant differences between sites in total cover for annual graminoids occurred for the spring 1985 sample and fall interval (Table 10). However, annual plant cover was in general greater in burned plots than in unburned, particularly during the summer when short lived "six-week" species were important. For the fall 1984 sample when annual plant cover was at its greatest, cover in burned areas was 554%, 883% and 335% greater than unburned on the south, east, and north slopes respectively. Of the three sites it was most important in burned plots on the north slope and made up 7.6 to 10.8% of the total cover for the fall samples.

*Andropogon cirratus* - Texas bluestem was most important on the east slope with 3.7% cover (32% of the perennial graminoids) while on the south it was 1.8% (9%) and on the north 0.9% (13%) in unburned areas (Figure 27). Significant differences in cover between sites were found for the spring 1984 and both 1985 sample periods and for the interval difference between the fall samples (Table 11). Contrasts for the three periods with significant differences showed greater cover on the east site compared to the south and north. Similarly, for the fall interval change on the east site was also greater. Results from the analysis of the frequency and density



data were similar to cover (Table 13 and 12). Differences occurred among sites for the last three periods with contrasts revealing frequency on the east site to be greater than on the south for the three samples and greater than on the north for the two 1985 samples. Density was only different for the two 1985 samples with greater density on the east slope compared to the north or south slopes which were not different. I also found significant site differences in live biomass during the fall 1985 sample but these differences were not consistent among treatments. No site differences in dead biomass were significant.

I found obvious fire effects for this species with the occurrence of initial declines



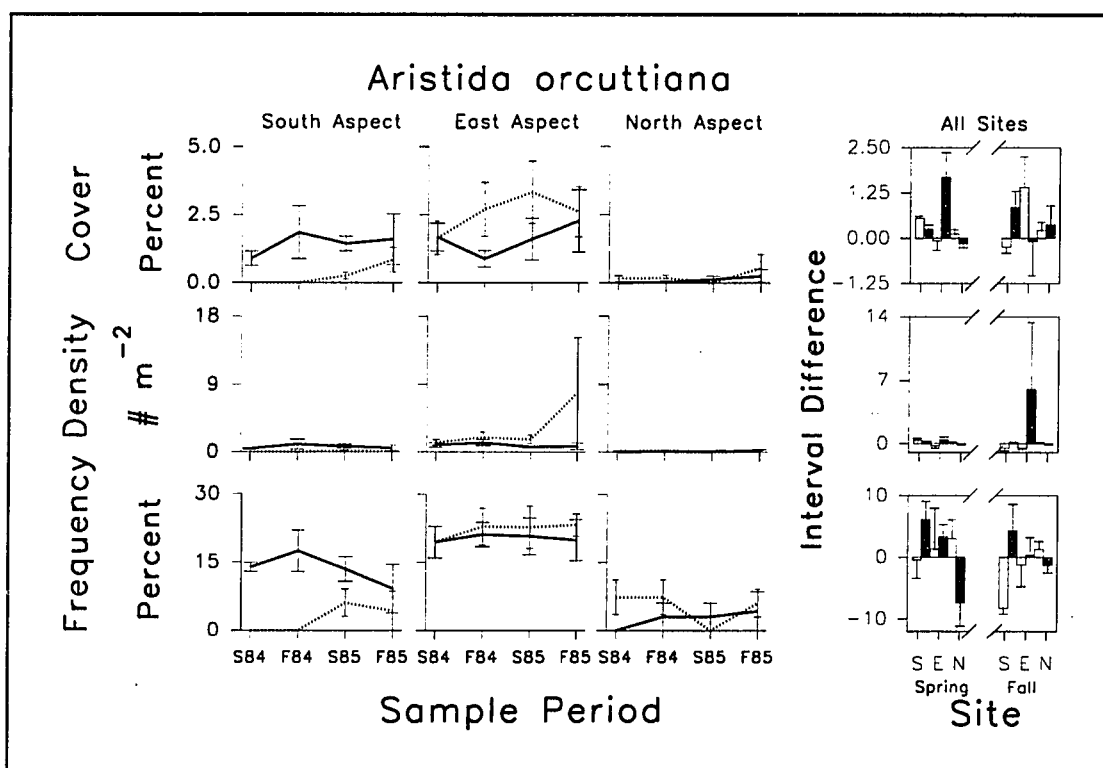
**Figure 27.** Cover, density, and frequency of *Andropogon cirratus* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

followed by rapid recovery. Cover was 93% less in burned plots relative to unburned on the south slope, 70% on the east, and 36% on the north for the spring 1984 sample. This was the only sample to have significant differences (Table 11). Similarly, frequency and density were also comparatively less in burned areas (Table 13 and 12). Significant differences in frequency were found for the 1984 samples and the spring interval. I found decreasing densities only for the spring 1984 sample. The small postfire frequency and density values for *A. cirratus* indicates mortality or reductions in plant size due to the fire. The 1985 samples show values in burned plots to be near unburned levels, evidence of recovery. A similar recovery pattern was observed by Niering and Lowe (1984) from data also collected in Molino Basin after an early summer burn in 1963 although the changes in my data were not as striking as what they report. I also found differences in live biomass (Figure 23) between burned and unburned areas for both 1985 samples and for the two spring samples for dead biomass (Table 15 and 16). Biomass was less in burned than in unburned areas, the case for all collections of this species (dead biomass in the spring indicates winter dieback). Fire effects on biomass of this species were difficult to ascertain precisely because the six biomass subsamples taken at each plot failed to sample this species adequately.

*Aristida orcuttiana* - Beggar-tick grass was most abundant on the east slope. In unburned plots cover ranged from 0% on the north slope to 1.7% (15% of perennial graminoids) on the east slope during the spring 1984 sample (Figure 28). Significant site differences were observed for cover (Table 11), frequency (Table 13) and density (Table 12). Cover differences were most pronounced during the spring samples with frequency differing for all samples and density only for the first three. Contrasts showed cover, frequency and density on the east slope

to be greater than on the south and north slopes which were not different. Biomass data were similar (Table 15 and 16). Only the spring interval difference for live biomass between sites was significant with the east slope different from the south and north with biomass tending to decrease over time (Figure 23).

The fire had little impact on *A. orcuttiana*, at least by the time sampling was started 10 months postburn. I detected no differences between burned and unburned areas or in the amount of change during either interval (Table 11, 12 and 13). The literature on fire effects on *Aristida*



**Figure 28.** Cover, density, and frequency of *Aristida orcuttiana* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

spp. is somewhat ambiguous with this in part a result of many authors only looking at this taxa at the generic level, not the specific. *A. orcuttiana* was one of three perennial species in this genus in the study area. In semi-desert grassland *Aristida* spp. Reynolds and Bohning (1956) report an increase while White (1965) found *A. ternipes* to decrease the first season but to have recovered by the second. Bock and Bock (1992a) report that *Aristida* spp. in semi-desert grassland in southeastern Arizona were greatly reduced by a July fire and remained so for at least three years postfire. Wright (1980) reports *Aristida* spp. to be moderately tolerant, recovering in two-to-three years with original basal area reduced 30-50%. Ahlstrand (1982) found *Aristida* spp. more frequently on burned than unburned sites.

*Bouteloua curtipendula* - Side-oats grama was one of the more important graminoid species in the study area with only *Muhlenbergia emersleyi* having greater cover. In unburned plots for the spring 1984 sample it made up 2% of the total cover (11% of perennial graminoids) on the south slope, 0.4% (1%) on the east and 0.6% (11%) on the north (Figure 29). Cover increased in both burned and unburned areas during the study, also similar to *M. emersleyi*. Significant site differences were present for all sample periods and intervals (Table 11). Cover on the south slope was greater than on the east or north slopes for all four sample periods with cover also increasing proportionally more during the study on the south slope than at the other sites. Results from the frequency (Table 13), density (Table 12) and biomass data (Table 15 and 16) were similar, with the exception that changes in frequency and density were not significant for either interval.

Side-oats grama appeared tolerant and responded positively to the postfire environment. This species increased following burning on the south (272% greater cover than in unburned areas) and east slope (478%) while declining on the north slope (58% less) which may be a marginal habitat for this species. Cover was generally different between burned and unburned plots while frequency and density were not (Table 11, 12 and 13). This indicated that the increases and decreases were a result of change in plant size not an increase or decrease in the number of plants. Live biomass was significantly greater in burned areas compared to unburned areas during the two 1984 samples and the fall 1985 sample while dead biomass was greater for

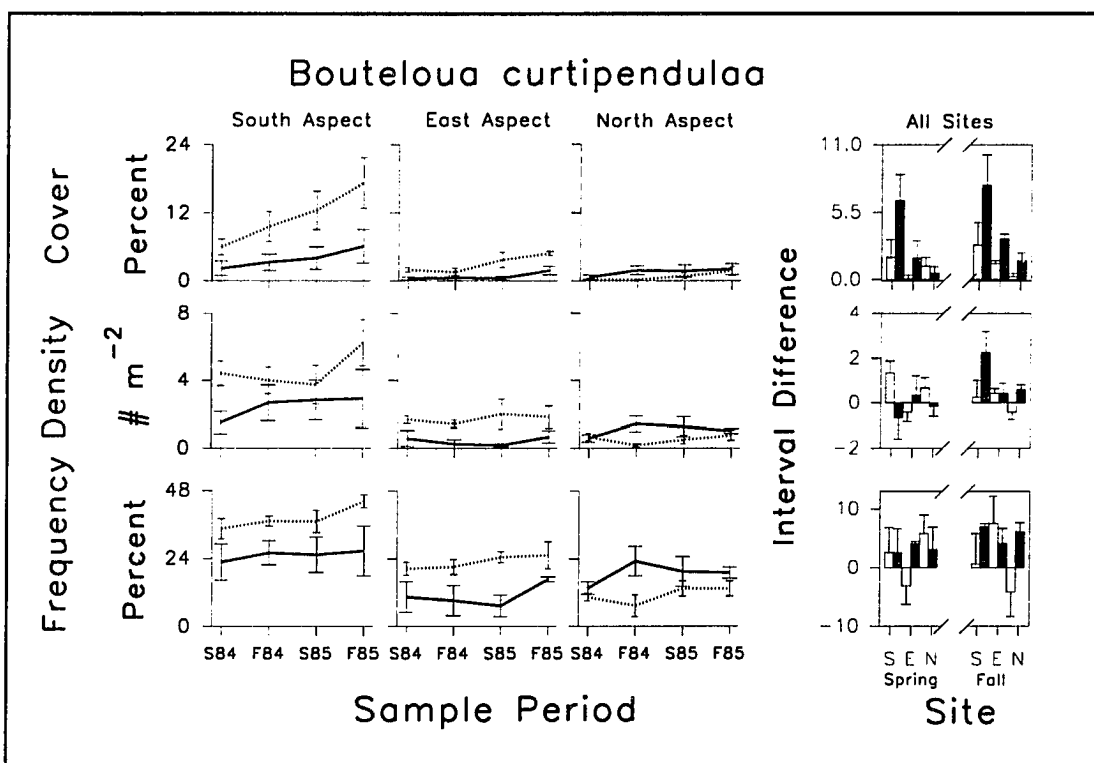
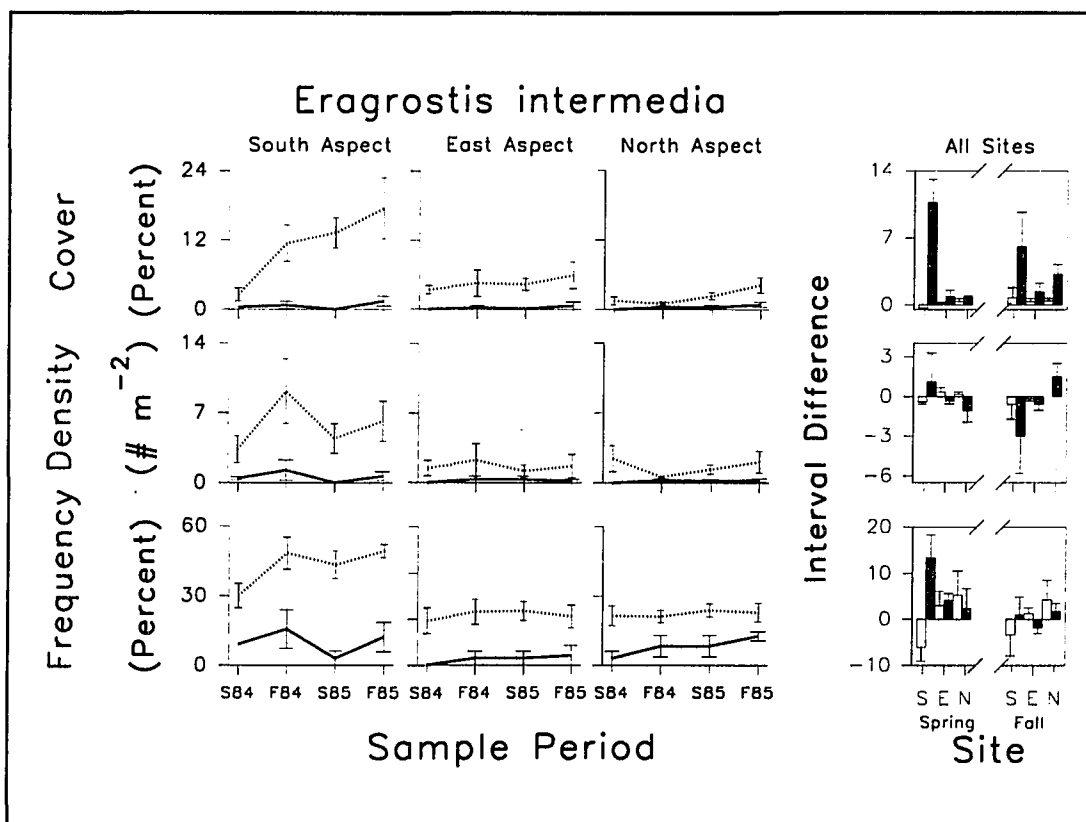


Figure 29. Cover, density, and frequency of *Bouteloua curtipendula* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

the spring 1984 and fall 1985 sample. Niering and Lowe (1984) report this species increased following a 1963 burn in Molino Basin while White (1965) and Bock and Bock (1992a) found it to decrease the first season after fire but to recover by the second. Other studies also report a reduction in this species following fire. Ahlstrand (1982) reports its frequency to be less on a three year old burn than in a control area in the Guadalupe Mountains and Bunting and Wright (1977) found drastic decreases in desert mountain scrub near Big Bend National Park, Texas. While making a general comparison of vegetation between Mexico and the United States in the 1930's Leopold (1937) described how Mexican mountains were lush with side-oats grama compared to the United States. He attributed this to the frequent fires and limited grazing in these areas of Mexico prior to that time while north of the border this species had declined due to overgrazing and fire suppression.

*Eragrostis intermedia* - Plains lovegrass was important at all burned sites but was only found in unburned plots on the south slope (0.4% cover) during the spring 1984 sample (Figure 30). Comparisons of the sites showed no significant site differences for the first sample for any data type although differences were found for both cover and frequency during the final three sample periods and density only for the fall 1984 (Table 11, 12 and 13). Linear contrasts of the cover data showed no differences in cover, frequency or density in unburned areas while in burned areas the south slope was significantly different from the east and north. Cover and biomass changes were also found for the spring interval. Like *B. curtipendula* cover increased at all sites across all treatments during the study. This may have been partly caused by greater than normal rainfall during the study period.

Significant differences in cover (Table 11), frequency (Table 13), density (Table 12), and biomass (Table 15 and 16) were found between burned and unburned areas during all sample periods. This was a strong result, displaying consistency across all sites and over time. It also showed there was an immediate response and recovery of this species. Cover increased at all sites following burning. Even by the spring 1984 sample cover was at least six times greater in burned compared to unburned areas. By the fall of 1985 a substantial part of the perennial graminoid cover at burned sites was made up of *E. intermedia*. On the south slope this was 27%



**Figure 30.** Cover, density, and frequency of *Eragrostis intermedia* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

of the perennial graminoids (17.5% total cover), 12% (5.9%) on the east slope and 66% (4.2%) on the north compared to 4%, 3%, and 7% respectively in unburned areas. The greatest absolute change in cover (14.9% increase) occurred on the south slope. No interval changes were of consequence although the species showed a consistent increase with time. Similar increases in this species are reported from Guadalupe Mountains National Park (Kittams 1972) and by Ahlstrand (1982) who states that frequency increased with at least 50% greater cover in burned than in unburned areas. White (1965) working in semi-desert grassland bordering oak woodland in south central Arizona also found this species to increase markedly the second year following burning after being reduced the first. Similarly, Bock and Bock (1992a) report a complex interaction with their data suggesting an initial fire-caused negative impact followed by a longer-term positive response.

The substantially greater increases of this species of bunchgrass in burned areas appeared to be a result of increased germination postfire with *E. intermedia* favored by burning. Increased germination in bunchgrasses and many other species following fire is probably due to the heating effects of fire on seed which results in seed coat scarification (Sweeny 1956; Whelan 1986; Ruyle et al. 1988; Sumrall et al. 1990). Postfire increases in species may also be a cause of fire induced flowering and resulting increase in seed production and germination (Daubenmire 1968a; Whelan 1986). Seasonal timing of the fire may be critical in producing this stimulus.

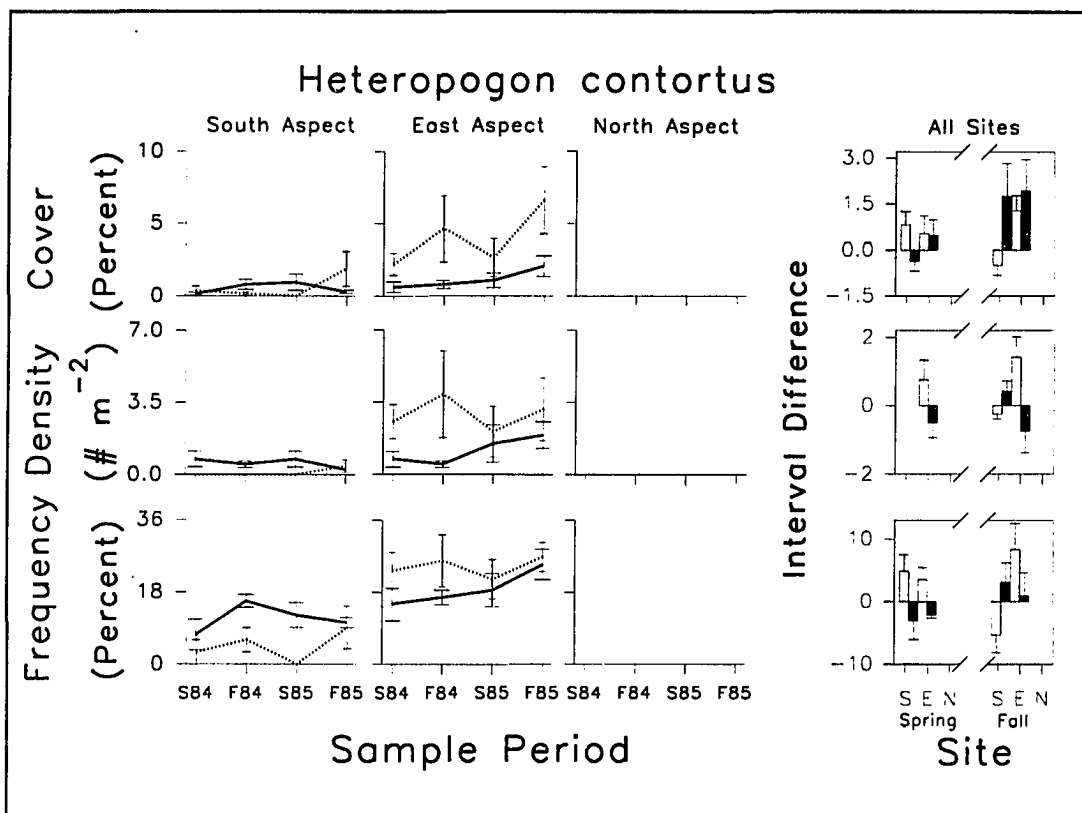
*Eragrostis lehmanniana* (Lehmanns lovegrass), an introduced species becoming widespread in the Southwest and considered obnoxious (Ruyle et al. 1988; Robinett 1992), was rare in Molino Basin. I observed only one small patch in the burned portion of the south slope and it did not appear to be expanding as a consequence of the burn, although higher seed germination rates have often been found when disturbances, fire or grazing, decrease canopy



cover (Ruyle et al. 1988; Sumrall et al. 1990). The lack of this species in the basin may be a result the higher, cool elevation, or because there is no livestock grazing to produce a long period of disturbance that would increase the likelihood of colonization and expansion.

*Heteropogon contortus* - Tangle-head or bunch spear grass, a subtropical graminoid species, was found only at sites on the south and east slope. This is a result of it being near its upper elevational limit (Kearney and Peebles 1960) and limited by cooler average temperatures on the north slope. It is a clonal species with clones often being quite large and covering whole hillsides. They are often visible during the fall and winter because the plants develop a reddish tinge as they become dormant and dry. *H. contortus* is a warm season C<sub>3</sub> species (Kearney and Peebles 1960; Wentworth 1985) which resulted in greater importance during the fall samples. Cover values were 0.1% and 0.6% during the initial spring 1984 sampling in unburned plots but this increased during the study (Figure 31). Significant differences among sites existed for cover (Table 11), frequency (Table 13) and density (Table 12) for all samples. However, live and dead biomass estimates showed no strong differences between the three sites, although *H. contortus* was the largest biomass component in unburned plots on the east slope (Figures 23 and 24). Contrasts showed that cover and density on the east slope were significantly greater than on the south. Frequency was similar but was greatest on the south slope.

Fire had little impact on tangle-head although major differences occurred between sites. Only during the fall 1985 sample was cover in burned plots significantly greater than in unburned plots (Table 11). No differences in frequency (Table 13), density (Table 12) or live and dead biomass (Table 15 and 16) were significant between burned and unburned areas. Only between the two spring samples was change in cover significant with there being more change in unburned



**Figure 31.** Cover, density, and frequency of *Heteropogon contortus* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

plots than burned. Other studies on how fire affects this species have reported varying results.

According to Wootton (1916) and Humphrey (1949), working in semi-desert grassland, this species decreased while Cable (1967, 1972) reports it was moderately affected. In contrast, White (1965), working in semi-desert grassland bordering oak woodland, reports cover and density to increase as did Shaw (1957) and Tothill (1969) in Australia. The Australian research indicates that under some conditions *H. contortus* can dominate a grassland in areas that burn frequently. This is partially a result of this species having seed with morphological

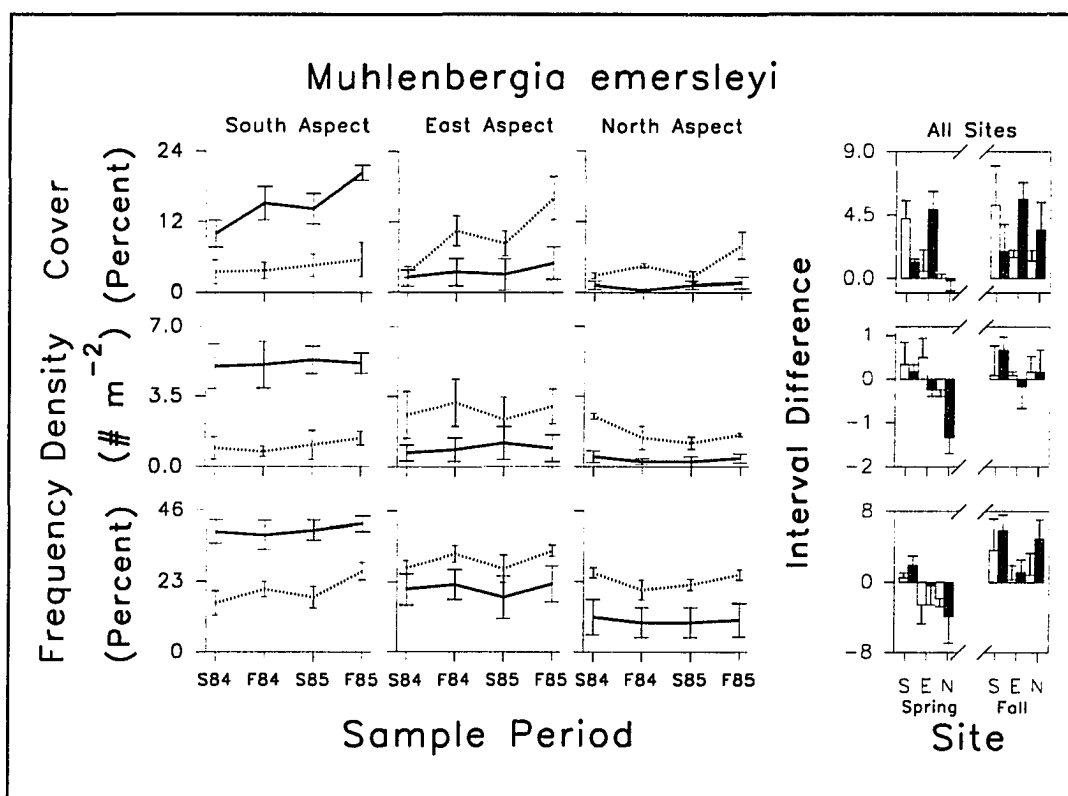
characteristics that allow it to burrow into the top 12 cm of soil and protect it from fire.

