

Mr. John Lissoway

March 31, 1980

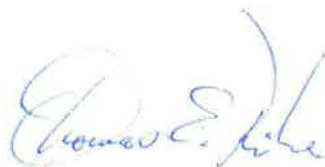
Division of Natural Resources

Bandelier National Monument

Sir,

Here is my ecological study which I have been working on for the last nine months. I hope this copy will find a place in the library there for the future.

Thanks again for your part in its preparation.

A handwritten signature in blue ink, appearing to read "Tom Kibe".

Tom Kibe

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DIVERSITY PATTERNS AND REVEGETATION OF
PONDEROSA PINE ZONE AFFECTED BY
WILDFIRE IN BANDELIER NATIONAL MONUMENT,
NEW MEXICO

by

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A thesis submitted to the Biology Board of Studies
in partial fulfillment of the requirements for the degree of

Bachelor of Arts

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ABSTRACT

This study was done two years after the La Mesa Fire of 1977 in Bandelier National Monument, New Mexico. Four study plots were delineated, two in unburned areas, one in a ground fire area, and one in a crown fire area, all within the ponderosa pine zone. The vegetation in these plots was censused and the diversity analyzed. Some ecological theory concerning diversity is presented and discussed.

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"In Hardwood Groves"

The same leaves over and over again!
They fall from giving shade above
To make one texture of faded brown
And fit the earth like a leather glove.

Before the leaves can mount again
To fill the trees with another shade,
They must go down past things coming up,
They must go down into the dark decayed.

They must be pierced by flowers and put
Beneath the feet of dancing flowers.
However it is in some other world
I know that this is the way in ours.

Robert Frost

INTRODUCTION

In 1875 Lt. Beale voyaged across northern Arizona to the Grand Canyon and to the volcanic peaks near present day Flagstaff. He travelled for days through ponderosa pine forests largely present today in this region, describing the nature of these forestlands as follows:

"We came to a glorious forest of lofty pines through which we have travelled ten miles. The country was beautifully undulating and although we usually associate the idea of barrenness with the Pine regions, it was not so in this instance; every foot being covered with the finest grass and beautiful broad grassy vales extending in every direction. The forest was perfectly open and unencumbered with brush wood so that travelling was excellent."

Tcday these ponderosa pine forests are often a tangle of fallen trees and dying saplings. Grass and wildflowers are scarce and travel without a path is rough. Why was this fcrest do different when it was true wilderness? Why are wilderness areas and wildland ponderosa forest different now, tangled and difficult to penetrate?

Ponderosa pine grassland is characterized by the occurrence and distribution of Pinus ponderosa. This forest type is distributed from the Fraser River Basin in British Columbia to Durango Mexico and from Nebraska to the Pacific coast. In all, 36 million acres of land are designated ponderosa pine forest (Cooper 1960).

This study concerns such forest, widespread in the mountains of northern New Mexico. The aim of this research is to observe and quantify the effects of the 1977 La Mesa fire in Bandelier National Monument on the plant life in the ponderosa pine zone. Attempting to establish the dependence of the ponderosa community on fire, I have studied the diversity of the botanical community in the ponderosa forest in variously burned and unburned sites in the area of the La Mesa fire. The fire markedly changed the appearance of some of the plant communities there.

Diversity is related to, among other things, the population dynamics of the species in the community. Diversity consists of species richness and the relative proportions of the species; these may be related to ways in which the plants in the community are interacting with each other and with the physical elements of their habitat. Diversity is the central focus of this study; it gives quantitative insight into the condition of the community studied here.

In recent years many ecological workers have begun to turn their attention to the problem of forest fuel buildup from dead plant material. Heavy buildups seriously limit the potential timber productivity of the ecosystem for human use and also decrease the aesthetic appeal of the wildland and its use for wildlife and recreation. The

absence of fire may be causing these undesirable effects (Gartner and Thompson 1972; Cooper 1960; Biswell 1972).

Fire is an ecological factor in most ecosystems. Due to the dramatic and often violent nature of fire, modern land managers have been compelled to control this force. The effects of fire suppression vary in different ecosystems but in many communities that have evolved with fire, it is an intrinsic ecological factor. Its elimination has caused changes in the natural system on which the biological elements of those communities depend.