Additionally, there is increased germination after fire has removed surface litter because soil temperature is greater during cool seasons when adequate moisture is available (Tothill and Shaw 1968; Tothill 1969), a response also important in North American prairie ecosystems (Anderson 1982).

*Muhlenbergia emersleyi* - Bull grass was the most abundant graminoid species in the study area and was the largest biomass component in unburned plots on the south slope (Figure 23 and 24). Cover in unburned areas during the spring 1984 sample averaged 10.0% on the south slope (52% of the perennial graminoids), 2.5% (22%) on the east, and 1.2% (22%) on the north (Figure 32). Cover increases in both burned and unburned areas were as great as 400% during the study indicating this species may have responded positively to the increased rainfall and lower temperatures during 1983 and 1984. Cover varied significantly between sites for all samples and the spring interval (Table 11). Site differences also were present for frequency during the last three sample periods (Table 13) and for density during the two 1985 samples (Table 12). All three categories of data had significant interaction terms. Linear contrasts showed the south slope to be consistently different from the east and north in unburned areas while in burned areas differences existed only during the fall samples when the south slope was different from the east and the east different from the north slope. Both live and dead biomass were similar among sites with the exception of the spring 1984 sample for dead biomass (Table 15 and 16).

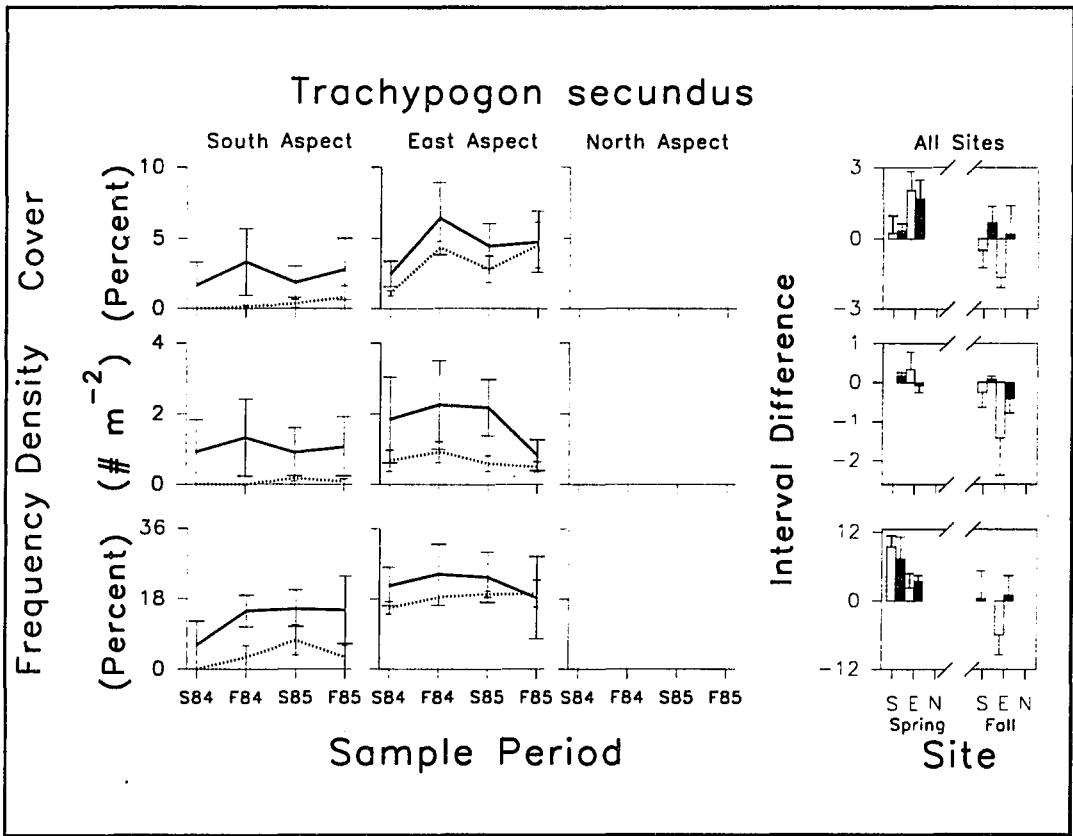
When I compared burned and unburned plots no significant differences in cover, frequency, density or biomass were observed (Table 11, 12, and 13). These data indicate bull

grass was not seriously impacted by burning. This contradicts the findings by Humphrey (1949), Wright (1980), Sourabie (1982) and Schmutz et al. (1985) working in semi-desert grassland at lower elevations. They report bull grass to be intolerant with decreases in density and cover occurring. In contrast, White (1965) found little change and Ahlstrand (1982) found reductions on three year old burns but no differences on six-to-seven year old burns in succulent vegetation in the Guadalupe Mountains National Park.



**Figure 32.** Cover, density, and frequency of *Muhlenbergia emersleyi* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

*Trachypogon secundus* - Crinkle-awn only occurred on the south and east slopes, a distribution similar to tangle-head. Cover ranged from 1.1% to 2.4% during the first sample and increased during the study (Figure 33). I found significant site differences in cover for the last three samples and for the spring interval (Table 11). Contrasts showed significantly more cover on the east slope than on the south. Contrasts for the spring interval also showed greater cover increases on the east slope than on the south. Site differences for frequency were significant for

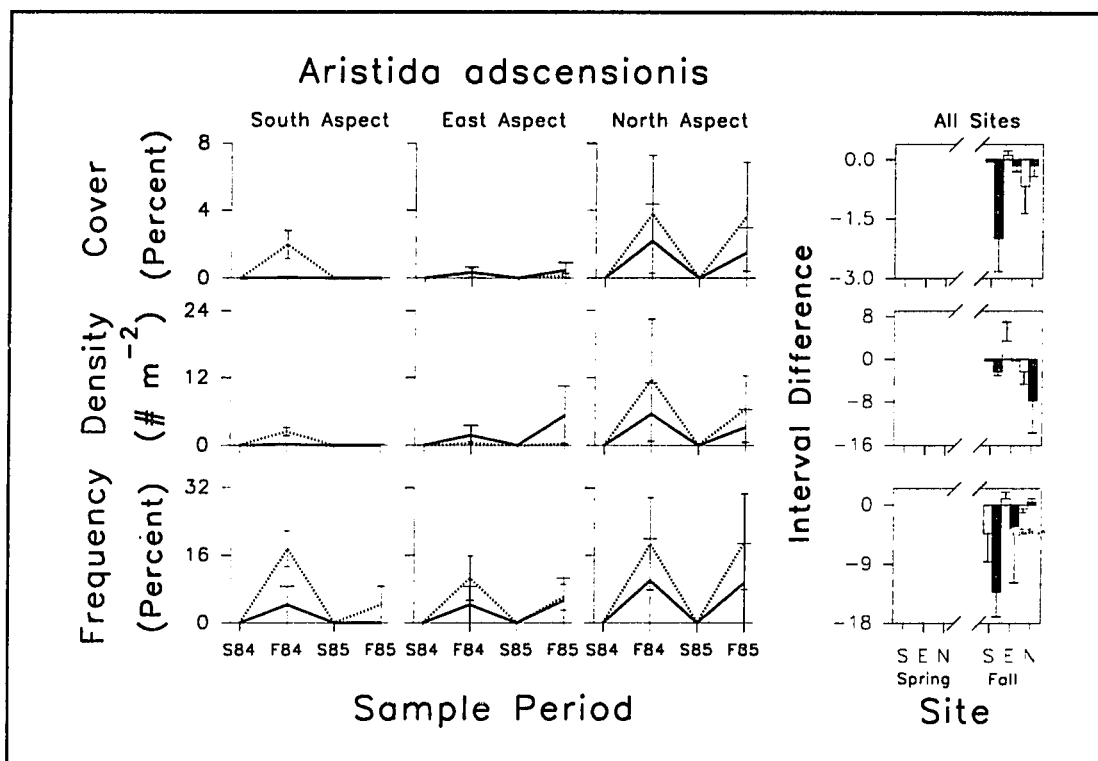


**Figure 33.** Cover, density, and frequency of *Trachypogon secundus* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. *T. secundus* was not recorded in plots on the north slope. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

all periods and the spring interval (Table 13). Contrasts showed frequency was greater on the east slope than on the south slope. For the spring interval the amount of change on the south slope was greater than on the east. In contrast, density (Table 12) and live biomass (Table 15) were not strongly different between sites with dead biomass (Table 16) only showing a significant site difference for the spring 1984 sample.

Burning had little impact on this species with only minor differences apparent between burned and unburned areas for any of the sample categories. However, although cover, frequency, density or live and dead biomass were not significantly different they often showed lower values in burned plots than in unburned (Table 11, 12, 13, 15, and 16).

*Aristida adscensionis* - Six-week three-awn is a summer annual and was found growing only during the fall samples. No significant differences between sites or burned and unburned areas were found for cover (Table 11), frequency (Table 13), density (Table 12) and live biomass (Table 15) although this species was generally more common in burned areas. Only dead biomass during the fall 1985 sample showed significant differences both among sites and between burned and unburned areas (Table 16). In general *A. adscensionis* was a minor graminoid except on the north slope where cover in unburned plots averaged 2.2% (36% of the graminoids) and on burned plots 3.8% (46% of the graminoids) for the fall 1984 sample (Figure 34). Cover on burned plots on the north slope appeared to have been very high the summer after the burn but this period was missed by the sampling. It was the main annual graminoid species in the study area and was usually found in disturbed areas, particularly on the north slope where large patches of *Selaginella* had been killed by a moderately hot fire. Wright (1980) lists *A. adscensionis* as favored, recovering in one year, with double the normal yield the first growing



**Figure 34.** Cover, density, and frequency of *Aristida adscensionis* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

season after fire if average or better rainfall occurs which was the case during my study. Its abundance is negatively correlated to the presence of perennials (Cable 1967, 1972).

**Non-flowering species (Pteridophyta)** - The most important non-flowering plants in the study area were restricted to several species of ferns and *Selaginella rupincola* with the latter usually the most common. I found significant differences in cover between sites and between burned and unburned areas for each of the four samples (Table 10). Contrasts for the periods

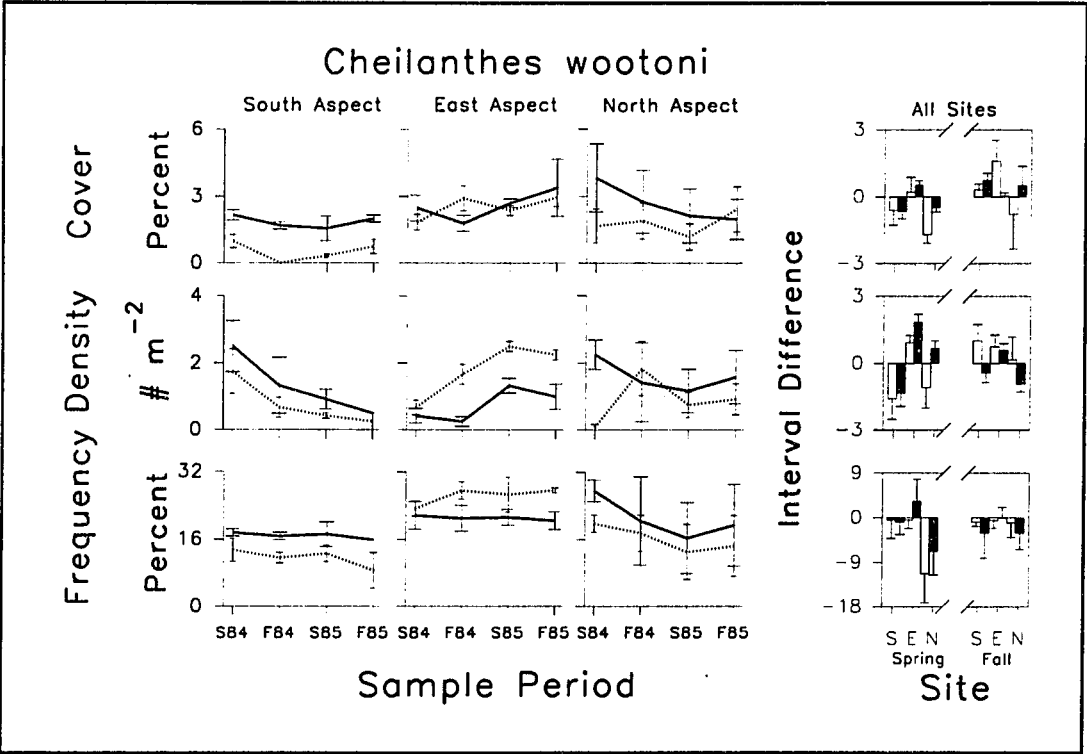
without interaction effects (both fall samples) showed significantly less cover on the south slope than on the east or north slopes (Figure 11). Linear contrasts for the two spring samples indicated significant differences among three sites in unburned areas with the greatest cover on the north and least on the south slope. They indicated no differences among burned areas. The lack of *Selaginella* differentiated the south slope from the east and north slope with respect to non-flowering species. Cover was greater in unburned areas in all cases. In burned plots on the south slope it was 2% less than in unburned (a 45% relative difference), 19.6% (83%) less on the east, and 34.7% (87%) less on the north. Postfire recovery was apparent but occurring slowly. Non-flowering species were the largest biomass or fine fuel component in unburned plots on the north slope (Figure 23).

*Ferns* - Ferns as a group recovered rapidly after the fire and displayed little long term effects (Figure 12). This was probably due to having rhizomes with the growing meristem located in a protected position below the ground surface. Ahlstrand (1978b, 1982) reports an apparent reduction of *Notholaena sinuata* (cloakfern) whereas I observed no striking differences in its cover between burned and unburned plots on the south slope where it was marginally common (Table 10).

All biomass collected for ferns was combined together and considered alive because plants become dry and appear dead during the spring drought and resurrect during the summer monsoons. Only during the fall 1985 sample were significant differences in biomass found between sites (Figure 23) with contrasts showing it to be greater on the north slope than on the drier southern exposures. Strong differences between burned and unburned areas were not observed.



*Cheilanthes wootoni* - Beaded-lip fern was the most important fern on all sites and of all non-flowering species on the south slope. Cover ranged from 1.7% to 3.8% with it making up 49% of non-flowering plant cover on the south slope, 10% on the east, and 4% on the north. No consistent cover (Table 11) or frequency (Table 13) site differences were found with one exception, while density (Table 12) was generally different among sites during the study (Figure 35). Only during the spring 1984 sample was frequency different among sites. Contrasts revealed frequency on the south slope to be less than either the east or north. Additional differences also existed for the spring interval with contrasts showing greater increases on the east



**Figure 35.** Cover, density, and frequency of *Cheilanthes wootoni* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

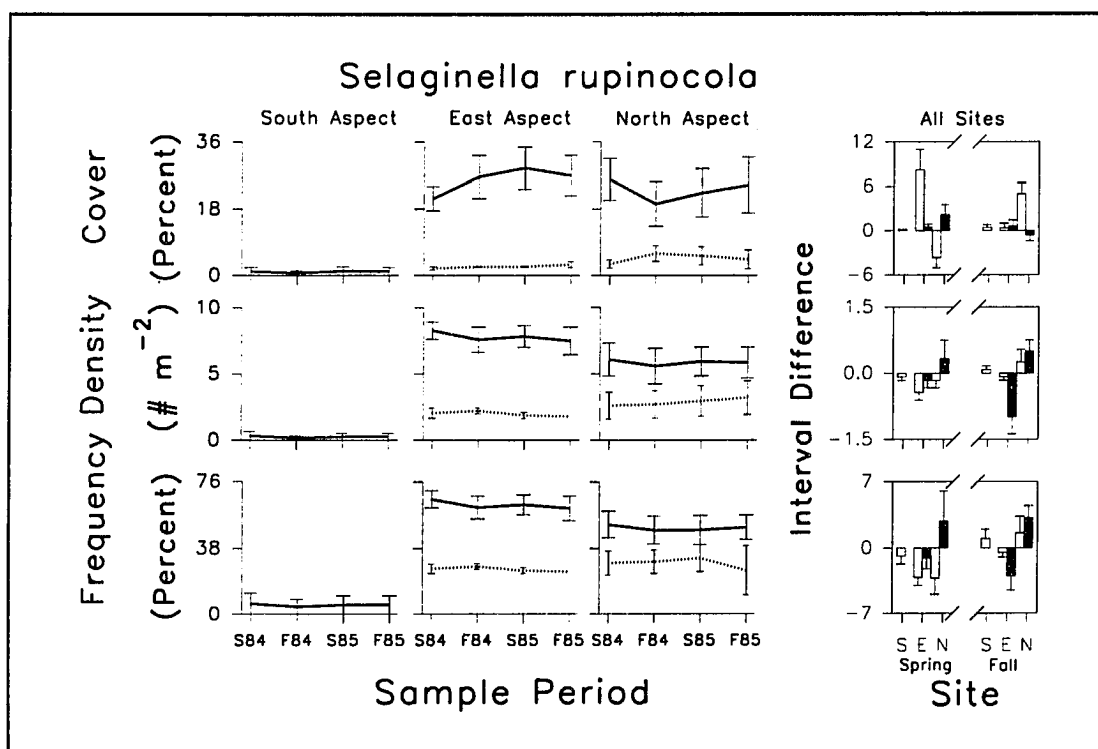
slope and decreases on the south and north. No reason for this is known. The fire had little impact on this species with no frequency differences and significantly less cover and density in burned areas relative to unburned for the spring 1984 sample only.

*Selaginella rupincola* - *Selaginella* was an important but inconspicuous species in the oak woodland. It had the greatest cover of any species and was most common in plots on the north and east slopes (Figure 36). Cover for the first sample averaged 1.1 to 26% in unburned plots. It made up 24% of the non-flowering plant cover on the south slope (1.1% of total cover), 88% on the east, and 65% on the north slope (24% of the total on the east and north). I found significant site differences for cover (Table 11), frequency (Table 13) and density (Table 12) during all sample periods and the spring interval. Site comparisons using linear contrasts showed the north and east slopes to be similar and to have significantly greater cover than the south in unburned areas while areas that were burned showed no significant site differences, a result of burning decreasing the occurrence of this species. Site differences for the fall interval were found, with contrasts showing a significant difference in the amount of change that occurred between the east and north slope sites with frequency on the east slope decreasing and increasing on the north.

Large differences in cover (Table 11), frequency (Table 13), density (Table 12) and biomass (Table 15 and 16) were found for each sample period with all less in burned areas. The apparent decrease in cover due to burning was 100% on the south slope, 91% on the east, and 88% on the north. This large reduction in cover was undoubtedly responsible the lack of significant site differences in burned areas (stated above) whereas sites appeared to have had some strong pre-burn differences. Little recovery of this species was noticed during the study.

Interval data for frequency showed significant differences for the spring interval with a decrease at unburned and little or no change at burned treatments. The reason for this pattern is unknown. The thin prostrate spreading stems of this species make it very susceptible to fire damage with no protection of growing meristems. It undoubtedly made up a major portion of the fuels on the north and east slope sites prior to the 1983 burn.

Like ferns all *Selaginella* biomass was considered alive because of its adaption to drought by drying and taking on a dead-like appearance (Figure 23). Contrasts of the biomass data between sites for the fall 1984 and spring 1985 sample period, without interaction, showed



**Figure 36.** Cover, density, and frequency of *Selaginella rupinocola* for the four sample periods (S84=spring 1984, F84=fall 1984, etc.) in burned and unburned areas at the three sites (S=south facing slope, E=east slope, N=north slope) with  $\pm 1$  SE. Solid lines with long headed error bars represent unburned areas and dotted lines with short headed error bars burned areas. Change in cover between the two spring samples and two fall samples is shown in bar plots. Filled bars in the biomass difference plots are for burned areas and open bars for unburned.

biomass on the south slope less than at either the east or north slopes which were not different (Table 15). Linear contrasts for the other two samples indicated that in unburned areas all sites were different. There were no differences among burned areas. The results also showed that biomass was significantly less in burned than unburned areas. I found no changes during the two intervals to be important.

Because of its high coverage on the east and north slopes *Selaginella* was one of the most important species in the oak woodland studied in Molino Basin. Although it was inconspicuous it was a major component of the vegetation structure and composition. Development of these mats and the importance of this species does not appear to be recent since they were observed by Shreve (1915) while conducting vegetation research in the Catalinas early in this century. It was also considered an important species in oak woodland of the Mule Mountains, Arizona by Wentworth (1981), who adds that it commonly forms mats on exposed rock surfaces. Haase (1970) felt it was important in modifying soil temperatures when he found very high densities on southwest slopes at a site in desert scrub at 930 m elevation on the fore-range of the Santa Catalina Mountains. However, with this species sensitivity to fire I doubt it would be common in any locality with a short fire return interval. It becomes important where grasses have declined in areas that have remained fire free for long periods. Its increase may be associated with increases in woody species at these same sites. Under these conditions it appears to be an important soil stabilizer, developing staircase-like formations in the soil, particularly in shallow rocky areas such as found on the north slope that are the most well developed in areas of reduced fire frequency. These formations appear as though they can persist for long periods, although the *Selaginella* cover may be killed. They appear partially stabilized by roots and the development of what seems to be a bryophytic cover. This interim feature may maintained them until *Selaginella* can

reestablish. However, the rills appear more susceptible to destruction during this time which I observed to occur during the very heavy rains at the end of September 1983.

### 5.5 Total Cover

Total cover in unburned areas increased slightly between the initial and final sampling whereas in burned areas a comparatively greater increase occurred (Figure 11 and Appendix 5 and 6) and tended to fluctuate by season. Increases on burned plots occurred during the summer and decreased or increased only slightly during the winter as a result of the dominant graminoid species that increased growth in the summer. Total cover was significantly less on burned areas when compared to unburned areas for the first three sample periods (Table 10). This difference was greatest between burned and unburned areas on the north and least on the south slope and decreased with time. By the final sample, total cover on the south slope was 17.9% greater in burned than in unburned plots, while 8.7% and 34.1% less on the east and north sites respectively. Site differences in total cover changed significantly between the two spring samples with contrasts showing the change on north slope to be significantly different and greater than on the south or east. In Chihuahuan Desert mountain shrub vegetation Ahlstrand (1982) reports 18% less total cover in burned areas three years postburn and 5% more cover at six-to-seven years postburn than in unburned areas.

### 5.6 Summary of Fire Effects and Postfire Responses of Individual Species

The immediate effect and subsequent response of species for two years following the fire was to decrease woody species and increase herbaceous species (Table 1). Of the eight

**Table 17.** Fire tolerance of the 21 major species used for detailed analysis. Percent difference is the difference between burned and unburned areas averaged over the three sites. Criteria for determining tolerance follow Wright (1980).

<i>Species Name</i>	Percent Difference			Tolerance
	Density	Cover	Frequency	Rating
<i>Quercus emoryi</i>	-77	-71	-48	Tolerant
<i>Quercus oblongifolia</i>	15	-41	21	Very Tolerant
<i>Arctostaphylos pungens</i>	-73	-91	-72	Not Tolerant
<i>Garrya wrightii</i>	-31	-81	-22	Tolerant
<i>Agave schottii</i>	-74	-93	-18*	Not Tolerant
<i>Dasylirion wheeleri</i>	-55	-86	-35	Mod./Not Tolerant
<i>Haplopappus laricifolius</i>	-90	-99	-60	Not Tolerant
<i>Nolina microcarpa</i>	44	-83	-1*	Tolerant
<i>Artemisia ludoviciana</i>	133*	145*	45	Favored
<i>Gnaphalium wrightii</i>	>2000	>2000	530	Favored
<i>Lotus rigidus</i>	105*	491*	26*	Tolerant
<i>Andropogon cirratus</i>	-69	-66	-59	Tolerant
<i>Aristida orcuttiana</i>	222*	433*	>2000*	Tolerant
<i>Bouteloua curtipendula</i>	131	166*	41*	Very Tolerant
<i>Eragrostis intermedia</i>	>2000	>2000	>2000	Favored
<i>Heteropogon contortus</i>	72*	229	-1*	Moderately Tolerant
<i>Muhlenbergia emersleyi</i>	202*	33*	34*	Tolerant
<i>Trachypogon secundus</i>	-82	-77	-63	Not Tolerant
<i>Aristida adscensionis</i> <sup>n</sup>	497	>2000	180	Favored
<i>Cheilanthes wootoni</i>	-22*	-46	-19	Moderately Tolerant
<i>Selaginella rupincola</i>	-78	-93	-68	Not Tolerant

\* Indicates the values shown were averaged from values which showed increases and decreases between the 3 sites.

<sup>n</sup> Based on fall 1984 because the species is a summer annual.

**Table 18.** Summary of fire tolerance information, postfire response and main regeneration means of the 21 major species in burned areas. The principal means of postfire recovery I observed for each species are listed in parenthesis.

- 
- Quercus emoryi* - Susceptible to scorch and death of crown but was a vigorous sprouter from root crown. Topkilled individuals grew up to 2.5 m in two years. No seed regeneration.. (Sprouter)
- Quercus oblongifolia* - Susceptible to crown scorch but moderately resistant to topkill. Good sprouter if crown killed. No seed regeneration observed. (Sprouter)
- Arctostaphylos pungens* - Killed by fire with regeneration from seed buried under clumps of plants which existed prior to burning. Repeated burning may eliminate. Regeneration appeared within one year with seedlings up to 50 cm in three years. (Seed)
- Garrya wrightii* - Topkilled with regeneration initially rapid from an enlarged lignotuber. Sprouts reached 50 cm in two years. (Sprouter)
- Agave schottii* - Severely reduced. No seedlings but limited vegetative sprouting was observed. Basal position of growing meristem may give some but limited protection from light fires. (Sprouter and Escape)
- Dasyliion wheeleri* - Moderately susceptible. Some apparent protection by layered leaves around stem but if penetrated by heat the plant is killed. (No reproduction observed)
- Haplopappus laricifolius* - Severely reduced. A few seedlings noticed in burned areas two yr postfire, particularly in vicinity of adult plants surviving the fire. (Seed)
- Nolina microcarpa* - Individual clump or aggregate size reduced but few killed. Aggregate centers died (or were already senescent), apparently due to fuel buildup, resulting in high fire severity, while sprouting occurred from clump fringes. (Sprouter)
- Artemisia ludoviciana* - Individuals topkilled but returned vigorously from sprouts and seed to most burned areas by two years postfire. (Sprouter + Seed)
- Gnaphalium wrightii* - Killed but returned rapidly from seed sources by two years postfire. Initial increase was followed by a decrease two years postfire. (Seed)
- Lotus rigidus* - Topkilled but resprouted moderately well from woody caudex. (Sprouter)
- Andropogon cirratus* - Topkilled with some mortality. Moderate ability to sprout. Some reduction by fire. (Sprouter)
- Aristida orcuttiana* - Topkilled with good ability to resprout. Little overall change. (Sprouter)
- Bouteloua curtipendula* - Topkilled with good sprouting ability plus some apparent regeneration from seed sources. (Sprouter + Moderate Seed)
- Eragrostis intermedia* - Topkilled with moderate mortality. Increased substantially within two years from seed sources with some individuals beginning to die by three years. (Sprouter + Seed)

Table 18 continued.

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<i>Heteropogon contortus</i> - Topkilled but good sprouter with individuals responding with increased growth. (Sprouter)
<i>Muhlenbergia emersleyi</i> - Topkilled but resprouted well. Some large senescent tufts with a large amount of fuel were killed. New individuals appeared within three years. (Sprouter + Seed)
<i>Trachypogon secundus</i> - Topkilled and decreased. Surviving individuals respond positively with good growth. (Sprouter)
<i>Aristida adscensionis</i> - Killed but returns rapidly from seed during summer. Increased vigorously on disturbed areas with continued importance for at least three years. (Seed)
<i>Cheilanthes wootoni</i> - Topkilled but recovered quickly from rhizomatous stems. (Sprouter)
<i>Selaginella rupincola</i> - Severely reduced. Slow vegetative regeneration, apparently from small clumps of former mats which survive the fire. (Escape)

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woody species (trees, shrubs, and subshrubs) intensively sampled as major species, four (50%) where not tolerant of fire while the remaining species were tolerant (Table 17). I only considered two (13.4%) of the 13 herbaceous species intensively sampled to be intolerant of fire, while seven (53.7%) were tolerant, and four (30.8%) strongly favored by fire. The tolerant species generally had good sprouting ability while favored species were often good sprouters that also increased their populations through seedling establishment (Table 18). Other favored species, such as *Gnaphalium wrightii* and *Aristida adscensionis*, were able to increase without resprouting, at least temporarily, from seed sources that appeared to be derived from seed banks. These differing survival and regeneration strategies are important in understanding long-term dynamics and interactions of vegetation and fire in oak woodlands.

I also reviewed the tolerances of species not considered major species (exclusive of those described in Table 17 and 18), that was based on less extensive field data due to these species being less common and thus not being as intensively sampled as the major species. This data was also supplemented by my personal field observations. However,



**Table 19.** Observational information on the ability of species not selected for analysis as "major species" to tolerate fire and their apparent main means of regenerating following fire in the oak woodland (SPRT=sprouter).

Species Name	Tolerance Rating	Regeneration Means
<b><u>TREES</u></b>		
<i>Juniperus deppeana</i>	MOD. TOL.	MOD. SPRT.
<i>Pinus discolor</i>	NOT TOL.	SEED REGEN.
<b><u>SHRUBS</u></b>		
<i>Crossosoma bigelovii</i>	TOLERANT	SPRT.
<i>Rhamnus crocea</i>	TOLERANT	VIG. SPRT.
<i>Rhus trilobata</i>	TOLERANT	VIG. SPRT.
<i>Vauquelinia californica</i>	NOT TOL.	POOR SPRT.
<b><u>SUBSHRUBS</u></b>		
<i>Acacia angustissima</i>	TOLERANT	VIG. SPRT.
<i>Agave palmeri</i>	NOT TOL.	?
<i>Asclepias linaria</i>	TOLERANT	VIG. SPRT.
<i>Ayenia pusilla</i>	TOLERANT	VIG. SPRT.
<i>Baccharis</i> spp.	TOLERANT	SPRT.
<i>Bouvardia glaberrima</i>	TOLERANT	VIG. SPRT.
<i>Brickellia californica</i>	FAVORED	SEED REGEN.
<i>Calliandra eriophylla</i>	TOLERANT	VIG. SPRT.
<i>Dalea pulchra</i>	TOLERANT	SPRT.
<i>Desmodium cinerascens</i>	TOLERANT	VIG. SPRT.
<i>Eriogonum wrightii</i>	TOLERANT	SPRT.
<i>Erythrina flabelliformis</i>	TOLERANT	SPRT.
<i>Ferocactus wislizeni</i>	NOT TOL.	?
<i>Gossypium thurberi</i>	FAVORED	SEED REGEN.
<i>Mammillaria</i> spp.	MOD. TOL.	?
<i>Mimosa biuncifera</i>	TOLERANT	SPRT.
<i>Opuntia engelmannii</i>	NOT TOL.	POOR SPRT.
<i>Selloa glutinosa</i>	TOLERANT	SPRT.
<i>Yucca schottii</i>	MOD. TOL.	MOD. SPRT.
<b><u>PERENNIAL FORBS</u></b>		
<i>Agastache breviflora</i>	FAVORED	SEED REGEN.
<i>Anemone tuberosa</i>	TOLERANT	SPRT.
<i>Arabis</i> spp.	TOLERANT	SPRT.
<i>Castilleja laxa</i>	TOLERANT	SPRT.
<i>Erigeron</i> spp.	FAVORED	SEED REGEN.

Table 19 continued.

Species Name	Tolerance Rating	Regeneration Means
<u>Perennial Forbs continued</u>		
<i>Galium microphyllum</i>	TOLERANT	?
<i>Gilia multiflora</i>	TOLERANT	SPRT.
<i>Iva ambrosiaefolia</i>	FAVORED	SEED REGEN.
<i>Penstemon parryi</i>	FAVORED	?
<i>Verbena ciliata</i>	FAVORED	SEED REGEN.
<u>ANNUAL FORBS</u>		
<i>Caucalis microcarpa</i>	FAVORED	SEED REGEN.
<i>Daucus pusillus</i>	FAVORED	SEED REGEN.
<i>Euphorbia melanadenia</i>	FAVORED	SEED REGEN.
<i>Ipomoea</i> spp.	FAVORED	SEED REGEN.
<i>Plantago purshii</i>	FAVORED	SEED REGEN.
<i>Solanum douglasii</i>	FAVORED	SEED REGEN.
<i>Sphaeralcea laxa</i>	FAVORED	SEED REGEN.
<u>PERENNIAL GRAMINOIDS</u>		
<i>Andropogon barbinodis</i>	TOLERANT	SPRT.
<i>Eragrostis lehmanniana</i>	TOLERANT	SPRT./SEED REG.
<i>Koeleria cristata</i>	TOLERANT	SPRT.
<i>Lycurus phleoides</i>	TOLERANT	SPRT.
<i>Muhlenbergia polycaulis</i>	TOLERANT	SPRT.
<i>Rhynchelythrum roseum</i>	FAVORED	SPRT./SEED REG.
<u>ANNUAL GRAMINOIDS</u>		
<i>Bouteloua aristidoides</i>	FAVORED	SEED REGEN.
<i>Bromus rubens</i>	FAVORED	SEED REGEN.
<i>Bulbostylis capillaris</i>	FAVORED	SEED REGEN.
<i>Enneapogon desvauxii</i>	FAVORED	SEED REGEN.
<i>Eragrostis cilianensis</i>	FAVORED	SEED REGEN.
<i>Vulpia octoflora</i> ( <i>Festuca</i> )	FAVORED	SEED REGEN.
<i>Muhlenbergia fragilis</i>	FAVORED	SEED REGEN.
<i>Panicum scribnerianum</i>	FAVORED	SEED REGEN.
<i>Poa biglovii</i>	FAVORED	SEED REGEN.
<i>Seteria viridis</i>	FAVORED	SEED REGEN.
<u>NON-FLOWERING PLANTS</u>		
<i>Bommeria hispida</i>	TOLERANT	SPRT.
<i>Notholaena aurea</i>	TOLERANT	SPRT.
<i>Notholaena sinuata</i>	TOLERANT	SPRT.
<i>Pellaea truncata</i>	TOLERANT	SPRT.

inclusion of a description of fire effects on these species (Table 19) allowed a much broader range of species and a more substantial review and interpretation of fire effects in oak woodland to be made. This information indicated that of the 25 woody species, five (19.2%) were intolerant of fire, 18 were tolerant (69.2%), while two, *Brickellia californica* and *Gossypium thurberi* were favored (7.7%). Although a higher proportion of these species were tolerant of fire than of the major species, they were overall less common in the oak woodland found in Molino Basin. Herbaceous species showed similar responses, with none intolerant of fire, 14 species (37.8%) tolerant, and 23 (62.2%) favored. This grouping of herbaceous species consisted of a much higher proportion of annuals (seven annual forbs and ten annual graminoids) than in the major species listing (with only one annual graminoid, *Aristida adscensionis*). The principal means of postfire recovery and increase in the herbaceous species was through seed regeneration (because most were annuals), while the woody species tended to be vigorous sprouters with less dependence on seed regeneration strategies. These data showed the very strong advantage the two oak species (*Quercus emoryi* and *Q. oblongifolia*) had over the other two tree species commonly seen in lower oak woodlands (*Juniperus deppeana* and *Pinus discolor*). Although the juniper is known as a postfire sprouter (Carmichael et al. 1978), it sprouted only to a limited extent and suffered considerable mortality following the Molino Basin fire, while piñon pine exhibited extreme sensitivity to fire with the few individuals present within the burn perimeter eliminated. These differences in tolerances to fire may help explain some of the distributional patterns of these species within southwestern ecosystems that may not be apparent now that fire suppression is so prevalent. With the reduction in fire occurrence over the last 100 years these data on fire tolerance indicate that these species should be expanding their local range (invading new sites on a local scale) and be increasing in density at sites where they were formerly more

restricted. Thus, as an example, I would expect older piñon pines or junipers to be restricted to well protected sites, such as rocky areas with low or discontinuous fuels, while young trees would be found in a much wider range of sites, in areas of heavier fuels, that they could not have previously occupied.

Some differences in postfire response were also observed within groups of species. This was noted by Dunne et al. (1991) who reports that shrubs reproducing from seed recovered slower than shrubs that resprouted. In my study subshrubs as a group showed a dichotomous response to fire. Many of the more succulent life-form species (*Opuntia* spp., *Agave palmeri*, *A. schottii*, *Ferocactus wislizeni*) and also *Haplopappus larifolius*, exhibited intolerance, with slow postfire recovery, while others showed rapid recovery from top-kill via vigorous sprouting from stem parts protected at or below the soil surface (*Acacia angustissima*, *Bouvardia glaberrima*, *Calliandra eriophylla*, *Ayenia pusilla*).

The time required for total vegetation cover to re-establish following the fire varied among the three sites. The most rapid recovery was on the south slope because of the dominance of perennial resprouting species that tended to be resilient to fire and slowest on the north slope where a high proportion of the vegetation before the burn was non-sprouting species that exhibited little resilience to fire (for example *Selaginella* and *Arctostaphylos*). The rapid recovery on the south slope may also be a function of time since the last fire. I would surmise that the open aspect of the vegetation is a result of both dry conditions and a higher fire frequency which may promote species which are better adapted to recovering from fires.

Biomass samples (all plant material <1.0 cm diameter) showed predictable recovery responses following the burn. Live and standing dead biomass recovered rapidly, a result of vigorous postfire growth of herbaceous species, primarily sprouting graminoids. This recovery

was quickest on the south and southeast slopes and less pronounced on the north slope where fewer sprouting herbaceous species existed. This fine fuels accumulation rate indicates that an area may be able to sustain a second burn within one or two years. Recovery of total biomass lagged that of standing biomass due to slower accumulation rates of litter. Additionally, differences in the spatial distribution of biomass between burned and unburned sites existed over the two-year-long study period, with biomass more evenly distributed across burned areas and more clumped in unburned areas. The more even distribution of biomass in burned areas appears to be a result of an increase in graminoids which tend to be more evenly distributed, with a concurrent decrease in shrubs which tend to have concentrations of associated litter fuels. This was most apparent in the live and standing dead categories, where the 1985 samples had greater variances in unburned samples than burned even though live biomass measurements were greater (Appendix 3).

The overall effect of the burn in Molino Basin was to cause shifts in species composition between burned and unburned areas, with the north slope sustaining the greatest change. Persistent sprouting species were most responsible for rapid vegetation recovery on the south slope with an open savanna character. However, while composition shifted, the actual number of species in any burned or unburned site remained nearly equivalent. Generally, species that were present in unburned areas were also present in burned areas. The fire increased the dominance (cover, density, and biomass) of herbaceous species, particularly graminoids, at the expense of woody species and *Selaginella*. The fire effects and postfire species responses observed during this study indicate that fire exclusion or greatly reduced frequencies since about 1880 have had a very strong influence on the patterns of vegetation change that have taken place in southeastern Arizona during this interval. In the past, fire in oak woodland probably also

played an important role in species distributions, at least on the local scale, though its effects were probably subject to the influence and interactions with such factors as climate, topography, moisture, temperature, and soils.

### **FIRE IN MADREAN OAK WOODLAND: SYNTHESIS OF EFFECTS AND RESPONSES TO FIRE**

Interpretation of specific effects of fire and responses on individual species is only one facet in understanding the role of fire in Madrean oak woodland. It also needs to be combined with information on how fire affects this biotic community as an assemblage of species and how important non-biotic factors might influence these effects. While this study primarily addressed the immediate effects of fire, a fuller understanding of fire's role and its impact on vegetation also needs to consider both short-term and long-term effects and how these vary over different spatial scales. Longer-term effects are important because they influence vegetation on both ecological-time scales and evolutionary-time scales (Fox and Fox 1987). In this section I will discuss and integrate a number of these influences, including seasonal timing of the burn, fuel loadings (incorporating both time since last fire and site productivity), the fire frequency regime, and fire intensity versus severity, with the fire effects that I observed in this study. Additionally, I will discuss: 1) postfire vegetation patterns, climate during the period when the burn occurred ( $\pm 2$ -3 yrs) and its implications on fire effects and postfire vegetation response and long term interactions of climate/topography and fire and its effect on vegetation structure. Many of these components have been investigated in other ecosystems (Heinselman 1973; Arno 1980; Romme and Knight 1981; Despain 1983; Hemstrom and Franklin 1982). Lastly, I will evaluate the role of fire in shaping and in the dynamics of Madrean oak woodlands, both in the past and present, and of what some of the possible management implications are of fire or lack of fire in Madrean oak woodland today.

## 6.1 Fire and Biotic Interactions

Season of fire - The particular season of a burn and the phenological and physiological state of each species during this season is important in understanding the impact of fire (Trabaud 1981; Rundel and Parsons 1981). These seasonal effects are also influenced by environmental factors such as air temperature, water availability, and humidity that control fire behavior (Fox and Fox 1987; Scifres and Hamilton 1993). Fire and the phenological condition and response of vegetation has been studied in a number of plant communities (Biswell and Lemon 1943; Curtis and Partch 1950; Jameson 1961; Hover and Bragg 1981; Abrahamson 1984b; Platt et al. 1988; Vose and White 1991; White et al. 1991; Spier and Snyder 1994). Phenological patterns of many species tend to be species-specific and variable, depending on factors such as, fire behavior, time since the last burn, and season of burn. For instance, Rundel and Parsons (1981) found that *Chamaebatia foliolosa*, in a chaparral-coniferous forest transition zone in the Sierra Nevada of California, responded with stimulated regrowth after spring (pre-growing season) and fall (post-growing season) fires, whereas summer burns (mid-growing season) resulted in reduced growth for two years. In the grasslands of the Flint Hills, Kansas, winter and early spring burns resulted in less production relative to unburned areas, while late spring burns had biomass production nearly equal to unburned areas (Anderson 1982). Finally, in addition to interacting with phenological conditions of the plant, the season of burn also interacts with the climate regime, resulting in a complex set of fire effects and postfire vegetation responses following each fire. I will discuss some of these more fully in the next section.

The 1983 fire in Molino Basin occurred at the height of the foresummer drought, which is the main period of lightning fire ignition and when most large fires occur in southeastern Arizona both presently and historically (Pearson 1922; Barrows 1978; Bock and Bock 1978; Baisan 1990,



1991). Although this is the driest and hottest period each year, fires during this season may result in rapid postfire recovery in graminoid dominated woodlands for at least two reasons. First, many species, particularly herbaceous species, are dormant during the consistently dry hot foresummer drought when most above ground plant parts are dead and thus not prone to injury (Ohr and Bragg 1985). Those above ground plant parts that are still alive and dormant would tend to be drought hardened, with reduced amounts of tissue moisture, which would result in greater heat resistance (Hare 1961; Scifres and Hamilton 1993). Additionally, plant parts and soil organisms near the soil surface would be better protected from heat penetration during the foresummer drought when soil moisture is low and less conductive (Alonso 1967; Frandsen and Ryan 1986; Frandsen 1987; Scifres and Hamilton 1993). Second, the foresummer dry period is usually followed by consistent summer monsoon rainfall and increasing soil moisture, permitting rapid growth and recovery. This seasonal climate pattern is different from many arid grassland ecosystems in North America where summers are dry and litter removal by fire results in increased moisture loss and decreased productivity (Anderson 1982; Knapp and Seastedt 1986). Phenologically, in southeastern Arizona, most of flowering and seed production in semi-desert graminoid species takes place in late summer and fall so seeds are likely to be already dispersed on or in the soil by the time the foresummer drought occurs, and thus be better protected from heating by a burn.

Woody species also show seasonal differences in fire effects. For example, oaks appear to have better carbohydrate reserves during the dry foresummer period when they are relatively dormant than a few months later in the summer when new growth and reproductive effort is being expended (Harrington 1989; Trabaud 1981, 1991). The physical impact of winter burns may be less than during a warmer period, but would be followed by drought which may produce

increased stress at a time when the oaks are recovering from fire caused injuries (Trabaud 1981). Summer or fall burns may cause injury to such species during a period when they are actively growing and flowering, resulting in a reduction or loss of that years reproductive effort.

In conclusion, the seasonal timing of fire can be critical in producing very different effects and postfire responses in many plant species. This is a result of differing impacts of fire, which depends on life-history traits, phenological development, and physical condition of an individual or species. In the Southwest, winter burns may be detrimental to cool-season species while benefiting warm-season species. Seasonal fire effects on broadleaf and long-lived perennial species may be less significant than on annual or biennial species because they often have the capability to regenerate from protected underground plant parts (Scifres and Hamilton 1993). In southern France, Trabaud and Lepart (1981) found the seasonal effects of fire to be the strongest factor influencing species diversity. Lastly, human induced changes in the fire regime, such as altered seasons of burning, may have significant impacts on the vegetation and dynamics of the ecosystem (Malanson 1987). This is an area that requires further study.

Climate conditions and fire effects - When attempting to understand fire effects and vegetation response in southern Arizona the importance of climatic conditions during the year of the fire and also for several years prior to and following the fire must be recognized. The specific composition of the vegetation after fire is closely associated with both the conditions of the environment prior to and following the fire (Trabaud 1981). These effects from single fires may then be compounded through repeated fires into long-term effects.

It has long been understood that in many grassland-shrubland fuel based ecosystems, such as in the Southwest, fire occurrence is more frequent following one-to-three years of wet weather

(Rogers and Steele 1980; Wright and Bailey 1982; McLaughlin and Bowers 1982; Rogers and Vints 1986). The implications of a greater probability of fire occurrence following wet periods does not solely involve the occurrence of fire but should also have a strong influence on how vegetation is affected and responds to fire. Postfire plant response to fire-caused injury after a wet period should in most cases be relatively greater than after a dry period. Jemeson (1961) reports that fires during dry, hot weather may be more damaging to vegetation than during cooler, wet weather. For instance, soil moisture and reserves of plant resources should be greater if a wet period preceded the fire. In some areas of arid North America, postfire grassland production was lower following fires during low rainfall years due to the removal of the litter layer and enhanced moisture loss (Anderson 1982). The ultimate outcome of this plant-climate interaction might be that many species would be better able to tolerate and re-establish after wet periods when there is a higher probability of fire. However, there could be confounding interactions between some species or ecosystems and weather patterns. For example, it has been shown that mesquite seedlings are more vulnerable to fire caused mortality following one-or-two years of above normal precipitation due to increased fine fuels from greater grass production (Cable 1972; Wright 1980). In other situations, the removal of litter cover and the exposure of mineral soil may increase moisture stress during critical dry seasons of a year.

Over the long term this plant-climate interaction may act as a feed-back mechanism selecting species that do well under such a regime. This could have important implications on the structure and dynamics of oak woodland and in other related vegetation types. One of the more important climatic influences producing recognizable variability in the climate of the Southwest (and other regions of the world) is the pattern of El Niño-Southern Oscillation (ENSO) events. Strong links between ENSO occurrence and seasons of increased fire activity in eastern Australia (Skidmore

1987) or decreased fire activity in the southeastern United States (Simard et al. 1985) have been found (during ENSO events it is dry in the western Pacific and wet in the southern United States). In the Southwest a weak link between fire occurrence and ENSO conditions has been noted (Swetnam and Betancourt 1990). Thus a pattern of positive ENSO events may have important implications on fire effects and long term fire-vegetation dynamics. Conversely, the frequency of fire after dry periods "La Nina" would also have important effects (possibly with plants being more susceptible to negative impacts). These effects should be strongest in locations where these climate patterns are dominant, such as in southern Arizona and south into Mexico. The specific pattern and timing of fire occurrence in relation to these two climatic events would be critical in how long-term fire effects may be expressed in the vegetation of the region. Such patterns could be modelled. Related patterns of drought associated with ENSO, such as during the 1950s, and its impact on vegetation is being investigated by Betancourt et al. (1993). They suggest that these patterns have important effects on plant communities in the Southwest. Thus a knowledge of when historic fires occurred climatologically will be important in understanding long-term fire effects and fire-vegetation interactions. Lack of consideration for this short-term climate variation may be partially responsible for some of the varied results produced by different fire effects studies that have been undertaken over a period of many years in southern Arizona and New Mexico.

Fuel conditions - Both short and long-term fuel conditions are important in understanding fire effects within an ecosystem. The frequency, behavior, and environmental impacts of fires on an ecosystem are mainly regulated by fuel accumulations (Agee et al. 1978; Christensen 1987). Fuel dynamics within an ecosystem may vary in scale, both temporally and spatially, and be

influenced by past history. Fuel conditions at a site are a response of such site factors as productivity and the potential vegetation that can occupy the site. Fuels can vary from year-to-year depending on how climate conditions effect biomass productivity, decomposition rates, in addition to the time since the last burn. Additionally, fuel would be influenced by persistence characteristics of ecosystem properties that regulate litter and biomass turnover rates. For example, how persistent will higher fuel conditions be following a period of increased productivity due to advantageous climate conditions.

The spatial heterogeneity of fuels will vary greatly depending on the composition and structure of the vegetation with this heterogeneity changing over time. In Molino Basin, aggregates of *Arctostaphylos pungens*, *Agave schottii*, and *Nolina macrocarpa* burned hot due the high fuel loads and/or flammable structural characteristics of plants within these aggregates. Fire within these aggregates usually resulted in much greater soil heating than in surrounding grassland areas, creating a mosaic of fire effects over the landscape. Over time, as the composition and structure of the vegetation change after a fire (as new aggregates of shrubs develop) the fuel structure, continuity, and composition will change.

The single burn in Molino Basin tended to change the areas discontinuous fuel character to one dominated by more evenly distributed fine fuels. Postfire production of fuels was great enough to permit reburns within two-years (and probably as short as one) as occurred when the lower portion of the 1983 burn, primarily in desert grassland vegetation, reburned during the summer of 1985. This rapid recovery of fine flashy fuels may be important in understanding past fire frequencies in southeastern Arizona because it suggests low intensity fires, spreading over large areas, could occur frequently. The removal of these fuels at lower elevations during the severe period of overgrazing in the late 1800's, rather than higher elevation fuels in pine-forest,

may have been a key link in reducing fire frequency of higher elevation areas with the areas interconnected through fire spread.