Ironically, as time goes on and fire suppression continues, the increase of fuel in the forest or chaparral leads to highly destructive wildfires. This in turn causes more concerted efforts along the lines of fire suppression and elimination, increasing the potential even more for devastating fires. The opposite reaction would be the appropriate one: to control burn the areas where fuel buildup is evident, thus decreasing the potential for serious wildfire in the future (Gartner 1972; Biswell 1972; Dickson 1976; Weaver 1974).

Such was the case in Bandelier National Monument and surrounding lands previous to the La Mesa fire. In June 1977, after a dry winter and spring, a small fire was started in the mixed conifer zone of the Jemez Mountains near Alamo Canyon. The fire, no bigger than a campfire at first, ultimately burned 15 thousand acres. My study

began two summers after the blaze, allowing enough time for some natural rehabilitation of the community to begin. These results represent a brief sampling in the long process of succession; the same study done earlier or later would probably yield different results.

MATERIALS AND METHODS

Study Sites

The Jemez Mountains of New Mexico rise five thousand feet from the Rio Grande valley to their summit at nearly eleven thousand feet. From the valley, mesas rise rapidly to five hundred feet, then gradually slope up to the foothills at an elevation of 7,500 feet. The vegetation changes constantly as the land rises. The Pinyon-Juniper zone extends from the base of the mesas to about 7,000 feet and is dominated by Pinus monophylla, Juniperus monospermum, and Juniperus scopulorum. This vegetation zone fades into an ecotone at 7,000 to 7,200 feet where Pinus ponderosa begins to occur at higher elevations until the pinyon pine fades altogether, leaving a consistent canopy of ponderosa with an occasional Juniperus in the understory. The sampling for this study took place in this ponderosa-pine dominated zone.

Above the ponderosa zone the mountains rise to their summits--between 10,500 and 11,000 feet, where the

community is "mixed conifer" which includes Pseudotsuga menziesii, Abies concolor, Picea pungens, Picea engelmannii, Pinus flexus, Pinus ponderosa, Populus tremuloides, and Quercus gambelii. Quercus gambelii occurs through all of the zones mentioned above and will be mentioned later in this study.

The above lists exclude riparian trees and shrubs which represent a complex taxonomy in the many canyon bottom stream beds of the Jemez Mountains. The many shades of ecotone and variety of habitats make this mountain range both picturesque and interesting to study.

Due to the large areas of crown fire affected land and the lack of living root systems and vegetative matter on the soil surface, there was extensive and severe flooding in Bandelier National Monument in the vicinity of the study sites in the summer months after the 1977 fire. Frijoles and Alamo Canyons were severely damaged by flood waters rushing off the highlands though the rains causing these floods were not unusually large. Due to the short time since the blaze, the ruderal vegetation had not yet moved into the crown fire areas. Because the severely burned area was so vast, invader species seeds were off site and slow to invade such a large area, especially when they have played a minor role in local ecology for many years (Fox 1978).

In an effort to control flooding, the following

native grasses were seeded in the La Mesa burn area in the summer of 1978 (Foxy 1978): Agropyron trachycaulum, Agropyron smithii, Bouteloua gracilis, Muhlenbergia wrightii, Sporobolus cryptandrus, and Festuca sp. All of these grasses are perennial and have been very successful regenerating after the fire. In the crown fire areas reseeded by the Forest Service, grasses totally dominate other herbaceous foliage and are also fairly common in areas affected by ground fire.

The four plots used in this study were selected on the basis of fire type or in terms of the typical vegetation found there. All are within the ponderosa Pine zone. The two control plots and the Ground Fire plot are located on Escobas Mesa in Bandelier National Monument at 7,540 feet elevation, about one mile from the North rim on Frijoles Canyon. The Crown Fire plot is located on Frijoles Mesa at approximately 7,250 feet and is about 100 yards from the edge of Water Canyon. The last plot is widely separated from the first three because the Forest Service reseeded all of the crown fire areas in Bandelier National Monument. The unseeded crown fire plot area was set aside by Los Alamos Scientific Laboratory as a control site to aid in the study of the fire and the effects of the seeding of other areas. Judging by the similarities in vegetation before the fire, undisturbed communities at these varied elevations appear similar.