Fire frequency - Patterns of vegetation over the landscape result from two overlain ecological processes: the patterns resulting from the disturbance regime and the patterns on species distributions imposed by environmental gradients and the dispersal ability of species (Romme and Knight 1982). Important attributes of the disturbance regime include frequency and return interval of events (Jackson 1968; Sousa 1984). To understand the patterns imposed by disturbance we must understand that disturbance effects may be severe and catastrophic but infrequent, making them very apparent, or of low severity with a high frequency, making them less apparent, but having a cumulative effect that may be as ecologically significant as the high severity disturbances. Changes in an ecosystem from one to the other pattern of disturbance may result in dramatic effects and changes to the vegetation. This is becoming apparent as fire regimes change throughout much of western North America, a result of fire suppression and fuel accumulations (Dodge 1972; Parsons and DeBenedetti 1979).

Interpretations about long-term fire effects need to account for the consequences of an oak woodland vegetation that developed under a regime of episodic fire over a long period prior to European settlement. While my research in Molino Basin only examined fire effects following one burn, using this information and integrating it with additional information about fire intervals from fire history studies in southwestern woodlands, does permit some extrapolation as to what the longer-term ramifications of certain fire frequencies might be on Madrean oak woodland. First, there appears to be two subsets of fire effects that may be distinguished in reference to episodic fires: that of frequency and that of repeated fires, although the effects of each are linked.

Fire frequency should refer to stochastic effects predominately in the time domain and at the community level, such as the effect on species distributions due to disturbance by fire, while the effects of repeated fire should describe physical effects of repeated fires (more than one fire), primarily at the individual or species level.

While effects of moisture and geomorphic processes are often the dominant factors responsible for species distributions (Shreve 1915; Whittaker and Niering 1964, 1965; Jackson 1968; Swanson et al. 1988), the overall effects of many repeated burns (the fire frequency regime) could influence the positioning of some community boundaries (Jackson 1968), although fire itself is partially constrained by interactions with the landform (Swanson et al. 1988). In some settings the boundary position may be dynamic while in other it may either static or unstable, such that once fire has produced vegetation changes the composition of the vegetation is forced over a threshold from which it cannot return (Tausch et al. 1993). Thus, through the action of differing frequencies, fire may be important in regulating or at least strongly modifying some plant community boundaries in southeastern Arizona (Sweeney 1969). While periodic burning can maintain an open grassland, so long as fuels remain available (Martin 1983; Scifres and Hamilton 1993), in southeastern Arizona it could also shift community vegetation composition toward grassland in areas where grassland-woodland vegetation meet (i.e. woodland being: oak woodland, pinon-juniper woodland, or desert scrub). As fire frequency increases, particularly in drier low elevation sites, semi-desert grassland would be favored, resulting in a shift of the oak woodland boundary upslope (conversely there would be a boundary shift of sonoran desert vegetation downslope with fire increases in bordering semi-desert grassland.). The end result could be an increase in semi-desert grassland (up to a point that productivity and fuel production could be maintained) with more frequent fires, with grassland moving both

upslope into oak woodland and downslope into desert vegetation. The sensitivity of lower elevation desert vegetation to fire has been documented in several studies (Rogers 1985, 1986; Roger and Vint 1987).

Grass species that comprise these semi-desert or woodland communities are often well adapted to fire. Species possess many adaptations that provide protection or escape from fire; buds buried in soil or protected in tussocks and bases of leaf tillers and sheaths. Through time episodic fires tend to favor prolific sprouters and rapidly growing species. Without fire, stratification of the vegetation occurs, with a shift toward the replacement of fire adapted forms by species less well adapted (Granier and Cabanis 1976). This may result in decreases in grass cover (Innes 1963, see Bock and Bock 1986) and frequently to an increase in woody species (Whitfield and Beutner 1938a, 1938b; Blackburn and Tueller 1970; Box et al. 1967; Amos et al. 1988; Gell et al. 1993).

The reoccurrence interval of fire at a site is an important component in understanding the ecological role of fire, particularly in grassland or shrubland communities where these intervals are often tied to site productivity and thus fuel production.

*"Fire variables such as frequency and intensity tend to determine relative dominance of species but rarely their presence or absence (Gill & Groves 1981; Abrahamson 1984a). Thus post-fire vegetation is a rearrangement of pattern and dominance of pre-fire vegetation not a succession of species replacements" (Robertus et al. 1989)*

What have these changes in fire meant for the Southwest?. It is apparent that fire intervals have gone from frequent burns (3-15 yrs) to a regime with little or no fire. This abrupt change in the fire regime must have produced pronounced impacts on woodland vegetation. Precisely determining what these impacts are may be difficult to impossible because little baseline



information exists. Traub (1982) working in *Q. coccifera* woodland felt the impact of fire leads to a change in vegetation structure of the upper layers of woody plants such that as they disappear herbaceous species increase. This may cause a transformation of shrubby woodlands into grasslands.

How did or would fire frequency affect the vegetation at the 3 sample sites? Of the vegetation on the three aspects in Molino Basin the areas with the most grassland type of aspect were the least impacted as far as the change in the dominant species concerned whereas areas with a large woody species component and in this study associated with Selaginella (important but inconspicuous) have a greater shift in species composition. This would indicate that fire is less frequent in the areas of woody species which are intolerant of fire and take a long period of time to regain their dominance, either through resprouting or from seed germination.

Area burned and fire spread - The size of the area burned is often referred to as an important factor in determining fire effects and postfire vegetation response (Miller 1982; Sousa 1984; Fox and Fox 1987, Malanson 1987). Area burned refers to the influence of patch size as a characteristic of disturbance that may affect community structure. However, the fire effects data from the Molino Basin study suggests that the size of the area burned would not be of great importance in many situations within oak woodland, because most species were sprouters or had seed banks rather than relying on dispersal for reestablishment postfire. This agrees with patterns reported by Malanson (1984) in which intensity or severity are identified as important aspects of the disturbance regime in a community composed of sprouting species, not size of burn. Thus, in communities dominated by sprouters, the size of the burned area would be less important than in

a community where postfire regeneration was primarily from seed and particularly from those derived from dispersed propagules.

Understanding past sources, spread patterns, frequency, and interval patterns of fire (the fire history) within the Southwest is necessary to adequately interpret long-term fire effects on the vegetation within the region. These patterns may then be linked with knowledge obtained about specific fire effects to provide a framework for a broader landscape scale fire vegetation relationships. Understanding the fire history of an area is important because it is a component of the fire regime that has a unique past pattern and has a strong influence on both current vegetation and fire regime characteristics (Fox and Fox 1987).

**Fire spread** - Large scale grassland fires are frequently common in areas with regularly alternating wet-and-dry growing seasons (Gillon 1983). These alternating seasons allow rapid fine fuel accumulations during wet seasons, with subsequent moisture loss during dry seasons, to permit fires. Burns in these settings, are usually intense burning fronts which pass rapidly, lasting only 5 to 10 minutes, with peak temperatures only persisting a few seconds (Alonso 1967; Gillon 1983; Hartford and Frandsen 1992; Scifres and Hamilton 1993). Climate patterns in southeastern Arizona fit this description. This suggests that historically large grassland fires were common and an important source of fires that spread into and across various ecosystems within the region.

Historic documents also suggest that fires of large size were not uncommon in the past. Replies from inquiries during the 1880 US census tell of large fires in western New Mexico and eastern Arizona during 1880 following a dry winter (Hough 1882):

*"Fires began in early May, 1880, and burned for weeks overrunning a portion of Socorro, Doña Aña, and a large part of Grant Counties, and extended into Arizona. The area was large, but cannot be estimated."*

Further, newspaper accounts cited in Bahre (1985, 1991) indicate that as late as the 1870's, large, fires were burning broad expanses of southeastern Arizona during the fore-summer dry season. Some accounts describe fires crossing semi-desert grasslands and spreading into local mountain ranges.

*"For the last month the country north, south and east of Tucson has been in a constant blaze. The grasses on the mesas, mountains and in the valleys, have been eaten up by the flames; during the last two days the fire has traveled over the Santa Catarina (Catalina) mountains and is burning now miles beyond. It has climbed almost to the summit of the Santa Rita, after devouring most of the pastures below,..." - Arizona Star, June 23, 1877.*

This fire or complex of fires was of extremely large size in comparison to the fires occurring in these mountains today. It also suggests that fires were burning across several vegetation types including semi-desert grassland, oak woodland and ponderosa pine forest and possibly spreading between mountain ranges.

Fires of this or greater magnitude may have provided large scale connections to the vegetation over the landscape in the past. Vegetation and fire mediated disturbances may be connected by fire spread across intervening grasslands. Connections would be strongest during the foresummer drought when grasslands are dry with fire spread hindered as summer monsoons begin and grasses green up with increased fuel moisture.

**Source of fires** - Both historical documents and contemporary fire behavior patterns suggest large fires, at least prior to the 1880s, often originated at lower elevations in semi-desert

grasslands and oak woodlands. An early biologist in the Southwest, J. Blumer made observations to that effect. In 1910 he wrote *"....the fire damage in mountainous regions is lessened by the fact that the discharges [lightning] are concentrated upon trees on high ridges and exposed peaks. As fire will not readily spread down hill under any conditions, and as it gathers its most destructive force in ascending a slope, the burnt areas will be limited."* (Blummer 1910a).

Additionally, the occurrence of lightning ignitions in grassland has usually been neglected by ecologists (Kormoreck 1968, 1971; Fonteyn et al. 1988). Today, the source areas of fires in southwestern mountain ranges is often assumed to be at higher elevations where lightning strikes and apparent fire ignition rates are greater with lower elevations neglected. However, this may be confounded for several reasons. For one, vegetation changes have occurred over the last century in many biotic communities in the Southwest - semi-desert grassland, oak woodland and pine forest (Hensel 1923; Leopold 1924; Brown 1950; Branscomb 1956,1958; Marshall 1957, 1963; Buffington and Herbel 1965; Hastings and Turner 1965; Reeves 1976, Bahre 1991) and may have altered the distribution of fire ignitions over the landscape. Thus, inferences about past ignitions based on the distribution of recent ignitions must be interpreted considering these landscape changes and the resulting fuel alterations. Such changes include increases in the dominance of woody plants and a corresponding decrease in dominance of herbaceous species as in Molino Basin. These shifts in the fuel matrix, particularly fine fuels, would have significantly affected ignitions and spread patterns of fires across the landscape in various vegetation types. Although the number of ignitions, currently or in the past, may have been greater at higher elevations (pine forest), the resulting fires may have been of smaller median size than fires originating at lower elevations. Although, fewer ignitions may have occurred in lower elevation grasslands or woodlands they could have resulted in fewer but larger burns covering more area. Second, these

fires originating at lower elevations could have been the important spreading fires found throughout a mountain range or in several nearby mountain ranges. However, in some situations it is conceivable that higher elevation fires may have been able to burn into lower elevation areas and thus acted as the source of fires that then could have subsequently spread through the grasslands into other areas. Fire history research along elevational transects on the west slope of the Sierra Nevada in California strongly suggest that low elevation fires were important in the spread of fires across this landscape and were generally the fires of large size (Caprio and Swetnam 1993, in press).

This evidence indicates that large fires may have often spread from points of ignition at lower elevations into higher elevations. Fire spread patterns for many recent large fires in the Madrean region of Arizona and New Mexico have exhibited this pattern. Examples of such burns include: burns on the forerange of the Santa Catalina Mountains (Pima and Soldier Canyons) in 1985, 1987, and 1994 (1985 area reburned); in Box Canyon, Santa Ritas Mountains in 1985; a 1984 burn in the Sunshine drainage in the Huachuca Mountains; the 1989 Chiva burn in the Rincons; the Coronado National Memorial boundary burn in 1989 (human caused); and very large burns in the Animas Mountains in both 1959 (Wagner 1977) and 1989 (Geoff Babb personal communication) that were ignited by lightning in lower elevation semi-desert grasslands or oak woodlands.

Intensity and severity - To properly identify how fire affects vegetation within an ecosystem, the relative importance of both fire intensity and fire severity needs to be considered in producing observed fire effects. Plant responses to fire are partially determined by fire intensity and duration, with intensity defined as the heat released per-unit time per area (flame lengths) and

lengths) and duration as a time-temperature relationship related to total fuel consumed and heat yield. Fire intensity can be a factor in controlling species composition and diversity by modifying seedling production of shrubs and herbaceous species and altering postfire seedling populations (Moreno and Oechel 1991). Intensity is most tied to effects on above ground plant parts (Van Wagner 1973, 1983; Trollope 1984; Morgan and Neunswander 1985). However, the response of plants to a particular fire is most dependant on fire severity, as a function of total heat yield and duration of heating, and more readily reflects the fire impact on the vegetation (Ryan and Noste 1983; Trollope 1984; Sousa 1984; Morgan and Neunswander 1985; Hartford and Frandsen 1992). Burn severity has been evaluated using measures of litter and duff consumption (Morgan and Neunswander 1985), char depth (Ryan and Noste 1983), depth of burn (Chandler et al. 1983; Van Wagner 1983; Rowe 1983), and burnout time (McArthur and Cheney 1966). McArthur and Cheney (1966) considered a number of factors important in determining their estimate of fire severity (burnout time or flame persistence). These included intra-annual timing of fire, amount of fuel available, time since last fire, wind velocity, slope, fire type (head versus backing), and humidity.

Long-term vegetation response would be largely determined by the severity of the areas' fire regime, with this regime a function of individual burn severity and the overall frequency with which these burns occurred. Frequency would affect floral composition by selecting those species most able to maintain viable populations under a specific regime (Chander et al. 1983). However, care must be taken in judging past severity conditions based on severity conditions observed today due the intervening period of fire suppression and resulting changes in the vegetation that have taken place.

Considering the oak woodland in Molino Basin, fire intensity effects were probably more important than fire severity effects because of the dominance of graminoids, which are considered flashy fuels (Sousa 1984), with little heavy duff and litter accumulations. Fire severity was important in only a few situations that were most common on the north slope. These were in clumps of manzanita that burned hot due to the standing and accumulations of downed fuel. I will discuss the spatial aspects of this below. In areas that had burned, particularly on the south and east slopes, these local areas of severe fire would have decreased, because a more even distribution of vegetation (fuels), primarily graminoids, developed on the sites. With continued episodic fire this distribution of fuels would be maintained, resulting in less severe fires overall. Finally, while topkilled oaks were primarily a result of crown scorch injury from long flame lengths, trees that died were frequently individuals that possessed cavities within trunks that allowed fire to enter and persist within the root crown area, which apparently produced severe heating and extensive internal bole damage, resulting in mortality.

## 6.2 Patterns of Post-Burn Vegetation Establishment and Response

Over the course of the study I observed several general patterns of postfire vegetation response at the three sites. These included both a time dependant response, which may be divided into several subcategories of responses, and a spatial response, that tended to be specific within micro-sites. How consistent these responses were from fire-to-fire could not be determined precisely but they most likely vary for reasons discussed in the above sections, such as year-to-year climate variability, differences in preburn fuel conditions or other site characteristics. The most important species response that affected postfire vegetation was the ability or lack of ability to resprout following the burn, followed by the ability to regenerate from seed banks. Specific

patterns of postfire plant composition and distribution will depend on such factors as pre-fire vegetation structure and species composition, specific site environments, local patterns of fire severity, and unpredictable postfire events, including year-to-year variations in weather (Yellowstone Report 1989) and species specific fire resistance and response patterns.

Temporal patterns - The four main time dependant responses I observed for the various species were: 1) rapidly emerging annuals, 2) slow to moderately establishing annuals and perennials with rapid growth, 3) species with rapid to moderate postfire growth followed by normal growth, 4) long response species with normal growth. These groups appeared to be associated with differing life history and reproductive strategies for sustaining populations in the oak woodland. The first group consisted of annual species (*Ipomea* spp. for example) that established during the first summer monsoon following the burn, within two months, and were common only for this one season. They then essentially disappeared with the arrival of winter. The rapid establishment of these species would be explained by the maintenance of a soil seed bank between fire events that would permit their utilization of the disturbance to reproduce. A second group, consisted primarily of biennials that established over the first one or two years after the burn, then developed high densities for several years with intense reproduction, and then declined to a low background level, but did not totally disappear. I observed such a strategy by *Artemisia ludoviciana* and *Gnaphalium wrightii*. A third group made up of both herbaceous and woody perennials (*Quercus* spp.) showed enhanced growth for a period of up to several years following the burn with a subsequent slowing to more "normal" growth after this period. The last group would be characterized by species such as (*Arctostaphylos pungens*, *Selaginella rupicola*) that established slowly following the burn but were present for long periods. Some



species, such as *Eragrostis intermedia*, appeared to have a mixed strategy, combining tolerance to fire (having good sprouting ability), with additional recruitment of new individuals into the population via postburn seed production and dispersal. The recovery of species that existed at the time of the burn was generally rapid for graminoids and forbs, intermediate for subshrubs, and longest for shrubs and trees.

While many species in the Molino Basin study area recovered from the burn by resprouting some species depended on seed recruitment as a recovery mechanism. Such recruitment may be important for these species because the fire-caused disturbance may provide an unusually advantageous opportunity for establishment (Christensen and Muller 1975; Schmida and Whittaker 1981; Malanson and O'Leary 1984; Troeger 1982; Whelan 1986; Davis et al. 1989). This recruitment can come from either seed banks or from postfire reproduction. In California chaparral, recruitment is achieved primarily from the germination of seed from soil seed banks, with the concentration and patterns of recruitment in this time especially important in the population biology of many species. (Davis et al. 1989; Sweeny 1956). The postfire increases due to postfire reproduction and seed release are important mechanisms for many herbaceous species, particularly graminoids. Fire may stimulate flowering, resulting in greater seed production soon after the burn. Seasonal timing of the burn may be critical in producing this stimulus (Daubenmire 1968a; Whelan 1986; Trabaud 1987b). An important implication for managers resulting from these strategies is that the lack of fire may have important impacts on the population dynamics of these species.

Spatial patterns - Non-random postfire spatial patterns of vegetation establishment were observed and occurred on a local scale within Molino Basin. Recruitment of herbaceous species

in areas with dense shrub canopies appeared to be dependant on preburn seed banks associated with patterns of canopy cover. These were particularly evident on the north slope and in areas with burned clumps of *A. pungens*. The dense clumped growth habit of this species (genets), often with substantial accumulations of dead woody fuel, produced severe localized burns (hot spots) in these clumps. Woody fuel in California chaparral can amount to 33 to 112 metric tons per hectare compared to 5.6 metric tons per hectare for a heavy stand of grass (Wells et al. 1979) (I calculated a maximum of 1.46 metric tons of non-woody fine fuels in Molino Basin). Little herbaceous vegetation was present under unburned clumps and did not appear in burned areas until the second season postburn (spring 1985) while in open areas between clumps, vegetation rapidly reestablished following the burn. Seed dispersal into these former clumps was apparently needed for establishment of herbaceous species. In interior chaparral with dense canopies few herbaceous species can be found, but after burns annuals and short-lived perennials become common (Pase and Brown 1982). Longevity of *A. pungens* clumps or burn severity in them may reduce soil seed banks and affect postfire plant distribution patterns in these areas. Seed pools in chaparral have been found to vary with stand age, composition and with respect to overstory location (Zammit and Zelder 1988). Reduced soil seed pools in "hot" spots under shrub canopies are reported by Evans and Young (1977) and Hassan and West (1986) in sagebrush-grass semidesert vegetation.

Spatial patterns of fire impacts have been investigated in several ecosystems. In oak woodlands of the Edwards Plateau, Texas, postfire community structure was often controlled by microhabitat variations in fire generated temperatures (Fonteyn et al. 1988). Burn temperatures varied under different species of oaks (evergreen and deciduous) and in grassy openings between oaks due to differing types and amounts of fuel accumulations. The authors also suggested that

these effects will vary between winter and summer burns with less variation predicted during summer burns. In California chaparral, variation in fire severity strongly altered postburn seedling populations and appeared important in controlling species composition and diversity (Wright 1931; Whelan 1986; Hobbs and Atkins 1988; Moreno and Oechel 1991; Marian and Acyl 1991). Such microscale vegetation patterns following fire were intensively investigated by Davis et al. (1989) in maritime chaparral. They found scale-dependant relationships between preburn canopy cover and seed bank composition, degree of soil heating during burning, and postburn seed bank composition and vegetation patterns. Preburn seed bank distributions were not random, with the postburn germination of various species enhanced, diminished or unchanged by burning, which resulted in patchy vegetation. Areas of preburn canopy gaps supported the most numerous seedlings, a pattern similar to that seen in burned areas of Molino Basin.

Such spatial patterns were not as well defined on the south slope, even in areas of former *A. pungens* genets. This may be a result of the more open character of the vegetation with a large pool of resprouting perennial species always present. These features may allow a larger more diverse seed bank to exist with an associated pool of nearby perennial species providing propagules for colonization which would permit rapid establishment of vegetation even in severely burned areas.

Sprouting response - Postburn sprouting by many species was the most important overall response to the impact of the burn that I observed, particularly on the south and east slopes. It was the main response of most species that were long-term constituents of the woodland vegetation. Thus, the dynamics and fire effects of species appeared to be explicitly linked to this

life history attribute, as in many other ecosystems (e.g. Keeley and Zedler 1978; Noble 1982, 1984; Zedler et al 1983; Malanson 1984; Bradstock 1985; Bradstock and Myerscough 1988; Johnson et al. 1986). Such sprouting may be important where fire regimes exist that have short rotation periods (Trabaud and Lepart 1981) and where fire intensity is a major factor in producing fire effects (Malanson 1984). For example, in garrique vegetation in southern France, even short fire rotation periods (as low as three years) result in few species disappearing, because most species are sprouters (Trabaud and Lepart 1981). Fire in this situation was not consider a severe ecological disturbance.

Sprouting species have an initial postburn recovery advantage over many species that depend on regeneration from seed . In high frequency fire regimes they will tend to dominate, though there are trade-offs. Given a long enough fire-free interval the seeders can equal or surpass sprouters in biomass accumulations (Keeley and Zedler 1978). This is a result of the biomass allocation patterns of the these two life-history strategies, with the sprouters having a high ratio of biomass allocated below ground relative to seeders (Johnson et al. 1986). This is important in understanding and interpreting the effects of fire frequency on these two regeneration strategies and indicates a strong advantage for the sprouters in an ecosystem with a high frequency fire regime. While species following each of these life history traits were found in Molino Basin the sprouters dominated the postburn vegetation.

### 6.3 Vegetation Structure - Topography and Fire

Vegetation patterns on the south slope of Santa Catalinas are determined primarily by moisture, strongly influenced by elevation and aspect (Shreve 1915; Whittaker and Niering 1964, 1965). However, Whittaker and Niering (1965) and Niering and Lowe (1984) did suggest the

importance of fire in the development and shaping of these communities and their plant composition but undertook no studies to investigate this hypothesis. My study provided some data and substance to these observations. Species assemblages and distributions on the south slope of the Santa Catalina Mountains would be a result of a host of interacting factors, primarily determined by moisture (the determinant of what species can exist at a location). Secondary factors, that may have strong influences in some situations, would include fire, which would have a role in shaping species composition (dominance of particular species) and distributions locally, in addition to soil or substrate. These may be viewed as ultimate versus proximal factors. Fire effects on a plant assemblage may act as an overlay to that produced by the moisture gradient and must be considered as an additional factor that must be accounted for in explaining plant community structure and distribution. Its role may vary from negligible to extremely important depending on the specific setting. In the case of Molino Basin, most species on the study site were present in both burned and unburned plots but abundances differed. Species common following the fire were often uncommon in unburned areas while in other cases species common in some unburned areas (*Haplopappus laricifolius*) were nearly absent from burned areas because they were severely impacted by the fire.

In addition to the importance of fire's presence and frequency in affecting community structure (see previous discussion), is the distribution of fire frequencies or fire return intervals (with frequency defined as how often an area burns, not how often fire starts occur) over the landscape, which is influenced by biological, climatic, and topographic factors. The distribution of lightning ignitions over the landscape has been used as an indicator of fire frequency at differing topographic positions, but it may be an inappropriate measure/recorder, particularly since fire suppression has begun. Fire starts do not necessarily equate with fire spread or

frequency patterns on the landscape. Lightning ignitions may be more common at one elevation but the plant community may be less flammable than a community at a different elevation where ignitions may be less frequent but which may have a greater fire spread probability. Thus, there may not be a continuous distribution of fire events across an elevation gradient or particular landscape.

With these varying influences in mind, I would hypothesize that prior to fire suppression there would have been spatial variations in fire frequencies over the south slope of the Santa Catalina Mountains that would have shown a certain distributional pattern. This pattern might have also applied to other areas in southeastern Arizona as well. Fire would have been rare in lower elevation sonoran desert communities inhabited by many species intolerant of fire, such as giant saguaro, cholla cactus, and palo verde (Rogers 1985, 1986; Phillips 1992; McLaughlin and Bowers 1982). Frequency would then have increased into semi-desert grassland and open oak woodland where one peak in the distribution would occur. Many fire tolerant and sprouting species occur in these biomes. In the transition zone between semi-desert grassland and upper Sonoran desert scrub, fire may act as a factor, in addition to temperature, that could limit the occurrence of saguaro cactus and other desert vegetation at some higher elevational sites. Conversely, the lack of fire may play a role in the upward expansion of desert species. In open oak woodland, Mexican blue oak is common and appears more resistant to fire than Emory oak (Caprio and Zwolinski 1992). As plant composition shifts to more closed canopy woodland and pygmy-conifer oak woodland, fire frequency would decrease. Pygmy-conifer oak woodland has a high abundance of piñon pine and juniper (alligator and one-seed) which are generally intolerant of fire, although alligator juniper has some ability to sprout after being burned. At higher, and at some sites intermixed with the oak woodland vegetation, is interior chaparral.

Dominant species include *Arctostaphylos* spp., junipers, piñons, and species generally intolerant of fire. The *Arctostaphylos* spp. must regenerate via seed and though the seeds are stimulated to germinate by fire, frequent burning could eliminate this species by not allowing soil seed pools to become established, destroying plants prior to maturity (seed production age) or to an age when seed pools are great enough to maintain a viable population level. At other sites, oak woodland grades into pine-oak woodland which would have a high fire frequency. Both chaparral and pine-oak woodlands grade into pine forest which generally has a high fire frequency, with a MFI as short as three years (Baisan 1990). Pine forest, at some sites, may develop into mixed conifer if fire frequencies are low.

Fire in southeastern Arizona can be viewed as an additional overlay to the topographical, soil, and moisture gradients that exist. The studies by Shreve (1915) and Whittaker and Niering (1964, 1965) primarily describe vegetation patterns on an elevational gradient due to geomorphic attributes. However, the relationship between fire and these attributes is intricate because the fire gradient over the landscape is not unidirectional being influenced by geomorphic, biotic, weather, and climatic factors. Taken together these combined processes may produce a more complex pattern of spatial variation in the vegetation, creating a highly diverse mosaic. This provides a more dynamic, process orientated view of vegetation patterns in Madrean oak woodlands.

## MANAGEMENT IMPLICATIONS

As both stewards and utilizers of the many resources in Madrean oak woodland we have come to appreciate and desire certain attributes about the landscape, such as an open grassy character to the vegetation, while disliking the encroachment of woody vegetation for both aesthetic and economic reasons. However, lack of fire in woodland vegetation, as found in Molino Basin, has led to an expansion of woody plants, particularly shrubs, with decreases in perennial herbaceous species. This has also been observed in other similar biotic communities, such as the Chihuahuan Desert (Ahlstrand 1982) and in Mediterranean ecosystems (Trabaud 1991). As I observed in Molino Basin, these changes are eventually manifested as more exposed soil and an increased number and size of shrubs. With time, I expect the vegetation in the woodland to acquire more attributes of interior chaparral. Coincidental with these changes in the vegetation is a change in the dynamics of the fire regime. As fire frequency decreases, due to shifts in fuel characteristics, ignition points, and spread patterns, the fires that do occur may be of increased intensity. This could result in more severe fires that replace tree stands and produce an increasing dominance of rapidly establishing or resprouting shrub species. This would also produce a visually less attractive landscape with a greater dominance of shrubs and sparsely vegetated intershrub areas. Conversely, episodic fires would maintain or decrease the number of shrubs while maintaining or increasing the dominance of herbaceous species which would increase the frequency of lower intensity fires as flashy fuels are maintained. My study indicated the continued occurrence of episodic fire in Madrean woodlands may be important for maintaining the vegetation in a state that could be considered "healthy". It also indicated that fires may have occurred at frequent intervals in the past (5-20 years) and that woodlands may have provided a connection for fire spread to-or-from semidesert grasslands into-or-from upper



elevational forests (such as ponderosa pine) while maintaining their integrity. This supports a hypothesis that large spreading fires in southeastern Arizona frequently originated in lower elevation grassland areas and carried into the mountains, allowing for very synchronous fire occurrence over large areas. However, it also makes apparent that a great deal more research on fire in oak woodlands is needed, particularly on seasonality and frequency of burns, on the effects of burning under differing climatic conditions, and on long-term plant species dynamics and demographics under a regime of repeated fires.

## CONCLUSIONS

This study provided a framework for understanding fire effects in Madrean oak woodland of southeastern Arizona and related these to fire effects observed in nearby associated plant communities. The data also provided quantitative information on the structure and dynamics of the woodland in relation to fire. It showed that there were a variety of species specific effects and responses to fire's impact. This knowledge about individual species response will be of value in making predictions about vegetation responses to burning in the woodland, both in the context of historical effects and for management decisions involving prescribed burns, although many questions about fire's role in the woodland remain unanswered.

The analysis of fire effects on 21 major species within the woodland showed that species varied from being intolerant to strongly favored by fire. A higher proportion of tolerant species were herbaceous, relative to woody. The overall effect of the burn in Molino Basin was to cause shifts in species composition between burned and unburned areas, with the north slope sustaining the greatest change. Persistent sprouting species were most responsible for rapid vegetation recovery on the south slope, which had an open savanna character. However, while composition shifted, the actual number of species in any burned or unburned site remained nearly equivalent. Generally, species that were present in unburned areas were also present in burned areas. The fire increased the dominance (cover, density, and biomass) of herbaceous species, particularly graminoids, at the expense of woody species and *Selaginella*. Live and standing dead biomass in burned areas generally exceeded unburned areas one year postburn while litter and total biomass recovered to near preburn levels by three-years postburn. These findings support the concept that *"post-burn community composition is predicted by pre-burn vegetation to a large degree through the adaptations and predictable responses of the most important species to fire"* (Rego et al. 1991).

The burn in Molino Basin was not a 'catastrophic' disturbance (Harper 1977) to most individuals in this woodland, but its occurrence should be viewed as an episodic feature of the ecosystem. Historic fire frequencies were apparently high enough that burns would have occurred during the life-span of most woodland species. Since fire occurred repeatedly within the 'evolutionary memory' of most species (Whelan 1986; Malanson 1987), it should be expected that many have developed adaptations and tolerances to this disturbance (Naveh 1975). However, these responses would be individualistic for each species, allowing repeated burns and varying fire intervals to have strong influences on woodland dynamics. The postburn regeneration that I observed within the woodland was related to the past predictability, frequency and severity of fire, or taken together, as its fire history. Because of the varied selective influences of fire effects and species specific postburn responses, on the short-term fire would play a major role in regulating features of this community such as composition and distribution.

Evidence suggests that in the past, fire in oak woodland played an important role in species distributions, at least on the local scale, although its effects were undoubtedly subject to influences and interactions with such factors as climate, topography, moisture, temperature, and soils. Over the long-term there would have been feedbacks between fire and these latter factors, in addition to the potential vegetation that could exist on a site, and the type of fire regime that this vegetation could support. The effect of fire exclusion or reduction in frequency since about 1880, in combination with grazing pressure and possible climate change, has been to disrupt the dynamic interchange and state among these interacting factors, resulting in a vegetation assemblage that is most likely undergoing changes toward a new dynamic state. These observations suggest that the most obvious changes would be the expansion or increase of woody species - oaks, juniper, piñon, and manzanita - in woodland and semi-desert grassland.

**Appendix A.** Cover data for bare ground and litter.

Mean and standard deviation of (%) cover for bare ground and litter from physical data for each of the four sample periods (S=south slope, E=east slope, N=north slope).

		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Percent Cover									
<i>Bare Ground</i>									
S	Unburned	18.44	4.13	12.96	7.20	9.55	4.70	15.03	2.72
	Burned	20.88	4.76	17.79	0.49	18.39	0.97	14.66	2.91
E	Unburned	18.43	10.26	18.76	6.31	23.36	7.30	20.14	7.96
	Burned	22.11	4.31	7.76	3.39	8.34	3.83	8.44	3.01
N	Unburned	15.58	4.34	16.89	8.19	18.10	12.96	14.93	7.59
	Burned	27.67	16.66	14.85	9.64	13.62	4.21	13.99	7.08
<i>Litter</i>									
S	Unburned	32.34	2.50	24.88	1.51	35.97	8.25	30.10	10.14
	Burned	22.23	5.18	20.69	0.32	30.91	5.79	39.58	0.85
E	Unburned	37.55	4.09	25.93	2.45	35.51	4.68	32.14	3.34
	Burned	16.50	1.25	21.61	5.03	29.81	2.46	34.79	4.72
N	Unburned	39.63	6.48	32.77	8.50	35.14	11.67	33.69	13.24
	Burned	12.39	1.04	15.76	2.38	29.69	9.33	30.31	8.99

**Appendix B.** Seasonal differences in cover for bare ground and litter.

Mean and standard deviation for differences in cover (%) by seasonal sample periods for bare ground and litter.

Site	Unburned				Burned			
	Spring		Fall		Spring		Fall	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Percent Cover								
<b><i>Bare Ground</i></b>								
S	-8.89	5.75	2.07	5.06	-2.49	5.21	-3.12	3.27
E	4.92	2.95	1.37	2.09	-13.77	2.84	0.68	0.38
N	2.52	9.03	-1.95	2.14	-14.04	13.23	-0.86	14.15
<b><i>Litter</i></b>								
S	3.62	8.61	5.22	9.61	8.68	6.18	18.89	1.03
E	-2.04	8.46	6.21	2.51	13.31	2.33	13.18	8.80
N	-4.49	7.33	0.91	5.09	17.29	8.44	14.55	11.35

**Appendix C. Summed biomass data.**

Mean and standard deviation of biomass data for all species summed into categories. Data from burned and unburned plots is presented for the four sample periods at the three sites (S=south slope, E=east slope, N=north slope).

Category	Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
	g · m <sup>-2</sup>							
<i>Live Biomass</i>								
S Unburned	31.1	12.9	51.0	11.8	36.3	19.1	54.0	21.9
Burned	42.9	23.4	70.8	31.4	46.6	10.3	70.0	5.7
E Unburned	27.8	12.7	54.8	32.8	39.1	24.2	57.2	20.6
Burned	74.8	13.4	98.7	48.1	52.8	8.2	84.1	17.9
N Unburned	61.5	14.4	71.4	39.0	37.0	16.8	83.0	40.3
Burned	53.1	13.1	90.5	13.8	37.9	6.4	54.5	24.0
<i>Dead Biomass</i>								
S Unburned	101.52	26.51	87.73	32.58	109.67	29.01	97.55	38.40
Burned	53.37	13.67	92.84	32.92	120.95	50.44	101.86	6.45
E Unburned	47.93	20.13	42.40	15.41	32.76	12.67	53.47	51.6
Burned	38.18	17.50	103.69	25.87	134.37	27.36	140.58	27.94
N Unburned	12.38	11.38	12.39	7.69	15.39	13.25	20.44	13.52
Burned	78.57	16.45	37.94	7.25	49.96	18.84	97.25	47.78
<i>Litter Biomass</i>								
S Unburned	391.5	59.5	157.8	14.5	341.2	116.5	470.7	480.5
Burned	11.2	10.4	41.9	25.4	197.8	245.0	81.2	18.8
E Unburned	235.6	11.6	277.0	32.2	250.2	126.7	375.0	53.9
Burned	35.2	10.8	116.3	64.0	120.6	71.6	145.7	51.4
N Unburned	131.1	58.3	270.6	332.7	100.1	38.8	168.8	74.1
Burned	4.3	1.1	13.8	1.4	52.4	6.9	101.9	86.0
<i>Total Biomass</i>								
S Unburned	524.25	64.60	296.66	21.78	487.31	91.89	622.36	422.61
Burned	107.49	40.26	205.64	16.25	365.50	202.30	253.22	19.45
E Unburned	311.50	24.62	374.22	66.26	322.21	102.48	485.75	57.23
Burned	150.02	16.84	318.84	84.46	307.82	48.91	370.45	42.75
N Unburned	205.28	66.65	354.47	293.84	152.57	46.59	272.28	46.22
Burned	136.06	28.71	142.30	10.56	140.38	23.94	253.74	78.90

**Appendix D. Summed biomass seasonal differences.**

Summed biomass interval differences at the three sites and between burned and unburned treatments (S=south slope, E=east slope, N=north slope).

Site	Unburned				Burned			
	Spring		Fall		Spring		Fall	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
$\text{g} \cdot \text{m}^{-2}$								
<b>Live Biomass</b>								
S	5.2	9.0	3.0	11.7	3.8	17.5	-0.8	32.9
E	11.3	22.9	2.5	14.7	-22.0	21.5	-14.6	34.7
N	-24.6	22.5	11.6	55.0	-15.2	16.6	-36.3	32.6
<b>Dead Biomass</b>								
S	8.15	23.08	9.82	68.36	67.58	38.87	9.02	39.36
E	-15.17	26.67	11.07	28.42	96.18	9.89	36.90	2.35
N	3.02	7.98	-21.71	23.06	-28.61	33.50	59.31	45.19
<b>Litter Biomass</b>								
S	-50.3	176.1	312.9	484.9	186.7	235.7	39.3	9.1
E	14.6	130.4	98.0	81.2	85.4	62.7	29.4	90.5
N	-31.0	32.0	-101.8	386.5	48.1	7.0	88.0	87.3
<b>Total Biomass</b>								
S	-36.94	145.12	325.70	405.51	258.00	199.73	47.58	30.20
E	10.71	126.17	111.53	97.30	157.79	60.40	51.61	124.49
N	-52.71	55.00	-82.19	339.94	4.32	51.47	111.44	73.31

**Appendix E. Cover data summed by major life-form group.**

Mean and standard deviation of cover (%) summed by major life form for each site and treatment for each sample period (S=south slope, E=east slope, N=north slope).

<i>Category</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Percent Cover									
<i>Trees</i>									
S	Unburned	10.93	6.06	9.97	4.98	12.09	5.67	10.53	5.82
	Burned	3.70	3.32	4.90	4.26	5.34	4.65	4.38	3.83
E	Unburned	15.76	8.94	12.63	6.45	16.40	9.42	14.37	7.14
	Burned	5.96	5.64	6.05	5.38	6.43	5.84	5.79	4.18
N	Unburned	15.34	11.22	15.00	11.22	15.43	11.74	15.35	10.87
	Burned	0.85	1.41	1.45	2.14	2.14	2.17	1.83	1.72
<i>Shrubs</i>									
S	Unburned	6.21	8.53	5.71	7.35	7.04	9.59	6.98	9.44
	Burned	0.46	0.49	0.56	0.59	0.78	0.67	0.65	0.56
E	Unburned	10.48	5.49	11.19	6.43	10.96	7.93	10.30	6.44
	Burned	0.45	0.41	0.70	0.76	1.11	0.81	1.15	0.67
N	Unburned	29.59	3.69	25.00	4.40	28.52	3.59	27.32	5.09
	Burned	4.06	1.43	4.45	1.56	4.66	1.09	6.02	0.89
<i>Subshrubs</i>									
S	Unburned	19.29	3.02	21.58	4.09	20.31	2.41	21.05	2.95
	Burned	9.37	3.06	13.13	2.79	11.70	2.65	15.10	7.33
E	Unburned	20.63	4.48	20.13	3.47	19.53	2.00	18.70	4.49
	Burned	3.28	1.66	8.09	6.53	6.28	3.71	12.39	8.39
N	Unburned	17.44	5.82	16.26	6.12	15.34	5.52	18.08	3.98
	Burned	4.21	1.95	8.28	5.22	7.63	3.18	9.41	4.90
<i>Woody</i>									
S	Unburned	36.43	1.86	37.27	4.88	39.45	3.02	38.45	4.13
	Burned	13.54	6.68	18.60	6.73	18.21	8.14	20.14	9.41
E	Unburned	46.73	11.45	43.74	9.73	46.78	9.37	43.21	10.81
	Burned	10.27	5.83	14.84	11.41	14.08	9.35	19.33	11.90
N	Unburned	62.38	9.29	56.15	9.66	59.17	11.18	60.62	12.30
	Burned	9.12	4.05	14.20	7.87	14.44	4.78	17.26	5.94
<i>Forbs</i>									
S	Unburned	11.19	9.29	10.48	9.48	10.96	9.05	4.58	3.31
	Burned	15.97	7.30	12.56	7.52	13.08	7.15	19.85	10.06
E	Unburned	4.01	3.73	4.56	1.76	3.20	1.50	2.94	1.92
	Burned	16.40	2.58	28.27	4.14	18.30	8.16	18.12	4.97
N	Unburned	1.31	0.97	3.30	0.75	4.31	1.36	2.40	2.46
	Burned	16.56	8.83	32.45	13.88	13.78	5.68	21.38	10.45

*Appendix E continued.*

<i>Category</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site Treatment		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Percent Cover									
<i>Perennial Forbs</i>									
S	Unburned	10.02	8.58	10.10	9.29	9.62	8.02	4.39	3.15
	Burned	12.88	5.44	10.89	7.63	10.47	6.49	18.29	9.71
E	Unburned	3.49	3.39	4.29	2.08	3.04	1.70	2.75	2.09
	Burned	15.38	2.14	28.14	4.28	17.78	7.47	17.30	5.82
N	Unburned	1.33	1.01	3.30	0.75	4.28	1.32	1.97	1.88
	Burned	16.12	8.18	32.13	13.37	12.34	6.66	20.53	10.81
<i>Annual Forbs</i>									
S	Unburned	1.16	0.74	0.37	0.34	1.33	1.20	0.18	0.25
	Burned	3.08	2.38	1.86	0.97	2.99	1.08	1.55	0.36
E	Unburned	0.36	0.50	0.05	0.08	0.03	0.04	0.02	0.04
	Burned	1.60	0.55	0.12	0.21	0.77	0.55	0.82	0.85
N	Unburned	0	0	0	0	0.02	0.04	0.43	0.61
	Burned	0.43	0.75	0.31	0.54	1.44	1.09	0.84	0.93
<i>Graminoids</i>									
S	Unburned	19.39	6.67	32.43	5.75	27.12	2.38	40.24	7.12
	Burned	22.16	4.13	43.06	6.52	44.27	7.34	64.69	2.19
E	Unburned	11.55	4.16	17.66	5.38	17.29	3.69	25.75	4.56
	Burned	15.90	3.62	33.65	9.99	27.33	8.09	49.85	11.60
N	Unburned	6.00	2.75	11.49	1.30	8.37	4.19	14.12	1.14
	Burned	8.20	2.01	18.28	3.68	9.91	2.95	26.91	7.13
<i>Perennial Graminoids</i>									
S	Unburned	19.39	6.67	31.60	5.24	27.11	2.38	40.24	7.11
	Burned	21.71	4.20	38.51	10.44	43.33	7.57	64.30	2.18
E	Unburned	11.54	4.15	17.30	4.84	17.28	3.69	25.28	3.75
	Burned	15.08	3.78	30.46	10.20	27.15	8.08	48.35	12.16
N	Unburned	5.55	3.48	9.12	2.78	8.20	4.01	12.34	3.75
	Burned	7.06	2.14	10.36	3.93	9.21	3.49	20.95	6.41
<i>Annual Graminoids</i>									
S	Unburned	0	0	0.82	1.35	0	0	0	0
	Burned	0.44	0.47	4.55	4.06	0.93	0.94	0.38	0
E	Unburned	0	0	0.36	0.56	0	0	0.46	0.80
	Burned	0.81	0.64	3.18	3.63	0.17	0.07	1.49	1.82
N	Unburned	0.44	0.76	2.36	4.08	0.16	0.19	1.77	3.06
	Burned	1.13	1.14	7.91	7.48	0.69	0.59	5.95	7.07



*Appendix E continued.*

<i>Category</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site Treatment		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Percent Cover									
<i>Herbaceous</i>									
S	Unburned	39.33	11.93	49.56	9.21	47.99	7.37	56.41	11.25
	Burned	42.94	8.37	58.64	10.42	59.78	12.08	89.43	8.48
E	Unburned	62.90	10.83	82.41	23.94	84.45	20.90	91.79	17.71
	Burned	40.54	3.62	73.39	15.56	55.86	3.30	82.80	8.95
N	Unburned	87.01	30.84	83.99	40.11	76.17	29.19	86.97	32.53
	Burned	35.04	8.99	66.83	13.91	39.26	10.19	73.91	13.32
<i>Non-Flowering Plants</i>									
S	Unburned	4.37	1.52	3.27	1.29	4.95	2.86	5.79	0.69
	Burned	2.40	1.49	1.41	1.39	1.21	0.71	2.44	2.47
E	Unburned	23.67	4.70	30.09	10.95	31.98	9.41	31.55	8.37
	Burned	4.12	0.09	5.73	0.98	5.11	0.33	7.41	1.10
N	Unburned	39.85	15.14	34.60	20.48	31.74	15.42	35.22	17.23
	Burned	5.13	2.72	8.05	4.63	7.78	5.08	12.81	10.13
<i>Ferns</i>									
S	Unburned	3.31	0.81	2.65	1.24	3.81	2.98	4.75	2.25
	Burned	2.40	1.49	1.41	1.39	1.21	0.71	2.45	2.48
E	Unburned	2.86	1.26	3.44	2.46	2.96	0.55	4.51	1.71
	Burned	2.25	0.65	3.43	0.87	2.76	0.36	4.47	1.59
N	Unburned	13.93	5.48	15.27	10.17	9.48	4.29	10.90	4.61
	Burned	2.04	1.54	2.13	1.75	2.51	1.49	7.51	7.05
<i>Total</i>									
S	Unburned	71.39	9.41	83.45	7.09	82.48	6.66	89.18	10.52
	Burned	54.07	13.30	75.83	18.06	76.77	20.63	107.12	19.56
E	Unburned	85.96	6.72	96.05	4.86	99.25	3.28	103.45	1.53
	Burned	46.68	2.42	82.49	9.02	64.83	6.27	94.71	10.08
N	Unburned	109.57	14.28	105.65	12.80	103.72	13.34	112.50	12.86
	Burned	39.02	13.39	72.97	18.37	45.91	12.30	78.36	4.53

**Appendix F. Cover data summed by major life-form group**

Mean and standard deviation of interval differences between seasons for cover (%) summed by major life-form category (S=south slope, E=east slope, N=north slope).

<i>Category</i>	Unburned				Burned			
	Spring		Fall		Spring		Fall	
<i>Site</i>	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Percent Cover								
<b><i>Trees</i></b>								
S	1.16	0.78	0.55	1.61	1.64	1.46	-0.51	1.04
E	0.64	0.87	1.74	2.04	0.47	0.30	-0.26	1.61
N	0.08	1.89	0.35	0.67	1.29	1.12	0.37	1.11
<b><i>Shrubs</i></b>								
S	0.82	1.06	1.27	2.10	0.31	0.38	0.08	0.27
E	0.48	2.47	-0.89	0.57	0.66	0.44	0.44	0.29
N	-1.07	1.57	2.32	1.52	0.60	0.57	1.56	0.73
<b><i>Subshrubs</i></b>								
S	1.99	1.68	1.83	1.51	1.95	1.69	-0.43	0.77
E	1.12	1.59	0.85	2.01	1.13	0.37	0.18	1.82
N	-0.99	3.31	2.67	1.01	1.89	1.37	1.94	1.82
<b><i>Woody</i></b>								
S	3.02	2.32	1.18	2.66	4.67	1.47	1.54	3.90
E	0.05	3.19	-0.52	1.10	3.82	3.72	4.49	1.63
N	-3.21	4.18	4.47	2.96	5.32	2.16	3.07	2.13
<b><i>Forbs</i></b>								
S	-0.24	6.43	-5.89	7.27	-2.89	5.54	7.09	3.20
E	-0.81	2.78	-1.62	0.84	1.90	6.00	-10.15	8.71
N	3.00	1.48	-0.90	1.09	-2.78	3.79	-11.07	3.98
<b><i>Perennial Forbs</i></b>								
S	-0.40	5.03	-5.70	7.10	-2.41	6.32	7.40	3.60
E	-0.45	2.28	-1.54	0.86	2.40	5.43	-10.84	9.60
N	2.94	1.47	-1.32	1.60	-3.78	2.49	-11.60	2.70
<b><i>Annual Forbs</i></b>								
S	0.16	1.42	-0.19	0.18	-0.09	1.32	-0.31	0.90
E	-0.33	0.53	-0.02	0.04	-0.82	0.89	0.69	0.89
N	0.02	0.04	0.43	0.61	1.00	1.74	0.53	1.40
<b><i>Graminoids</i></b>								
S	7.73	5.22	7.81	11.23	22.11	3.2	21.63	4.53
E	5.74	1.60	8.09	1.37	11.43	4.55	16.20	3.76
N	2.37	2.27	2.63	2.12	1.70	1.51	8.63	4.43

**Appendix F continued.**

<i>Category</i> Site	Unburned				Burned			
	Spring		Fall		Spring		Fall	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Percent Cover								
<b><i>Perennial Graminoids</i></b>								
S	7.72	5.21	8.63	11.41	21.62	3.36	25.79	8.56
E	5.74	1.60	7.98	1.53	12.07	4.66	17.89	2.26
N	2.65	2.16	3.22	1.30	2.15	1.34	10.58	5.95
<b><i>Annual Graminoids</i></b>								
S	0	0	-0.82	1.34	0.48	0.46	-4.16	4.07
E	0	0	0.10	0.24	-0.64	0.72	-1.69	1.81
N	-0.27	0.83	-0.59	1.02	-0.44	0.85	-1.96	1.52
<b><i>Herbaceous</i></b>								
S	8.66	16.67	6.96	12.69	16.84	10.19	30.79	3.56
E	21.55	12.60	9.38	7.12	15.32	1.58	9.42	8.91
N	-10.84	8.74	2.98	14.57	4.22	8.33	7.08	18.72
<b><i>Non-Flowering Plants</i></b>								
S	0.58	3.44	2.52	1.10	-1.19	0.77	1.03	1.13
E	8.31	5.83	1.46	2.94	0.99	0.42	1.68	0.80
N	-8.10	3.36	0.62	5.26	2.65	2.42	3.77	7.89
<b><i>Ferns</i></b>								
S	0.50	3.47	2.10	1.77	-1.19	0.78	1.03	1.14
E	0.10	1.09	1.07	1.86	0.51	0.29	1.04	0.78
N	-4.45	2.11	-4.37	7.17	0.47	0.09	5.38	7.19
<b><i>Total</i></b>								
S	11.09	13.12	5.73	10.49	22.69	10.69	31.29	5.01
E	13.29	9.97	7.40	5.04	18.14	4.59	12.22	9.07
N	-5.85	7.99	6.85	11.54	6.89	7.31	4.40	13.90

**Appendix G.** Cover data for major species.

Mean and standard deviation of cover (%) for major species at the three sites sampled (S=south slope, E=east slope, N=north slope).