Due to the drought conditions experienced in the southwest in the summers of 1976 and 1977, the forest in this area was extremely dry. Seventy years of Park Service fire suppression on Escobas and Frijoles mesas created a heavy buildup of fuels. Most of the ponderosa zone on Escobas Mesa was a large "doghair thicket" (Biswell 1972). It had an extremely high fire potential and when the fire, driven by high winds, crossed the nearby Frijoles Canyon, it burned through the crowns of the trees and the understory as well.

Sampling Methods

The control plots are located near the edge of the main fire pathway. The Ground Fire plot is located directly on the periphery of the main fire pathway. The ground fire in this area scarred the large trees (0.5 m DBH) up to seven meters from their bases. Medium sized trees (25 cm DBH) experienced burns up to three meters from their bases, smaller trees (15 cm DBH) up to two meters from their bases. This intense ground fire eliminated nearly all of the litter on the forest floor.

The two control plots were selected randomly from a wide area of unaffected land along the edge of the burn. In selecting a plot for the ground fire survey, I chose one that was far enough away from the crown fire areas to be unaffected by the native grass reseeding efforts of the

summer after the burn. This was my only consideration in this selection. The crown fire plot was randomly selected from a wide expanse of similar forest area. Using a meter tape I measured seven by fifteen meter rectangular plots, large enough to include significant numbers of all the understory species and a good cross sections of the trees through their different ages; it is important how the young trees in the various sites responded to the intensities of fire to which they were exposed.

A complete census of all of the plants was taken in all of the plots except the crown fire plot. This was done by partitioning off strips three meters wide across the whole plot. In each of these the species were counted individually and the trees measured. It was effectively impossible to accurately count the grasses over the whole plot because there were so many of them and many species occur in clumps rather than as individual plants. Therefore censusing these in terms of individuals was not done; grasses were considered in terms of the area they occupied.

In the crown fire plot there were so many individuals of all species that a complete census was impossible. There are about 17,120 individual plants in the crown fire plot. Therefore I haphazardly selected one square meter plots within the main 7x15 meter plot and counted all the individuals in these. All the plants within the plot that

were not among the six dominant species were censused completely.

I measured the depth of the pine litter at haphazard points within the various plots. These results are averaged in table two. Many plants are incapable of successfully germinating in an area with a deep litter layer (Esau 1977). The litter depth is therefore a factor in the richness of the understory.

I measured the diameters of understory plants and of tree trunks to determine the area occupied by the trunk itself. These data are used for calculating diversity.

Calculations

Indices are used to quantify some aspects of a community for comparison with other communities. These results summarize many elements of ecological structure and their interactions. Diversity is a concept and a general ecological quality of a community which has two component parts. These are evenness (or equitability) and species richness. Equitability is the distribution of individuals among the species present. Richness is the number of different species present.

One particular index commonly used is the Shannon-Wiener index, derived originally from the field of information science. This function describes the average

degree of uncertainty of occurrence of a particular symbol (or individual) at a given point in a message (or community) and the amount of information conveyed as a consequence. When applied to a biotic community, it describes the average degree of uncertainty of predicting the species of a given individual picked at random from a community. This uncertainty will increase as the individuals are distributed more equitably among the species or as the number of species increases. The basic form of this index is:

Equation 1

$$H = - \sum p_i \log_2 p_i$$

Where: p = decimal fraction of total individuals belonging to a particular species

I used a converted form of the index in the base 10 (Zar 1977; Pielou 1975) which is much easier to calculate:

Equation 2

$$H = 3.3219 \left(\log_{10} N - \frac{1}{N} \sum n_i \log_{10} n_i \right)$$

Where: N = total number of individuals of all species
 n = number of individuals of a particular species
 H = diversity index
 3.3219 = conversion factor from log to log

I used the Shannon-Wiener index to analyze diversity on the basis of abundance of individual organisms and the area occupied by individuals from each species. When diversity was based on area, then n (equation 2) represents the area in cm occupied by individuals of a

particular species.