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Percent Cover									
<i>Quercus emoryi</i>									
S	Unburned	0.68	1.17	0.57	0.99	0.77	1.33	0.72	1.25
	Burned	0.47	0.8	0.57	0.99	0.40	0.70	0.36	0.62
E	Unburned	9.12	5.59	6.56	3.11	9.77	5.35	8.49	4.39
	Burned	0.47	0.40	0.46	0.48	0.51	0.56	0.85	0.48
N	Unburned	3.59	2.32	3.48	2.56	3.90	2.65	3.67	2.61
	Burned	0.51	0.83	0.83	1.07	1.47	1.46	1.08	0.96
<i>Quercus oblongifolia</i>									
S	Unburned	10.25	5.62	9.40	4.91	11.32	5.35	9.80	5.42
	Burned	3.22	3.22	4.32	3.95	4.93	4.42	4.02	3.48
E	Unburned	6.33	3.48	5.74	3.76	6.31	4.73	5.47	3.22
	Burned	5.49	6.00	5.58	5.86	5.92	6.39	4.93	4.65
N	Unburned	0	0	0	0	0.15	0.27	0.19	0.34
	Burned	0	0	0	0	0.19	0.34	0.21	0.37
<i>Arctostaphylos pungens</i>									
S	Unburned	5.64	8.02	4.87	6.73	6.32	9.16	6.27	9.13
	Burned	0	0	0	0	0	0	0	0
E	Unburned	5.33	4.92	5.87	5.94	6.45	6.68	5.66	4.90
	Burned	0.30	0.52	0.32	0.56	0.46	0.59	0.62	0.57
N	Unburned	4.26	3.55	2.99	3.67	4.03	4.32	4.06	4.08
	Burned	0.91	1.58	0.93	1.61	0.79	1.37	0.93	1.61
<i>Garrya wrightii</i>									
S	Unburned	0.27	0.47	0.30	0.46	0.32	0.56	0.23	0.39
	Burned	0.13	0.23	0.17	0.29	0.27	0.47	0.30	0.51
E	Unburned	3.61	1.02	3.73	1.19	2.77	1.11	2.96	1.28
	Burned	0.03	0.05	0.38	0.33	0.53	0.47	0.52	0.45
N	Unburned	24.53	5.79	21.42	6.51	23.99	5.49	22.57	5.94
	Burned	1.82	0.34	2.05	0.15	2.06	0.52	3.12	0.99
<i>Agave schottii</i>									
S	Unburned	2.64	2.34	2.79	2.69	2.27	2.29	3.13	2.98
	Burned	0.32	0.28	0.44	0.19	0.65	0.43	0.74	0.71
E	Unburned	8.31	2.22	8.44	1.31	7.85	2.05	8.08	2.31
	Burned	0.21	0.36	0.15	0.27	0.36	0.58	0.39	0.68
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0

**Appendix G continued.**

<b>Species</b>		<b>Spring 1984</b>		<b>Fall 1984</b>		<b>Spring 1985</b>		<b>Fall 1985</b>	
<b>Site</b>	<b>Treatment</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>
<b>Percent Cover</b>									
<b><i>Dasyllirion wheeleri</i></b>									
S	Unburned	5.13	1.26	5.07	1.19	5.30	1.67	5.21	1.64
	Burned	0.65	0.57	0.38	0.33	0.38	0.43	0.34	0.60
E	Unburned	5.71	1.88	5.15	2.25	6.43	2.17	6.23	3.33
	Burned	1.31	1.26	1.37	1.22	1.31	1.46	1.92	1.48
N	Unburned	0.82	1.06	1.17	1.11	1.16	1.42	1.48	1.48
	Burned	0.05	0.09	0.39	0.68	0.43	0.74	0.41	0.71
<b><i>Haplopappus laricifolius</i></b>									
S	Unburned	1.18	1.15	1.64	1.06	1.76	1.76	1.99	1.60
	Burned	0	0	0	0	0	0	0	0
E	Unburned	2.90	2.10	2.52	1.68	1.92	1.04	1.62	1.12
	Burned	0.08	0.13	0	0	0.07	0.12	0.05	0.09
N	Unburned	0.56	0.51	0.49	0.62	0.35	0.36	0.71	0.63
	Burned	0	0	0.14	0.12	0.17	0.14	0.25	0.23
<b><i>Nolina microcarpa</i></b>									
S	Unburned	3.50	1.66	2.93	0.70	3.83	1.04	3.18	1.13
	Burned	1.39	1.52	2.17	1.52	2.40	1.46	3.78	0.82
E	Unburned	1.32	2.28	1.28	2.21	1.41	2.44	0.78	1.35
	Burned	0	0	0	0	0	0	0	0
N	Unburned	14.40	5.15	12.28	5.50	12.21	6.19	14.31	4.18
	Burned	1.44	0.33	1.54	0.58	1.61	0.21	1.80	0.44
<b><i>Artemisia ludoviciana</i></b>									
S	Unburned	4.12	5.21	4.66	5.65	3.92	3.52	2.89	2.75
	Burned	1.89	0.95	2.96	3.01	2.83	2.62	6.82	3.03
E	Unburned	0.72	0.86	0.46	0.51	0.49	0.47	0.62	0.77
	Burned	2.85	3.60	6.40	5.96	6.56	6.90	5.83	5.07
N	Unburned	0.67	0.46	1.21	1.06	1.85	1.30	1.07	1.79
	Burned	1.96	1.35	5.29	2.72	3.96	3.66	7.63	2.55
<b><i>Gnaphalium wrightii</i></b>									
S	Unburned	0.03	0.04	0	0	0	0	0.12	0.21
	Burned	0.51	0.69	0.32	0.28	0.23	0.13	0.70	0.48
E	Unburned	0.51	0.76	0.86	1.12	0.05	0.04	0.12	0.21
	Burned	3.97	1.15	12.74	7.44	1.06	0.33	0.30	0.25
N	Unburned	0	0	0.12	0.21	0.08	0.08	0.02	0.04
	Burned	7.77	4.09	15.77	7.52	0.70	1.01	0.53	0.07

## Appendix G continued.

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Percent Cover									
<i>Lotus rigidus</i>									
S	Unburned	4.25	4.37	4.53	3.87	2.84	2.15	0.51	0.69
	Burned	0.81	0.83	2.53	2.35	3.86	3.23	7.47	5.50
E	Unburned	0.78	0.96	1.25	2.16	0.96	1.65	0.87	0.84
	Burned	1.19	0.70	1.26	1.44	2.26	1.10	0.28	0.16
N	Unburned	0.05	0.08	0.05	0.08	0.12	0.21	0	0
	Burned	0.80	1.32	0	0	0.02	0.04	0	0
<i>Andropogon cirratus</i>									
S	Unburned	1.80	1.65	1.96	1.80	1.32	1.43	1.80	1.72
	Burned	0.12	0.21	0	0	0.12	0.21	0.43	0.75
E	Unburned	3.74	1.97	4.05	3.18	5.57	3.07	7.52	3.20
	Burned	1.13	0.67	1.35	0.19	1.76	0.67	5.37	0.51
N	Unburned	0.91	0.33	0.97	0.76	0.74	0.86	1.86	1.44
	Burned	0.58	0.66	2.09	2.56	1.40	2.42	3.81	4.38
<i>Aristida orcuttiana</i>									
S	Unburned	0.89	0.47	1.85	1.69	1.44	0.47	1.60	1.62
	Burned	0	0	0	0	0.25	0.21	0.84	0.79
E	Unburned	1.68	0.89	0.88	0.52	1.61	1.34	2.28	1.98
	Burned	1.65	1.07	2.70	1.72	3.33	1.98	2.61	1.59
N	Unburned	0	0	0.02	0.04	0.12	0.21	0.25	0.43
	Burned	0.15	0.19	0.17	0.19	0	0	0.54	0.87
<i>Bouteloua curtipendula</i>									
S	Unburned	2.21	2.26	3.28	2.49	4.04	3.44	6.11	5.15
	Burned	6.01	2.45	9.60	4.54	12.49	5.88	17.28	7.73
E	Unburned	0.41	0.42	0.51	0.82	0.46	0.51	1.82	1.24
	Burned	1.96	0.71	1.54	1.28	3.73	2.34	4.87	0.59
N	Unburned	0.62	0.67	1.84	1.28	1.73	1.84	2.08	1.62
	Burned	0.30	0.19	0.16	0.21	0.84	0.88	1.71	1.33
<i>Eragrostis intermedia</i>									
S	Unburned	0.38	0	0.72	1.10	0.02	0.04	1.46	1.50
	Burned	2.60	1.92	11.46	5.51	13.29	4.55	17.53	9.18
E	Unburned	0	0	0.31	0.54	0.12	0.21	0.64	1.12
	Burned	3.49	1.21	4.53	3.96	4.35	1.74	5.89	3.96
N	Unburned	0	0	0.40	0.41	0.34	0.53	0.84	0.73
	Burned	1.51	1.17	1.01	0.47	2.31	0.97	4.20	2.26

**Appendix G continued.**

<b>Species</b>		<b>Spring 1984</b>		<b>Fall 1984</b>		<b>Spring 1985</b>		<b>Fall 1985</b>	
<b>Site</b>	<b>Treatment</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>
<b>Percent Cover</b>									
<b><i>Heteropogon contortus</i></b>									
S	Unburned	0.13	0.21	0.80	0.60	0.95	0.98	0.30	0.19
	Burned	0.36	0.56	0.15	0.20	0	0	1.89	2.08
E	Unburned	0.58	0.65	0.80	0.48	1.10	0.88	2.08	1.23
	Burned	2.21	1.33	4.68	3.96	2.67	2.24	6.62	4.03
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0
<b><i>Muhlenbergia emersleyi</i></b>									
S	Unburned	9.99	3.97	15.17	4.90	14.23	4.47	20.37	2.17
	Burned	3.44	3.54	3.69	2.37	4.60	3.32	5.59	5.04
E	Unburned	2.52	2.32	3.44	3.95	3.05	4.58	4.95	4.79
	Burned	3.41	1.73	10.43	4.40	8.30	3.63	16.05	6.34
N	Unburned	1.22	1.16	0.37	0.37	1.23	1.17	1.63	1.63
	Burned	2.81	0.84	4.50	0.60	2.62	1.56	7.94	3.99
<b><i>Trachypogon secundus</i></b>									
S	Unburned	1.66	2.88	3.33	4.12	1.90	1.95	2.82	3.80
	Burned	0	0	0.12	0.21	0.34	0.52	0.81	1.40
E	Unburned	2.42	1.58	6.42	4.40	4.46	2.76	4.76	3.77
	Burned	1.09	0.32	4.34	0.85	2.79	1.64	4.54	2.82
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0
<b><i>Aristida adscensionis</i></b>									
S	Unburned	0	0	0.03	0.05	0	0	0	0
	Burned	0	0	1.99	1.43	0	0	0	0
E	Unburned	0	0	0.33	0.58	0	0	0.46	0.80
	Burned	0	0	0.31	0.45	0	0	0.15	0.20
N	Unburned	0	0	2.18	3.77	0	0	1.49	2.58
	Burned	0	0	3.78	6.04	0	0	3.63	5.57
<b><i>Cheilanthes wootoni</i></b>									
S	Unburned	2.15	0.40	1.68	0.28	1.55	0.97	2.00	0.27
	Burned	0.97	0.51	0	0	0.32	0.15	0.74	0.56
E	Unburned	2.48	1.01	1.79	0.63	2.70	0.34	3.39	2.22
	Burned	1.84	0.61	2.92	0.98	2.37	0.39	2.97	0.74
N	Unburned	3.82	2.63	2.75	2.45	2.12	2.11	1.96	1.57
	Burned	1.66	1.32	1.89	1.42	1.17	1.02	2.41	1.76

**Appendix G continued.**

<b>Species</b>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
<b>Site</b>	<b>Treatment</b>	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Percent Cover									
<b><i>Selaginella rupicola</i></b>									
S	Unburned	1.06	1.84	0.62	1.08	1.14	1.98	1.04	1.80
	Burned	0	0	0	0	0	0	0	0
E	Unburned	20.81	5.69	26.65	10.10	29.02	9.80	27.04	9.38
	Burned	1.87	0.72	2.30	0.11	2.36	0.14	2.94	1.40
N	Unburned	25.92	9.67	19.33	10.41	22.26	11.24	24.32	12.99
	Burned	3.09	1.87	5.92	3.72	5.27	4.23	4.31	4.40



**Appendix H.** Seasonal differences in cover data by major species.

Mean and standard deviation of cover by major species for seasonal differences for the three sites sampled (S=south slope, E=east slope, N=north slope).

<i>Species</i>	Unburned				Burned			
	Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Mean	SD	Mean	SFD	Mean	SD	Mean	SD
Frequency								
<i>Quercus emoryi</i>								
S	0.09	0.15	0.15	0.25	-0.06	0.11	-0.21	0.36
E	0.65	1.34	1.93	1.44	0.04	0.38	0.39	0.07
N	0.31	0.89	0.18	0.12	0.95	0.82	0.25	0.63
<i>Quercus oblongifolia</i>								
S	1.07	0.94	0.40	1.36	1.71	1.54	-0.30	1.29
E	-0.02	1.26	-0.27	0.75	0.43	0.39	-0.65	1.56
N	0.15	0.27	0.19	0.34	0.19	0.34	0.21	0.37
<i>Arcostaphylos pungens</i>								
S	0.68	1.13	1.40	2.42	0	0	0	0
E	1.12	2.17	-0.20	1.37	0.16	0.14	0.30	0.39
N	-0.23	0.78	1.07	1.04	-0.12	0.20	0	0
<i>Garrya wrightii</i>								
S	0.05	0.09	-0.07	0.07	0.14	0.24	0.13	0.22
E	-0.83	0.83	-0.76	0.61	0.50	0.46	0.14	0.13
N	-0.54	0.49	1.14	0.94	0.23	0.18	1.07	1.13
<i>Agave schottii</i>								
S	-0.37	0.56	0.33	0.36	0.32	0.27	0.30	0.53
E	-0.46	0.84	-0.35	1.40	0.15	0.21	0.23	0.40
N	0	0	0	0	0	0	0	0
<i>Dasyllirion wheeleri</i>								
S	0.16	0.43	0.13	1.18	-0.26	0.72	-0.03	0.56
E	0.72	0.59	1.07	1.96	0	0	0.55	0.72
N	0.34	0.44	0.31	0.37	0.37	0.64	0.01	0.02
<i>Haplopappus laricifolius</i>								
S	0.58	0.61	0.34	0.65	0	0	0	0
E	-0.98	1.24	-0.90	1.43	-0.01	0.01	0.05	0.09
N	-0.22	0.19	0.22	0.56	0.17	0.14	0.11	0.13
<i>Nolina microcarpa</i>								
S	0.33	0.66	0.25	0.60	1.00	1.37	1.61	1.78
E	0.09	0.15	-0.50	0.86	0	0	0	0
N	-2.18	1.70	2.02	1.78	0.16	0.39	0.26	0.23

**Appendix H continued.**

Appendix 12 continued.								
	Unburned				Burned			
<i>Species</i>	Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Mean	SD	Mean	SD	Mean	SD	Mean	SD
	Frequency							
<i>Artemisia ludoviciana</i>								
S	-0.20	2.87	-1.76	3.20	0.94	2.05	3.86	3.20
E	-0.23	0.87	0.16	0.28	3.70	3.30	-0.57	1.49
N	1.17	0.91	-0.13	0.78	2.00	2.44	2.33	0.37
<i>Aristida orcutatia</i>								
S	0.55	0.10	-0.24	0.30	0.25	0.21	0.84	0.79
E	-0.07	0.45	1.40	1.47	1.68	1.18	-0.09	1.64
N	0.12	0.21	0.22	0.38	-0.15	0.19	0.37	0.91
<i>Bouteloua curtipendula</i>								
S	1.83	2.53	2.83	3.18	6.48	3.62	7.68	4.31
E	0.05	0.54	1.31	0.42	1.76	2.47	3.33	0.69
N	1.10	1.23	0.23	0.44	0.54	0.92	1.55	1.12
<i>Eragrostis intermedia</i>								
S	-0.35	0.04	0.74	1.82	10.69	4.19	6.07	6.27
E	0.12	0.21	0.33	0.57	0.85	1.16	1.36	1.56
N	0.34	0.53	0.43	0.43	0.79	0.25	3.19	1.81
<i>Heteropogon contortus</i>								
S	0.81	0.77	-0.49	0.57	-0.36	0.56	1.74	1.88
E	0.52	1.02	1.28	0.85	0.46	0.90	1.93	1.78
N	0	0	0	0	0	0	0	0
<i>Muhlenbergia emersleyi</i>								
S	4.24	2.19	5.20	4.85	1.16	0.34	1.90	3.35
E	0.53	2.57	1.50	0.86	4.89	2.24	5.62	2.05
N	0.01	0.52	1.25	1.25	-0.18	1.15	3.44	3.39
<i>Trachypogon secundus</i>								
S	0.24	1.27	-0.50	1.29	0.34	0.52	0.68	1.18
E	2.04	1.39	-1.66	0.75	1.70	1.37	0.20	2.07
N	0	0	0	0	0	0	0	0
<i>Aristida adscensionis</i>								
S	0	0	-0.03	0.05	0	0	-1.99	1.44
E	0	0	0.12	0.21	0	0	-0.15	0.26
N	0	0	-0.68	1.18	0	0	-0.15	0.48

**Appendix H** *continued.*

<i>Species</i>	Unburned				Burned			
	Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Frequency								
<i>Cheilanthes wootoni</i>								
S	-0.60	1.17	0.32	0.46	-0.64	0.60	0.74	0.56
E	0.22	1.15	1.60	1.63	0.53	0.34	0.05	0.24
N	-1.70	0.67	-0.78	2.72	-0.48	0.34	0.51	1.50
<i>Selaginella rupincola</i>								
S	0.08	0.14	0.41	0.72	0	0	0	0
E	8.21	4.78	0.39	1.09	0.49	0.69	0.64	1.46
N	-3.65	2.40	4.99	2.58	2.18	2.40	-0.62	1.36

# Appendix I. Density data for major species.

Mean and standard deviation of density data for major species, giving number of plants per hectare for woody species and number per square meter for herbaceous species. Data is given for burned and unburned areas of the south slope (S), east slope (E), and north slope (N).

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Number · ha <sup>-1</sup>									
<i>Quercus emeryi</i>									
S	Unburned	15	13	15	13	7	13	7	13
	Burned	15	26	15	26	15	26	7	13
E	Unburned	81	46	104	46	126	64	96	71
	Burned	7	13	30	13	52	34	22	22
N	Unburned	104	46	126	56	111	59	104	13
	Burned	22	22	74	56	89	59	81	46
<i>Quercus oblongifolia</i>									
S	Unburned	59	34	89	67	89	67	89	39
	Burned	81	78	104	112	111	102	59	56
E	Unburned	111	44	74	13	104	13	111	38
	Burned	59	51	81	78	89	89	67	59
N	Unburned	7	13	7	13	7	13	7	13
	Burned	15	13	15	13	15	13	15	13
<i>Arctostaphylos pungens</i>									
S	Unburned	178	289	348	546	400	693	348	528
	Burned	0	0	0	0	0	0	0	0
E	Unburned	274	379	318	344	400	521	363	477
	Burned	22	22	7	13	22	22	30	34
N	Unburned	96	167	81	122	119	151	163	189
	Burned	67	115	96	167	104	180	170	295
<i>Garrya wrightii</i>									
S	Unburned	22	22	22	22	15	13	22	22
	Burned	22	38	15	26	15	26	15	26
E	Unburned	67	38	52	26	67	44	81	56
	Burned	74	71	81	46	59	64	67	44
N	Unburned	1000	226	792	68	978	357	1141	245
	Burned	274	56	326	112	311	59	185	13
<i>Agave schottii</i>									
S	Unburned	12844	8827	9377	6653	8933	5600	13466	10676
	Burned	2978	1897	1867	933	2222	1426	2667	2117
E	Unburned	13556	10331	16222	7795	19778	7974	17689	4097
	Burned	533	923	439	947	444	770	444	770
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0

**Appendix I continued.**

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Number · ha <sup>-1</sup>									
<i>Dasyllirion wheeleri</i>									
S	Unburned	533	231	533	231	533	352	444	204
	Burned	133	133	89	154	89	154	133	133
E	Unburned	1156	429	1244	734	1111	504	844	468
	Burned	711	308	578	204	577	204	444	278
N	Unburned	178	77	178	77	133	133	178	77
	Burned	89	77	89	77	89	77	89	154
<i>Haplopappus laricifolius</i>									
S	Unburned	1378	734	1556	908	1689	781	1644	964
	Burned	400	693	89	154	222	385	267	462
E	Unburned	1200	933	1111	868	1289	1069	1022	601
	Burned	0	0	0	0	44	77	0	0
N	Unburned	222	77	311	154	267	133	222	77
	Burned	133	231	133	133	178	154	133	231
<i>Nolino microcarpa</i>									
S	Unburned	89	77	0	0	44	77	178	77
	Burned	222	154	356	204	133	0	178	204
E	Unburned	89	154	133	231	89	154	133	231
	Burned	0	0	0	0	0	0	0	0
N	Unburned	1289	468	1100	601	711	278	933	481
	Burned	489	734	589	505	400	581	356	278
Number · m <sup>-2</sup>									
<i>Artemisia ludoviciana</i>									
S	Unburned	2.59	2.77	1.50	1.64	4.00	3.68	1.25	1.25
	Burned	1.50	0.66	0.42	0.38	2.25	1.89	1.33	0.38
E	Unburned	0.58	0.58	0.17	0.14	0.75	0.66	0.58	0.63
	Burned	2.33	3.18	1.92	1.51	4.83	5.13	1.58	1.70
N	Unburned	1.67	1.42	1.25	1.30	2.00	2.29	1.25	1.32
	Burned	4.00	2.22	2.08	1.13	4.17	2.63	2.33	1.53
<i>Gnaphalium wrightii</i>									
S	Unburned	0	0	0	0	0	0	0.08	0.14
	Burned	0.50	0.25	0.25	0.25	2.00	1.56	1.42	0.87
E	Unburned	0.58	0.52	0.33	0.58	1.42	1.66	0	0
	Burned	4.75	0.90	3.58	1.61	1.25	0.25	1.00	1.32
N	Unburned	0.10	0.14	0.17	0.14	0.50	0.50	0	0
	Burned	7.05	2.25	4.42	2.67	0.42	0.14	3.00	2.18