The indices for diversity and equitability were calculated using four different data categories for each plot. Each index was calculated taking into account 1) trees and understory including grasses, 2) trees and understory excluding grasses, 3) understory including grasses, and 4) understory excluding grasses. This allowed me to estimate the potential influence of the trees on the indices.

The equitability of each study site was also calculated using the Shannon-Weiner function. This index describes the evenness of the distribution among the species. When an area is dominated by a particular species, or if there are many rare species and only a few dominant ones, the index will be low, indicating great variability in relative abundance. The form of this calculation is:

Equation 3

$$J = \frac{H}{H_{max}}$$

Where: J = equitability
H = diversity index (from equation 2)

H is derived by distributing the total number of individuals (N) in a plot evenly among the number of species found at that site. This is a theoretical and ideal number-the optimum even distribution of individuals

among species. MacArthur has argued that the J obtained using this derivation of H is inaccurate since H is so ideal. He proposes finding the optimal "possible" equitability by observing natural abundances and deriving H from the natural species curves.

Table one shows the area covered with living plants and other materials at the four study sites. This is calculated by dividing the total area of the study plot by the area that was actually covered by each plant species. The circular area value of plants is derived by measuring the plants at the widest part of their crown and calculating the area of a circle of this diameter. The trees are analyzed in terms of the area that their trunks occupy, not the area that may be shaded by the crown of the tree. The canopy affects the amount of light and rain that reaches the floor and influences the distribution of the moisture slightly. The shaded area is difficult to calculate because the habit of each tree species varies and the spread of the crown is different. It is difficult to analyze the ecological domination that the tree exerts on the understory. These effects vary greatly among canopy species. In the ponderosa forest the shadow cast by the trees is not a dark one. The narrow needles allow some light to pass through the canopy, creating patchy shade.

RESULTS

Physical Characteristics

Although each species of plant has different nutrient requirements, broad differences in nutrient levels in the soil at the different sites may be important in determining the species composition and density at the various sites. Table eight summarizes the change in nutrient availability at the various plots.

Following the pattern described by Kilgore (1973), organic matter at the crown fire site decreased as the fire burned the soil to a depth of a few centimeters. There is a marked decrease in the amount of available Nitrogen (NH_3), Nitrate (NO_3), Magnesium, Manganese, Sodium, and to some extent Calcium in the crown fire site. Phosphorus, Potassium, Sulphate, and Chloride all increased with the intensity of burning. The most dramatic increase involves Sulphate.

The overall decrease in Nitrogen in all forms may be explained by the fact that this study was done two summers after the fire and much of the Nitrogen at the crown fire plot could have been leached out of the soil by precipitation in the interim. It is also possible that these compounds were oxidized by the heat of the fire or that significant amounts have already been integrated into new plant tissues and organic matter.

Interestingly, all of the measured nutrients decreased in the process of the ground fire's occurrence and the time before measurement. The only exception is phosphorus which increased gradually in proportion to the intensity of the ground fire. Some of the nutrients increased when the intense crown fire occurred, but twice as many decreased in this situation.

It is not possible to correlate high nutrient levels with high diversity directly. It appears that at these study sites the available species are adapted for more limited nutrient levels.

Table one shows the percentages of various ground covers in the four study sites as extrapolated from line transects. Sampling done at 0.5 meter intervals revealed that in the control sites, an average of 93% of the ground is covered with pine litter, needles, branches, or logs. In the ground fire site, 20% less or 70% of the ground is covered with litter. More of the area is covered with living plants and there is some bare ground which is receptive to colonization. In the crown fire plot a very small portion of the area is covered by pine litter. Most of the area is covered with forbs or is bare.

The crown fire plot has the largest coverage of living plants and bare ground. The area in the Crown Fire Plot was dominantly bare ground according to line transect sampling although the appearance is one of nearly total

plant coverage.