## Appendix I continued.

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Number · m <sup>-2</sup>									
<i>Lotus rigidus</i>									
S	Unburned	0.83	0.80	0.67	0.63	0.58	0.63	0.25	0.25
	Burned	0.67	0.63	0.33	0.38	0.50	0.25	0.75	0.66
E	Unburned	0.25	0.25	0.25	0.43	0.17	0.29	0.25	0.25
	Burned	0.58	0.14	0.25	0.25	0.50	0.25	0.17	0.14
N	Unburned	0.17	0.14	0.17	0.29	0.08	0.14	0	0
	Burned	0.50	0.66	0	0	0.08	0.14	0	0
<i>Andropogon cirratus</i>									
S	Unburned	1.92	0.58	1.25	1.25	0.92	0.88	1.08	0.95
	Burned	0.17	0.29	0	0	0.08	0.14	0.17	0.29
E	Unburned	3.92	2.74	3.08	2.13	3.42	2.40	3.50	2.46
	Burned	0.83	0.63	0.50	0.25	1.17	0.29	1.50	0.50
N	Unburned	0.92	0.80	0.33	0.38	0.67	0.63	0.42	0.52
	Burned	0.58	0.63	0.92	1.59	0.75	1.09	1.25	1.09
<i>Aristida orcuttiana</i>									
S	Unburned	0.42	0.14	1.00	1.15	0.75	0.43	0.50	0.66
	Burned	0	0	0	0	0.17	0.14	0.08	0.14
E	Unburned	0.92	0.52	1.25	0.66	0.67	0.14	0.75	0.75
	Burned	1.25	0.66	1.92	1.26	1.67	1.01	7.92	12.63
N	Unburned	0	0	0.08	0.14	0.08	0.14	0.17	0.29
	Burned	0.08	0.14	0.17	0.14	0	0	0.08	0.14
<i>Bouteloua curtipendula</i>									
S	Unburned	1.50	1.15	2.67	1.84	2.83	2.04	2.92	3.00
	Burned	4.42	1.28	4.00	1.39	3.75	1.98	6.25	2.38
E	Unburned	0.58	0.80	0.25	0.43	0.17	0.14	0.67	0.63
	Burned	1.67	0.38	1.42	0.38	2.00	1.52	1.83	1.15
N	Unburned	0.58	0.38	1.42	0.80	1.25	1.00	1.00	0.25
	Burned	0.67	0.38	0.17	0.14	0.50	0.43	0.75	0.50
<i>Eragrostis intermedia</i>									
S	Unburned	0.42	0.29	1.25	1.75	0	0	0.67	0.76
	Burned	3.33	2.31	9.17	5.64	4.42	2.57	6.17	3.51
E	Unburned	0	0	0.33	0.58	0.33	0.58	0.17	0.29
	Burned	1.50	1.32	2.25	2.84	1.17	1.01	1.67	2.04
N	Unburned	0	0	0.25	0.25	0.17	0.29	0.25	0.25
	Burned	2.42	2.24	0.58	0.14	1.33	0.80	2.08	1.88

## Appendix I continued.

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Number · m <sup>2</sup>									
<i>Heteropogon contortus</i>									
S	Unburned	0.75	0.66	0.50	0.25	0.75	0.66	0.25	0
	Burned	0	0	0	0	0	0	0.42	0.52
E	Unburned	0.75	0.66	0.50	0.25	1.50	1.56	1.92	1.13
	Burned	2.58	1.44	3.92	3.64	2.08	2.13	3.17	2.63
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0
<i>Muhlenbergia emersleyi</i>									
S	Unburned	5.00	1.95	5.08	2.02	5.33	1.18	5.17	0.88
	Burned	0.92	0.95	0.75	0.43	1.08	1.23	1.42	0.58
E	Unburned	0.67	0.72	0.83	1.01	1.17	1.42	0.92	1.15
	Burned	2.58	2.02	3.17	2.04	2.33	1.94	3.00	1.50
N	Unburned	0.50	0.50	0.25	0.25	0.25	0.43	0.42	0.38
	Burned	2.50	0.25	1.43	1.01	1.17	0.52	1.58	0.14
<i>Trachypogon secundus</i>									
S	Unburned	0.92	1.59	1.33	1.89	0.92	1.18	1.08	1.46
	Burned	0	0	0	0	0.17	0.14	0.08	0.14
E	Unburned	1.83	2.10	2.25	2.17	2.17	1.38	0.83	0.76
	Burned	0.67	0.52	0.92	0.52	0.58	0.38	0.50	0.25
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0
<i>Aristida adscensionis</i>									
S	Unburned	0	0	0.17	0.29	0	0	0	0
	Burned	0	0	2.42	1.23	0	0	0.08	0.14
E	Unburned	0	0	1.75	3.03	0	0	5.25	9.09
	Burned	0	0	0.33	0.58	0	0	0.25	0.25
N	Unburned	0	0	5.50	9.53	0	0	3.17	5.48
	Burned	0	0	11.58	18.78	0	0	6.42	10.26
<i>Cheilanthes wootoni</i>									
S	Unburned	2.50	1.32	1.33	1.46	0.92	0.52	0.50	0.00
	Burned	1.75	1.15	0.67	0.52	0.42	0.14	0.25	0.43
E	Unburned	0.42	0.38	0.25	0.25	1.33	0.38	1.00	0.66
	Burned	0.67	0.38	1.67	0.52	2.50	0.25	2.25	0.25
N	Unburned	2.25	0.75	1.42	2.04	1.17	1.13	1.58	1.38
	Burned	0.08	0.14	1.83	1.38	0.75	0.66	0.92	0.80

**Appendix I continued.**

<b>Species</b>		<b>Spring 1984</b>		<b>Fall 1984</b>		<b>Spring 1985</b>		<b>Fall 1985</b>	
<b>Site</b>	<b>Treatment</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>
<b>Number · m<sup>-2</sup></b>									
<b><i>Selaginella rupincola</i></b>									
S	Unburned	0.33	0.58	0.17	0.29	0.25	0.43	0.25	0.43
	Burned	0	0	0	0	0	0	0	0
E	Unburned	8.27	1.12	7.58	1.66	7.83	1.42	7.50	1.80
	Burned	2.00	0.66	2.17	0.38	1.83	0.38	1.75	0.00
N	Unburned	6.08	2.13	5.58	2.32	5.92	1.88	5.83	2.01
	Burned	2.58	1.77	2.67	1.81	2.92	2.02	3.17	2.24



**Appendix J. Seasonal differences of density data major species.**

Mean and standard deviation for seasonal differences of density data for major species in burned and unburned areas at the three sites (S=south slope, E=east, N=north).

	Unburned				Burned			
<i>Species</i>	Spring		Fall		Spring		Fall	
Site	Mean	SD	Mean	SD	Mean	SD	Mean	SD
	Number · ha <sup>-1</sup>							
<i>Quercus emoryi</i>								
S	-7	13	-7	13	0	0	-7	13
E	44	22	-7	34	44	44	-7	13
N	7	34	-22	44	67	32	7	34
<i>Quercus oblongifolia</i>								
S	30	34	-.03	39	30	26	-44	59
E	-7	34	37	34	30	51	-15	26
N	0	0	0	0	0	0	0	0
<i>Arctostaphylos pungens</i>								
S	222	404	0	22	0	0	0	0
E	126	143	44	135	0	0	22	22
N	22	39	81	68	37	64	74	128
<i>Garrya wrightii</i>								
S	-7	26	0	0	-7	13	0	0
E	0	22	30	34	-15	13	-15	13
N	-22	182	348	210	37	26	-141	114
<i>Agave schottii</i>								
S	-6133	3289	4089	4801	-756	601	800	1272
E	6222	5317	1467	4955	-89	154	-44	77
N	0	0	0	0	0	0	0	0
<i>Dasylirion wheeleri</i>								
S	0	133	-89	77	-44	77	44	77
E	-44	77	-400	266	-133	133	-133	133
N	-44	203	0	0	0	0	0.03	133
<i>Haplopappus laricifolius</i>								
S	311	77	89	154	-178	308	178	308
E	89	154	-89	278	44	77	0	0
N	44	78	89	77	44	204	0	267
<i>Nolina microcarpa</i>								
S	-44	77	178	77	-89	154	-178	204
E	0	0	0	0	0	0	0	0
N	-578	204	-178	154	-89	204	-133	267

**Appendix J continued.**

Appendix 3 continued

Species	Unburned				Burned			
	Spring		Fall		Spring		Fall	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Site	Number · m <sup>-2</sup>							
<i>Artemisia ludoviciana</i>								
S	1.416	1.282	-0.250	0.433	0.750	1.391	0.916	0.144
E	0.166	0.520	0.416	0.520	2.500	1.952	-0.333	1.040
N	0.333	1.376	0	0	0.166	0.763	0.250	1.639
<i>Gnaphalium wrightii</i>								
S	0	0	0.083	0.144	1.500	1.520	1.166	0.629
E	0.833	1.233	-0.333	0.577	-3.500	0.750	-2.583	1.040
N	0.416	0.629	-0.166	0.144	-7.083	2.126	-1.416	4.639
<i>Lotus rigidus</i>								
S	-0.250	1.000	-0.416	0.381	-0.166	0.381	0.416	0.381
E	-0.083	0.144	0	0	-0.083	0.381	-0.083	0.144
N	-0.083	0.144	-0.166	0.288	-0.416	0.520	0	0
<i>Andropogon cirratus</i>								
S	-1.000	0.433	-0.166	0.520	-0.083	0.144	0.166	0.288
E	-0.500	0.500	0.416	0.381	0.333	0.878	1.000	0.433
N	-0.250	0.433	0.083	0.144	0.166	0.520	0.333	0.520
<i>Aristida orcuttiana</i>								
S	0.333	0.381	-0.500	0.500	0.166	0.144	0.083	0.144
E	-0.250	0.433	-0.500	0.250	0.416	0.520	6.000	12.847
N	0.083	0.144	0.083	0.144	-0.083	0.144	-0.083	0.144
<i>Bouteloua curtipendula</i>								
S	1.333	0.946	0.250	1.322	-0.666	1.607	2.250	1.639
E	-0.416	0.721	0.416	0.381	0.333	1.527	0.416	0.803
N	0.666	0.803	-0.416	0.577	-0.166	0.763	0.583	0.381
<i>Eragrostis intermedia</i>								
S	-0.416	0.288	-0.583	1.941	1.083	3.818	-3.000	4.867
E	0.333	0.577	-0.166	0.288	-0.333	0.381	-0.583	0.803
N	0.166	0.288	0	0	-1.083	1.464	1.500	1.732
<i>Heteropogon contortus</i>								
S	0	0	-0.250	0.250	0	0	0.416	0.520
E	0.750	1.000	1.416	1.040	-0.500	0.750	-0.750	1.089
N	0	0	0	0	0	0	0	0

**Appendix J continued.**

Appendix 3								
	Unburned				Burned			
<i>Species</i>	Spring		Fall		Spring		Fall	
Site	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Number · m <sup>2</sup>								
<i>Muhlenbergia emersleyi</i>								
S	0.333	0.878	0.083	1.181	0.166	0.288	0.666	0.520
E	0.500	0.750	0.083	0.144	-0.250	0.250	-0.166	0.878
N	-0.250	0.250	0.166	0.629	-1.333	0.629	0.166	0.878
<i>Trachypogon secundus</i>								
S	0	0	-0.250	0.661	0.166	0.144	0.083	0.144
E	0.333	0.763	-1.416	1.664	-0.083	0.288	-0.416	0.629
N	0	0	0	0	0	0	0	0
<i>Aristida adscensionis</i>								
S	0	0	-0.166	0.288	0	0	-2.333	1.154
E	0	0	3.500	6.062	0	0	-0.083	0.381
N	0	0	-2.333	4.041	0	0	-7.750	10.253
<i>Chielanthes wootoni</i>								
S	-1.583	1.626	1.000	1.299	-1.333	1.040	-0.416	0.763
E	0.916	0.577	0.750	0.901	1.833	0.629	0.583	0.520
N	-1.083	1.607	0.166	1.755	0.666	0.577	-0.916	0.629
<i>Selaginella rupincola</i>								
S	-0.083	0.144	0.083	0.144	0	0	0	0
E	-0.433	0.317	-0.083	0.144	-0.166	0.288	-1.000	0.661
N	-0.166	0.288	0.250	0.500	0.333	0.721	0.500	0.433

## Appendix K. Frequency data for major species.

Mean and standard deviation of frequency data for major species. Data has been transformed with an arcsine transformation (S=south slope, E=east slope, N=north slope).

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Frequency									
<i>Quercus emoryi</i>									
S	Unburned	11.68	20.24	23.37	20.24	23.37	20.24	23.37	20.24
	Burned	11.68	20.24	11.68	20.24	11.68	20.24	11.68	20.24
E	Unburned	66.67	38.01	88.67	19.63	88.67	19.63	66.67	33.50
	Burned	22.11	38.01	44.48	19.12	66.33	33.50	44.48	19.12
N	Unburned	67.94	0	78.11	20.59	66.22	20.59	66.62	20.24
	Burned	30.00	27.81	71.68	31.71	78.11	20.59	66.62	20.24
<i>Quercus oblongifolia</i>									
S	Unburned	60.00	27.81	71.68	31.71	59.79	27.87	78.31	20.24
	Burned	48.31	45.36	60.00	51.96	60.00	51.96	60.00	51.96
E	Unburned	60.00	27.81	47.90	11.12	54.33	0.00	54.33	0.00
	Burned	48.31	45.36	60.00	51.96	36.22	31.36	60.00	51.96
N	Unburned	11.68	20.24	11.68	20.24	11.68	20.24	11.68	20.24
	Burned	23.37	20.24	23.37	20.24	23.37	20.24	23.37	20.24
<i>Arctostaphylos pungens</i>									
S	Unburned	41.68	45.36	41.68	45.36	41.68	45.36	48.31	45.36
	Burned	0	0	0	0	0	0	0	0
E	Unburned	60.00	27.81	66.22	20.59	66.22	20.59	54.94	0
	Burned	23.37	20.24	23.37	20.24	23.37	20.24	23.37	20.24
N	Unburned	41.68	45.36	29.79	27.54	41.68	45.36	53.37	31.71
	Burned	18.31	31.71	18.11	31.36	18.11	31.36	18.31	31.71
<i>Garrya wrightii</i>									
S	Unburned	30.00	27.81	23.37	20.24	23.37	20.24	23.37	20.24
	Burned	18.31	31.71	11.68	20.24	11.68	20.24	11.68	20.24
E	Unburned	60.00	27.81	47.90	11.12	59.79	27.87	59.79	27.87
	Burned	60.00	27.81	59.79	27.87	53.37	31.71	48.31	11.47
N	Unburned	90.00	0	90.00	0	90.00	0	90.00	0
	Burned	66.62	20.24	71.68	31.71	78.11	20.59	71.68	31.71
<i>Agave schottii</i>									
S	Unburned	46.92	6.66	46.92	6.66	46.92	6.66	51.14	12.10
	Burned	60.00	26.61	47.30	13.97	47.30	13.97	35.01	7.30
E	Unburned	90.00	0	90.00	0	90.00	0	72.29	15.33
	Burned	16.92	29.31	16.92	29.31	16.92	29.31	13.07	22.64
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0

**Appendix K continued.**

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Frequency									
<i>Dasylium wheeleri</i>									
S	Unburned	42.70	13.97	50.77	0	42.70	13.97	43.08	18.73
	Burned	21.93	20.02	13.07	22.64	13.07	22.64	17.71	15.34
E	Unburned	51.14	12.10	63.44	0	72.29	15.33	59.21	7.31
	Burned	38.85	12.10	43.07	6.66	43.07	6.66	38.85	12.10
N	Unburned	26.57	0	26.57	0	17.71	15.34	26.57	0
	Burned	17.71	15.34	17.71	15.34	17.71	15.34	21.93	20.02
<i>Haplopappus laricifolius</i>									
S	Unburned	64.22	25.39	73.08	29.31	73.08	29.31	60.00	26.61
	Burned	13.08	22.65	9.74	16.88	13.08	22.65	8.86	15.34
E	Unburned	55.37	13.98	55.37	13.98	55.37	13.98	59.22	7.32
	Burned	0	0	0	0	8.86	15.34	0	0
N	Unburned	30.79	7.31	35.01	7.31	35.01	7.31	30.79	7.31
	Burned	13.08	22.65	17.71	15.34	15.34	20.02	17.71	15.34
<i>Nolina microcarpa</i>									
S	Unburned	17.71	15.34	17.71	15.34	17.71	15.34	26.57	0
	Burned	30.79	7.30	34.63	13.97	17.71	15.34	21.93	20.02
E	Unburned	13.07	22.64	16.92	29.31	13.07	22.64	13.07	22.64
	Burned	0	0	0	0	0	0	0	0
N	Unburned	68.07	20.02	60.00	26.61	51.14	12.10	59.21	7.31
	Burned	21.93	20.02	34.63	13.97	34.63	13.97	38.85	12.10
<i>Artemisia ludoviciana</i>									
S	Unburned	18.66	16.98	17.97	16.77	19.83	17.89	16.36	16.61
	Burned	19.19	1.31	20.64	2.17	18.80	5.20	22.74	2.01
E	Unburned	12.21	5.39	6.06	5.25	8.33	7.97	9.18	9.22
	Burned	21.44	7.51	24.12	7.95	24.98	10.36	19.72	11.31
N	Unburned	17.20	5.06	18.05	4.94	20.44	4.42	15.58	8.14
	Burned	26.78	6.91	28.99	7.82	29.68	7.05	29.88	13.20
<i>Gnaphalium wrightii</i>									
S	Unburned	6.06	5.25	0	0	0	0	3.03	5.25
	Burned	11.64	2.20	8.61	7.45	19.45	6.16	18.80	5.20
E	Unburned	10.59	9.17	11.21	10.46	6.06	5.25	0	0
	Burned	36.15	5.52	40.54	8.84	19.68	4.54	8.61	7.45
N	Unburned	3.03	5.25	3.03	5.25	9.60	8.44	0	0
	Burned	41.13	5.09	40.98	11.96	11.64	2.20	22.60	4.06

## Appendix K continued.

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Frequency									
<i>Lotus rigidus</i>									
S	Unburned	20.88	6.56	22.29	6.67	20.13	9.59	10.45	9.46
	Burned	16.77	6.99	21.05	5.34	27.52	5.27	27.85	7.85
E	Unburned	10.37	2.20	6.14	10.64	8.33	7.97	8.33	7.97
	Burned	15.75	2.76	14.76	3.18	14.47	4.82	10.37	2.20
N	Unburned	7.34	6.63	4.30	7.45	3.03	5.25	0	0
	Burned	10.63	11.47	3.03	5.25	4.30	7.45	0	0
<i>Andropogon cirratus</i>									
S	Unburned	16.90	15.35	16.90	15.35	13.54	12.53	17.42	7.86
	Burned	6.06	5.25	0	0	3.03	5.25	4.30	7.45
E	Unburned	29.98	9.26	31.74	8.31	28.56	11.25	29.98	9.26
	Burned	13.48	4.69	20.64	2.17	19.10	2.78	19.79	3.53
N	Unburned	20.71	0	15.51	4.49	11.44	9.99	11.21	10.46
	Burned	8.61	7.45	14.15	13.36	11.90	11.42	17.18	8.80
<i>Aristida orcuttiana</i>									
S	Unburned	13.91	1.71	17.42	7.86	13.48	4.69	9.18	9.22
	Burned	0	0	0	0	6.06	5.25	4.30	7.45
E	Unburned	19.45	6.00	21.13	4.64	20.76	7.04	19.89	7.80
	Burned	19.45	6.00	22.89	7.05	22.74	8.06	23.24	4.26
N	Unburned	0	0	3.03	5.25	3.03	5.25	4.30	7.45
	Burned	7.34	6.63	7.34	6.63	7.34	6.64	6.06	5.25
<i>Bouteloua curtipendula</i>									
S	Unburned	22.79	11.06	26.07	7.39	25.39	10.80	26.71	15.26
	Burned	34.59	6.18	37.24	3.08	37.11	6.80	44.21	3.89
E	Unburned	10.45	9.46	9.18	9.22	7.34	6.63	16.74	1.47
	Burned	20.49	3.98	21.13	4.64	24.61	3.38	25.28	8.29
N	Unburned	13.62	3.92	23.16	9.03	19.48	9.19	19.04	3.48
	Burned	10.37	2.20	10.37	2.20	13.48	4.69	13.48	4.69
<i>Eragrostis intermedia</i>									
S	Burned	9.10	0	15.58	14.37	9.18	9.22	12.20	10.83
	Burned	30.05	9.21	48.42	11.82	43.42	10.31	49.35	5.00
E	Unburned	0	0	3.03	5.25	3.03	5.25	4.30	7.45
	Burned	19.37	9.67	23.09	9.46	23.54	7.12	21.21	8.55
N	Unburned	3.03	5.25	8.33	7.97	8.33	7.97	12.63	3.40
	Burned	21.44	7.51	21.13	4.64	23.83	5.00	22.89	7.05

**Appendix K continued.**

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Frequency									
<i>Heteropogon contortus</i>									
S	Unburned	7.34	6.63	15.75	2.76	12.21	5.39	10.37	2.20
	Burned	3.03	5.25	6.06	5.25	0	0	9.18	9.22
E	Unburned	14.93	7.06	16.60	3.18	18.46	7.17	24.93	6.59
	Burned	23.43	7.88	25.92	11.28	21.21	8.55	26.83	6.23
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0
<i>Muhlenbergia emersleyi</i>									
S	Unburned	39.11	6.51	38.06	8.21	39.63	5.61	41.72	4.25
	Burned	15.92	6.84	20.44	4.42	17.84	6.14	26.34	4.95
E	Unburned	20.45	8.71	21.98	8.44	17.88	12.05	22.28	10.23
	Burned	27.59	4.16	32.03	4.72	27.21	7.76	33.16	3.13
N	Unburned	11.44	9.99	9.60	8.44	9.60	8.44	10.45	9.46
	Burned	25.89	2.82	20.30	5.57	21.98	3.22	25.28	2.80
<i>Trachypogon secundus</i>									
S	Unburned	6.14	10.64	14.93	7.06	15.58	8.14	15.29	15.00
	Burned	0	0	3.03	5.25	7.34	6.63	3.03	5.25
E	Unburned	21.21	8.55	24.28	13.51	23.53	11.10	20.80	13.65
	Burned	15.75	2.76	18.44	0	19.19	1.31	19.45	6.00
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0
<i>Aristida adscensionis</i>									
S	Unburned	0	0	4.30	7.45	0	0	0	0
	Burned	0	0	17.53	7.37	0	0	4.30	7.45
E	Unburned	0	0	4.30	7.45	0	0	5.29	9.17
	Burned	0	0	10.59	9.17	0	0	6.06	5.25
N	Unburned	0	0	10.00	17.32	0	0	9.44	16.35
	Burned	0	0	18.73	18.88	0	0	19.22	19.62
<i>Cheilanthes wootoni</i>									
S	Unburned	17.59	1.47	16.74	1.47	17.20	5.06	15.89	0
	Burned	13.48	4.69	11.64	2.20	12.63	3.40	12.92	0
E	Unburned	21.73	5.70	21.05	5.34	21.29	3.18	20.53	3.63
	Burned	23.35	2.97	27.64	3.57	26.69	7.19	27.73	1.01
N	Unburned	27.58	4.46	20.44	18.17	16.34	14.65	19.44	16.85
	Burned	19.79	3.53	17.53	7.37	13.05	11.35	14.50	12.60

**Appendix K continued.**

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Frequency									
<i>Selaginella rupincola</i>									
S	Unburned	6.14	10.64	4.30	7.45	5.29	9.17	5.29	9.17
	Burned	0	0	0	0	0	0	0	0
E	Unburned	66.14	8.55	61.44	11.26	63.02	9.85	60.96	12.04
	Burned	26.38	4.64	27.68	2.69	25.28	2.80	24.73	0
N	Unburned	51.75	13.04	48.48	13.78	48.55	14.36	50.07	11.98
	Burned	29.63	11.89	30.36	11.47	32.44	13.35	25.29	24.67



**Appendix L.** Seasonal differences of frequency data.

Mean and standard deviation of seasonal differences for frequency data by major species at the three sites (S=south slope, E=east slope, N=north slope).

	Unburned				Burned			
<i>Species</i>	Spring		Fall		Spring		Fall	
Site	Mean	SD	Mean	SD	Mean	SD	Mean	SD
	Frequency							
<i>Quercus emoryi</i>								
S	0	0	0	0	0	0	0	0
E	18.11	17.55	-18.11	17.56	59.79	27.87	44.22	50.99
N	11.28	20.59	-11.48	20.42	48.11	11.30	-5.06	27.81
<i>Quercus oblongifolia</i>								
S	-0.20	0.35	6.62	11.47	11.68	20.24	0	0
E	-5.67	27.81	6.83	11.31	-12.09	20.42	0	0
N	0	0	0	0	0	0	0	0
<i>Arctostaphylos pungens</i>								
S	-11.68	20.24	6.62	11.47	0	0	0	0
E	6.22	11.31	-11.28	27.87	0	0	11.68	20.24
N	11.68	20.24	23.57	20.42	-0.20	0.35	0.20	0.35
<i>Garrya wrightii</i>								
S	-6.62	36.89	0	0	-6.62	11.47	0	0
E	-0.20	0.35	12.09	20.42	-6.62	11.47	-11.48	20.42
N	0	0	0	0	11.48	20.42	0	0
<i>Agave schottii</i>								
S	0	0	4.22	7.31	-8.85	15.33	-12.29	12.10
E	0	0	-17.70	15.33	0	0	-3.84	6.66
N	0	0	0	0	0	0	0	0
<i>Dasyllirion wheeleri</i>								
S	0	0	-7.69	18.73	-8.85	15.34	4.63	20.02
E	21.14	7.43	-4.22	7.31	4.22	18.23	-4.22	7.30
N	-8.85	15.34	0	0	0	0	4.22	7.31
<i>Haplopappus laricifolius</i>								
S	12.70	13.32	-13.08	22.65	0	0	-4.22	7.31
E	0	0	3.45	6.66	8.56	15.34	0	0
N	4.22	7.31	-4.22	7.31	8.86	27.06	0	0
<i>Nolina microcarpa</i>								
S	-8.85	15.34	8.86	15.34	-4.22	7.31	-3.85	6.66
E	0	0	-3.85	6.66	0	0	0	0
N	-16.92	20.16	-0.78	22.33	12.70	13.32	4.22	7.31

## Appendix L continued.

	Unburned				Burned			
<i>Species</i>	Spring		Fall		Spring		Fall	
Site	Mean	SD	Mean	SD	Mean	SD	Mean	SD
	Frequency							
<i>Artemisia ludoviciana</i>								
S	1.16	1.02	-1.60	2.78	-0.39	4.44	2.09	4.18
E	-3.88	4.69	3.11	5.39	3.54	5.28	-4.39	4.29
N	3.24	4.05	-2.46	6.03	2.90	0.92	0.89	5.37
<i>Gnaphalium wrightii</i>								
S	-6.06	5.25	3.03	5.25	7.80	5.41	10.19	2.58
E	-4.52	12.64	-11.21	10.46	-16.46	5.17	-31.93	4.31
N	6.57	13.65	-3.03	5.25	-29.48	3.50	-18.38	14.89
<i>Lotus rigidus</i>								
S	-0.75	6.59	-11.84	6.46	10.74	2.79	6.79	2.57
E	-2.04	6.28	2.18	6.12	-1.27	3.37	-4.38	4.69
N	-4.30	4.56	-4.30	7.45	-6.32	5.49	-3.03	5.25
<i>Andropogon cirratus</i>								
S	-3.36	2.92	0.52	7.58	-3.03	5.25	4.30	7.45
E	-1.41	2.55	-1.76	1.62	5.61	5.20	-0.85	5.24
N	-9.26	9.99	-4.30	7.45	3.29	5.69	3.03	5.25
<i>Aristida orcuttiana</i>								
S	-0.42	5.16	-8.24	1.69	6.06	5.25	4.30	7.45
E	1.30	11.53	-1.24	6.09	3.29	3.46	0.35	4.90
N	3.03	5.25	1.27	2.20	2.11	1.83	-1.27	2.20
<i>Bouteloua curtipendula</i>								
S	2.59	7.37	0.63	9.01	2.52	7.10	6.97	0.92
E	-3.11	5.39	7.56	7.97	4.12	0.60	4.14	4.44
N	5.86	5.41	-4.12	7.27	3.11	6.60	3.11	2.83
<i>Eragrostis intermedia</i>								
S	0.08	9.22	-3.38	7.91	13.37	8.60	0.93	6.82
E	3.03	5.25	1.27	2.20	4.16	2.55	-1.88	2.02
N	5.29	9.17	4.30	7.45	2.38	7.57	1.75	3.04
<i>Heteropogon contortus</i>								
S	4.87	4.58	-5.37	4.82	-3.03	5.25	3.11	5.39
E	3.52	3.40	8.33	7.24	-2.22	0.68	0.91	6.47
N	0	0	0	0	0	0	0	0

**Appendix L continued.**

<i>Species</i>	Unburned				Burned			
	Spring		Fall		Spring		Fall	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Site								
Frequency								
<i>Muhlenbergia emersleyi</i>								
S	0.52	0.91	3.66	6.08	1.92	1.91	5.90	2.99
E	-2.57	3.73	0.29	2.84	-0.38	3.79	1.13	2.51
N	-1.84	1.60	0.85	4.30	-3.90	5.25	4.98	3.58
<i>Trachypogon secundus</i>								
S	9.43	3.32	0.36	8.46	7.34	6.63	0	0
E	2.32	4.30	-1.64	1.44	3.44	1.80	1.01	6.00
N	0	0	0	0	0	0	0	0
<i>Aristida adscensionis</i>								
S	0	0	-4.30	7.45	0	0	-13.22	6.49
E	0	0	0.99	1.71	0	0	-4.52	12.64
N	0	0	-0.56	0.96	0	0	0.49	0.84
<i>Cheilanthes wootoni</i>								
S	-0.39	6.48	-0.85	1.47	-0.85	4.30	1.27	2.21
E	-0.44	2.95	-0.52	2.66	3.33	7.63	0.09	3.45
N	-11.23	10.23	-1.00	5.01	-6.74	8.21	-3.03	5.65
<i>Selaginella rupincola</i>								
S	-0.85	1.47	0.99	1.71	0	0	0	0
E	-3.11	1.53	-0.48	0.83	-1.10	1.91	-2.95	2.69
N	-3.20	3.02	1.59	3.01	2.81	5.55	3.17	2.22

**Appendix M. Live biomass of major herbaceous species.**

Mean and standard deviation of live biomass for major non-woody species at the three sites (S=south slope, E=east slope, N=north slope).

**LIVE BIOMASS DATA**

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
g · m <sup>-2</sup>									
<i>Artemisia ludoviciana</i>									
S	Unburned	2.42	4.18	4.86	8.41	2.57	3.39	4.44	7.06
	Burned	1.93	2.26	16.53	28.35	11.52	8.49	4.84	5.27
E	Unburned	0	0	0	0	0.32	0.55	0.07	0.12
	Burned	17.40	11.30	19.00	18.76	10.82	9.34	6.65	8.93
N	Unburned	0.02	0.04	0.97	0.76	0.50	0.61	0.29	0.50
	Burned	1.33	1.36	18.10	1.48	2.96	1.98	3.10	2.03
<i>Gnaphalium wrightii</i>									
S	Unburned	1.85	1.60	0	0	0.02	0.04	0.02	0.04
	Burned	0.19	0.19	2.98	5.17	0.09	0.12	1.20	1.34
E	Unburned	0.78	1.02	0.20	0.31	0	0	0	0
	Burned	11.72	3.00	17.78	21.64	5.54	5.12	0.28	0.26
N	Unburned	0	0	0.05	0.09	0.02	0.03	0.01	0.01
	Burned	14.28	4.24	27.69	7.76	0.02	0.04	0.18	0.17
<i>Lotus rigidus</i>									
S	Unburned	5.43	3.18	11.59	6.79	4.54	1.61	1.59	1.29
	Burned	1.55	2.07	0.16	0.22	0.87	0.32	0.57	0.43
E	Unburned	0.21	0.22	0.29	0.50	2.33	2.46	0.70	1.11
	Burned	0.60	0.25	0.74	1.09	0.70	0.87	0.37	0.64
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0
<i>Andropogon cirratus</i>									
S	Unburned	0.66	0.87	0.04	0.08	0.91	0.98	0.35	0.60
	Burned	0.05	0.08	1.19	1.25	0.25	0.44	0	0
E	Unburned	1.53	0.30	0.64	0.51	0.50	0.52	8.72	3.09
	Burned	0.24	0.42	0.82	1.42	0	0	0.04	0.06
N	Unburned	0.57	0.50	0.77	0.45	0.71	0.40	0.65	0.52
	Burned	0.97	1.6	0	0	0	0	1.93	3.34
<i>Aristida orcuttiana</i>									
S	Unburned	0.25	0.34	1.26	1.14	0.53	0.81	1.77	2.86
	Burned	0	0	0.09	0.16	0.55	0.26	0.80	1.36
E	Unburned	1.54	0.98	0.42	0.41	0.30	0.23	0.89	1.41
	Burned	0.96	0.88	0.34	0.59	0.32	0.56	1.13	1.95
N	Unburned	0.01	0.01	0.49	0.57	0.59	0.96	0.68	1.18
	Burned	0.07	0.06	0	0	0	0	0.03	0.05

## Appendix M continued.

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
g · m <sup>-2</sup>									
<i>Bouteloua curtipendula</i>									
S	Unburned	0.54	0.58	6.55	4.81	3.34	3.72	3.53	1.87
	Burned	9.42	2.36	18.80	12.14	8.81	4.71	17.24	6.82
E	Unburned	0.18	0.32	0.43	0.27	0.35	0.60	1.15	1.62
	Burned	0.77	1.34	1.36	2.02	1.24	0.78	3.49	4.73
N	Unburned	0	0	0.77	0.01	0.14	0.18	1.21	0.65
	Burned	0.84	0.88	5.61	2.44	0.53	0.83	1.12	1.14
<i>Heteropogon contortus</i>									
S	Unburned	0.14	0.24	0	0	0.40	0.61	3.09	3.83
	Burned	0.15	0.25	0	0	0.15	0.18	0	0
E	Unburned	0.26	0.23	0.71	0.42	0.45	0.38	2.42	0.39
	Burned	0.57	0.72	3.74	6.47	0.65	1.13	2.20	2.93
N	Unburned	0	0	0	0	0.01	0.02	0	0
	Burned	0	0	0	0	0	0	0	0
<i>Eragrostis intermedia</i>									
S	Unburned	0.10	0.17	0.76	0.90	0.61	0.93	0.92	1.32
	Burned	2.44	3.27	6.39	2.18	6.06	5.17	10.85	1.82
E	Unburned	0	0	0.11	0.20	0.02	0.04	0	0
	Burned	1.95	2.49	1.35	1.00	2.78	0.59	0.94	1.27
N	Unburned	0	0	0	0	0.05	0.09	0.36	0.63
	Burned	2.31	2.04	1.69	0.71	1.47	0.97	3.05	2.69
<i>Muhlenbergia emersleyi</i>									
S	Unburned	11.69	3.04	16.07	6.12	9.99	7.32	18.81	5.28
	Burned	3.77	5.48	1.17	1.53	8.89	13.78	1.98	1.31
E	Unburned	2.17	1.59	3.29	1.90	2.43	1.94	9.82	2.44
	Burned	19.09	17.50	11.89	8.80	14.34	13.51	25.95	8.63
N	Unburned	0.16	0.28	0.14	0.25	0	0	0.31	0.47
	Burned	8.48	8.48	2.95	4.18	1.49	1.34	15.60	12.66
<i>Trachypogon secundus</i>									
S	Unburned	0	0	0	0	0.48	0.84	3.95	5.52
	Burned	0	0	0	0	0	0	0	0
E	Unburned	0	0	0.63	0.54	1.48	1.09	0.89	1.14
	Burned	1.12	1.09	2.13	3.05	4.14	7.18	0.59	1.03
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0

**Appendix M continued.**

<b>Species</b>		<b>Spring 1984</b>		<b>Fall 1984</b>		<b>Spring 1985</b>		<b>Fall 1985</b>	
<b>Site</b>	<b>Treatment</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>
<b>g · m<sup>-2</sup></b>									
<b><i>Aristida adscensionis</i></b>									
S	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0
E	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0.03	0.03
<b><i>Ferns</i></b>									
S	Unburned	6.66	7.47	5.54	4.27	8.50	7.47	5.47	3.41
	Burned	0.60	0.76	2.62	1.17	0.88	0.31	1.89	1.95
E	Unburned	1.60	1.62	2.83	2.39	3.10	0.10	4.24	1.97
	Burned	3.93	1.86	5.71	3.51	4.67	3.02	5.49	2.12
N	Unburned	7.75	4.81	11.38	8.91	4.10	2.73	13.03	5.62
	Burned	9.67	6.21	8.33	6.86	5.19	4.27	11.14	8.01
<b><i>Selaginella rupincola</i></b>									
S	Unburned	0	0	0	0	0	0	0.89	1.55
	Burned	0	0	0	0	0	0	0	0
E	Unburned	16.10	11.55	43.95	35.18	26.40	17.48	26.20	12.06
	Burned	0.29	0.26	0.98	1.49	0	0	0.46	0.71
N	Unburned	51.37	11.84	51.38	25.39	29.53	14.02	64.60	35.48
	Burned	2.77	3.79	16.68	14.03	17.06	4.68	9.51	11.62

# Appendix N. Dead biomass of major herbaceous species.

Mean and standard deviation for dead herbaceous biomass by major species (S=south slope, E=east slope, N=north slope).

## DEAD BIOMASS DATA

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
g · m <sup>-2</sup>									
<i>Artemisia ludoviciana</i>									
S	Unburned	4.16	7.21	1.23	2.14	3.67	5.47	4.11	7.13
	Burned	0.38	0.66	1.60	2.78	14.90	10.36	4.28	4.07
E	Unburned	0	0	0	0	0.34	0.60	0.02	0.04
	Burned	0	0	0.01	0.01	24.72	11.70	10.23	12.65
N	Unburned	0.06	0.10	0.22	0.38	1.56	2.71	0.66	1.14
	Burned	0.09	0.15	0	0	0.85	0.79	8.20	9.20
<i>Gnaphalium wrightii</i>									
S	Unburned	1.62	1.39	0.03	0.05	0	0	1.45	2.52
	Burned	0	0	0	0	0.33	0.54	2.16	2.40
E	Unburned	1.17	0.39	0	0	0.85	1.27	1.08	0.97
	Burned	0.08	0.15	0.22	0.39	16.62	13.26	20.66	8.73
N	Unburned	0.18	0.31	0	0	0	0	0.80	1.39
	Burned	0.62	1.08	1.23	0.52	29.45	13.73	13.17	14.14
<i>Lotus rigidus</i>									
S	Unburned	3.55	2.36	5.56	7.05	5.18	1.39	10.88	8.58
	Burned	0.35	0.60	0.05	0.09	0.26	0.06	0.60	0.59
E	Unburned	0.18	0.31	0.31	0.54	3.25	3.58	0.82	0.99
	Burned	0	0	0.24	0.39	1.84	2.39	1.03	0.95
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0
<i>Andropogon cirratus</i>									
S	Unburned	4.66	7.06	0.01	0.01	3.55	3.23	0.07	0.12
	Burned	0.16	0.27	3.55	5.22	0.71	1.23	-	-
E	Unburned	17.21	10.32	7.43	6.40	2.71	2.27	11.51	6.38
	Burned	0	0	0.99	1.72	0	0	0.17	0.30
N	Unburned	7.86	7.62	3.24	1.37	6.20	2.84	8.92	8.26
	Burned	5.69	9.86	0	0	0	0	6.99	12.10
<i>Aristida orcuttiana</i>									
S	Unburned	0.09	0.08	1.59	1.38	1.01	1.60	4.65	7.42
	Burned	0	0	0.19	0.33	1.09	0.92	1.26	2.02
E	Unburned	7.38	6.35	1.91	2.35	0.71	0.26	1.36	2.17
	Burned	0.37	0.64	0.26	0.46	1.33	2.30	2.22	3.85
N	Unburned	0.11	0.18	1.34	2.01	3.09	4.87	1.18	2.05
	Burned	0.70	0.81	0	0	0	0	0.03	0.06

**Appendix N continued.**

<b>Species</b>		<b>Spring 1984</b>		<b>Fall 1984</b>		<b>Spring 1985</b>		<b>Fall 1985</b>	
<b>Site</b>	<b>Treatment</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>	<b>Mean</b>	<b>SD</b>
<b>g · m<sup>-2</sup></b>									
<b><i>Bouteloua curtipendula</i></b>									
S	Unburned	1.86	2.08	5.78	3.41	12.88	15.55	3.61	1.38
	Burned	15.85	8.35	21.08	15.48	26.61	12.07	20.43	9.27
E	Unburned	1.94	3.37	1.45	1.35	0.97	1.28	1.29	1.82
	Burned	0.08	0.14	1.48	1.83	4.49	2.75	7.36	11.57
N	Unburned	0	0	1.04	0.41	1.51	2.27	2.06	1.21
	Burned	8.78	8.01	5.78	1.55	3.05	3.33	5.03	5.53
<b><i>Eragrostis intermedia</i></b>									
S	Unburned	0.52	0.91	1.03	0.91	2.61	3.92	1.81	2.65
	Burned	3.40	4.41	16.70	7.51	16.62	16.41	24.85	6.71
E	Unburned	0	0	0.91	1.34	0.05	0.07	-	-
	Burned	1.04	1.23	5.88	4.71	9.45	5.60	1.95	2.82
N	Unburned	0	0	0	0	1.02	1.76	0.54	0.94
	Burned	9.01	7.82	1.76	0.79	4.01	4.06	3.49	2.85
<b><i>Heteropogon contortus</i></b>									
S	Unburned	0.39	0.68	0	0	2.36	2.08	1.97	3.13
	Burned	1.04	1.81	0	0	0.86	0.75	0	-
E	Unburned	3.07	2.78	2.48	1.97	4.08	3.36	3.87	3.46
	Burned	3.33	2.90	3.39	5.87	1.86	3.23	2.68	2.94
N	Unburned	0	0	0	0	0.11	0.20	0	-
	Burned	0	0	0	0	0	0	0	-
<b><i>Muhlenbergia emersleyi</i></b>									
S	Unburned	83.38	20.06	67.09	38.47	63.10	47.29	55.94	10.80
	Burned	7.13	9.23	8.15	13.70	30.38	45.99	4.54	3.79
E	Unburned	13.57	9.67	22.28	12.81	9.94	8.40	28.01	13.18
	Burned	23.41	22.34	59.83	49.45	46.34	33.89	67.27	38.22
N	Unburned	0.54	0.94	0.58	1.00	0	0	1.64	2.35
	Burned	31.55	31.57	10.86	15.77	6.35	7.04	28.71	33.74
<b><i>Trachypogon secundus</i></b>									
S	Unburned	0	0	0	0	4.18	7.25	5.18	7.18
	Burned	0	0	0	0	0	0	0	0
E	Unburned	0	0	1.79	2.08	8.36	6.35	1.36	1.42
	Burned	1.27	1.10	6.00	8.88	16.04	27.78	1.22	2.11
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0



**Appendix N continued.**

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
$\text{g} \cdot \text{m}^{-2}$									
<i>Aristida adscensionis</i>									
S	Unburned	0	0	0	0	0	0	0	0
	Burned	0.17	0.29	1.64	2.10	0	0	0	0
E	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0.87	1.50	0	0	0	0
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	8.73	10.02	0	0	20.60	12.74

**Appendix O.** Seasonal differences in biomass of major species.

Mean and standard deviation for seasonal differences of plant biomass for major non-woody species. Data from burned and unburned plots presented for the four sample periods at the three sites (S=south slope, E=east slope, N=north slope).

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
g · m <sup>-2</sup>									
<i>Artemisia ludoviciana</i>									
S	Unburned	0.15	1.06	-0.48	1.83	-0.41	1.41	2.88	4.98
	Burned	9.59	10.36	14.52	11.00	-11.69	31.21	2.67	6.15
E	Unburned	0.32	0.55	0.34	0.60	0.07	0.12	0.02	0.04
	Burned	-6.57	19.39	24.72	11.70	-12.35	22.28	10.22	12.65
N	Unburned	0.47	0.64	1.50	2.77	-0.68	0.45	0.43	0.75
	Burned	1.63	1.28	0.76	0.92	-14.99	2.84	8.20	9.20
<i>Gnaphalium wrightii</i>									
S	Unburned	-1.83	1.64	-1.62	1.39	0.02	0.04	1.42	2.54
	Burned	-0.09	0.28	0.33	0.54	-1.78	6.19	2.16	2.40
E	Unburned	-0.78	1.02	-0.32	0.87	-0.20	0.31	1.08	0.97
	Burned	-6.18	6.36	16.53	13.38	-17.50	21.90	20.43	8.43
N	Unburned	0.02	0.03	-0.18	0.31	-0.04	0.10	0.80	1.39
	Burned	-14.25	4.23	28.82	14.52	-27.50	7.62	11.94	13.62
<i>Lotus rigidus</i>									
S	Unburned	-0.88	2.14	1.63	3.41	-10.00	7.09	5.32	9.92
	Burned	-0.68	2.37	-0.09	0.61	0.41	0.42	0.55	0.51
E	Unburned	2.11	2.23	3.07	3.29	0.41	1.45	0.51	1.34
	Burned	0.10	0.92	1.84	2.39	-0.37	1.48	0.79	0.69
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0
<i>Andropogon cirratus</i>									
S	Unburned	0.24	1.41	-1.11	8.68	0.30	0.65	0.06	0.13
	Burned	0.20	0.35	0.55	0.95	-1.19	1.25	-3.55	5.22
E	Unburned	-1.03	0.72	-14.50	12.47	8.08	2.87	4.07	7.06
	Burned	-0.24	0.42	0	0	-0.78	1.46	-0.82	1.88
N	Unburned	0.13	0.83	-1.66	8.46	-0.12	0.61	5.68	8.40
	Burned	-0.97	1.69	-5.69	9.86	1.93	3.34	6.98	12.09
<i>Aristida orcuttiana</i>									
S	Unburned	0.28	1.00	0.92	1.55	0.50	2.76	3.06	6.89
	Burned	0.55	0.25	1.09	0.92	0.71	1.43	1.06	2.19
E	Unburned	-1.23	1.20	-6.67	6.42	0.47	1.08	-0.54	0.44
	Burned	-0.64	0.93	0.96	2.67	0.78	1.36	1.96	3.39
N	Unburned	0.58	0.96	2.98	4.97	0.18	1.39	-0.15	3.41
	Burned	-0.07	0.06	-0.70	0.80	-0.03	0.05	0.03	0.05

## Appendix O continued.

Species		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
g · m <sup>-2</sup>									
<i>Bouteloua curtipendula</i>									
S	Unburned	2.80	4.14	11.02	17.10	-3.02	4.05	-2.16	4.18
	Burned	-0.61	6.26	10.75	18.97	-1.56	6.37	-0.64	6.95
E	Unburned	0.16	0.81	-0.97	3.98	0.72	1.38	-0.16	0.51
	Burned	0.46	1.81	4.41	2.76	2.13	2.76	5.88	9.83
N	Unburned	0.14	0.18	1.51	2.27	0.44	0.65	1.02	0.81
	Burned	-0.31	0.38	-5.72	7.01	-4.49	3.06	-0.75	4.77
<i>Eragrostis intermedia</i>									
S	Unburned	0.50	0.75	2.08	3.01	0.16	1.68	0.78	2.42
	Burned	3.62	3.47	13.22	12.45	4.46	4.01	8.14	12.90
E	Unburned	0.02	0.04	0.05	0.07	-0.11	0.20	-0.91	1.34
	Burned	0.83	1.90	8.40	4.39	-0.40	1.84	-3.92	6.81
N	Unburned	0.05	0.09	1.01	1.76	0.36	0.63	0.54	0.94
	Burned	-0.84	2.00	-5.00	5.85	1.36	3.34	1.73	2.53
<i>Heteropogon contortus</i>									
S	Unburned	0.26	0.77	1.96	2.52	3.09	3.82	1.97	3.12
	Burned	0.00	0.34	-0.18	1.58	0	0	0	0
E	Unburned	0.19	0.55	1.01	5.41	1.71	0.47	1.39	4.50
	Burned	0.08	1.51	-1.47	3.32	-1.53	8.05	-0.71	6.91
N	Unburned	0.01	0.01	0.11	0.19	0	0	0	0
	Burned	0	0	0	0	0	0	0	0
<i>Muhlenbergia emersleyi</i>									
S	Unburned	-1.70	7.96	-20.27	29.40	2.74	5.54	-11.15	43.60
	Burned	5.12	8.37	23.25	37.22	0.80	2.81	-3.61	17.48
E	Unburned	0.26	0.71	-3.63	2.60	6.53	4.14	5.72	16.28
	Burned	-4.75	6.50	22.93	12.01	14.05	-1.92	7.44	16.35
N	Unburned	-0.16	0.28	-0.54	0.94	0.17	0.22	1.06	1.36
	Burned	-6.98	9.47	-25.19	34.77	12.65	8.47	17.85	18.52
<i>Trachypogon secundus</i>									
S	Unburned	0.48	0.84	4.18	7.25	3.95	5.52	5.18	7.18
	Burned	0	0	0	0	0	0	0	0
E	Unburned	1.48	1.09	8.36	6.35	0.26	0.83	-0.43	2.22
	Burned	3.02	7.20	14.77	27.16	-1.53	2.03	-4.78	6.78
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	0	0

**Appendix O continued.**

<i>Species</i>		Spring 1984		Fall 1984		Spring 1985		Fall 1985	
Site	Treatment	Mean	SD	Mean	SD	Mean	SD	Mean	SD
$\text{g} \cdot \text{m}^{-2}$									
<i>Aristida adscensionis</i>									
S	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	-0.17	0.29	0	0	-1.64	2.10
E	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0	0	-0.87	1.50
N	Unburned	0	0	0	0	0	0	0	0
	Burned	0	0	0	0	0.03	0.03	11.86	21.96
<i>Ferns</i>									
S	Unburned	1.84	5.52	0	0	-0.06	1.90	0	0
	Burned	0.28	0.76	0	0	-0.73	0.86	0	0
E	Unburned	1.50	1.69	0	0	1.41	2.09	0	0
	Burned	0.73	2.26	0	0	-0.21	5.50	0	0
N	Unburned	-3.65	2.14	0	0	1.64	13.44	0	0
	Burned	-4.47	9.87	0	0	2.81	3.42	0	0
<i>Selaginella rupincola</i>									
S	Unburned	0	0	0	0	0.89	1.55	0	0
	Burned	0	0	0	0	0	0	0	0
E	Unburned	10.30	15.99	0	0	-17.75	24.45	0	0
	Burned	-0.29	0.26	0	0	-0.52	1.95	0	0
N	Unburned	-21.84	20.94	0	0	13.22	44.74	0	0
	Burned	14.29	3.93	0	0	-7.17	5.19	0	0

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