The extensive mat of pine litter in the control plots and absence of bare ground is an important limiting factor in plant growth and propagation of these sites. The decrease in pine litter at the ground fire plot is one factor allowing for the increase in diversity there.

The control plots had almost six times more pine litter on the forest floor than did the ground fire plot. Not only had the litter buildup in the ground fire plot been broken down by the fire and nutrients returned to the soil (in part), but also seedlings are more able to receive light when litter is decreased. It is likely that the buildup of needles prevents some precipitation from being absorbed into the soil. Also, many seeds are unable to reach the soil due to litter buildup.

The crown fire plot had no litter buildup as all potential litter was consumed by the fire. There were numerous fallen logs at this site and eventually all of the standing carcasses will fall.

Biological Conditions

In the absence of regular ground fire, the many pine saplings which sprout under an established ponderosa canopy grow into a dense tangle called a "doghair thicket." Due to canopy shading and competition among the

saplings for space, moisture, and nutrients, these trees weaken and die between the ages of five to thirty. Alive or dead they constitute a mass of highly flammable fuel which serves as a ladder for a ground fire to spread into the canopy. Regular ground fire would select against the weaker saplings. If such trees were growing under a healthy ponderosa canopy, nearly all would be restrained due to shading and root competition and most would be selected against by ground fire.

In measuring the individuals in my study plots, it was necessary to look at the interactions between the canopy and the understory. The canopy trees may exert a dominating effect on the understory vegetation by shading and root competition, but those plants beneath them are evolved for this and other kinds of stress (Grime 1977). Understory species also exert considerable stresses on each other and may be considered separately from the overstory. The former interactions are especially important in this study since I am comparing an intact forest with one in which trees had been killed by wildfire.

In the understory of the unburned plot there are far fewer plants than are found in the crown fire plot where the trees are all dead. Several important influencing factors differ here including light availability in the understory, soil nutrient levels, and the amount of ground open to successful germination (Connell 1978).

The trees in the crown fire site were bare of leaves. The skeletons that remained exerted little shadow on the understory compared to living trees in the shaded unburned plot. Therefore the plants found in the understory of the crown fire plot are not enduring restricted light to the degree that the understory species in the unburned plot are. This could be one factor in the greater number of plants in the crown fire plot.

In the crown fire plot, all of the trees were dead; only the understory could be examined. The grasses were separated because it is possible that their populations in the study sites were influenced by a Forest Service reseeding campaign after the fire. The control sites were selected from an area that was far from reseeded areas and probably not affected by the campaign. The crown fire plot was selected from an area positively not seeded.

The ponderosa drops a lot of litter to the forest floor, a very important factor in the ecology of the ponderosa pine community. Due to the dry climate of northern New Mexico and anatomical features of the ponderosa, this litter takes a very long time to decompose. Many species are unable to germinate successfully with extreme litter buildups. The litter also limits the amount of moisture reaching the soil surface and many individuals or species become locally extinct as a result. The number of species in the community are thus lowered. The accumulation of

litter increases until reduced by ground fire (see table one).

In the understory of the virgin plots, various composites were dominant in terms of abundance. Unless one were to study the morphology of the root systems, their nutrient uptake relative to the amount of available nutrients, the uptake of the other competing species, and competition factors, it would be difficult to determine if the number of individuals imposes significant restrictions on colonization by new individuals or species. I think rather that the litter buildup and the overpopulation by young pines, factors that would be corrected by frequent ground fire, are the important factors limiting diversity in the unburned plots. Notably, the ground fire site has no single dominant species in the understory and has the most equitable distribution of individuals among the species. There are five co-dominant species here. ✓

The plot affected by crown fire is populated by pioneer species which are r-selected plants. R-selection is characterized by dominant amounts of photosynthate being directed to propagule production rather than morphological features that would contribute to interference competition with neighboring species or individuals. The dominant species in this plot is Chenopodium album, found in many different areas of the Southwest on disturbed soils such as gopher piles at higher elevations in the

Jemez Mountains. It has nearly 10,000 more individuals than the next most abundant species in the crown fire plot.

Table three shows the numbers of understory species found in the different plots. Members of the Gramminea are not considered here. The increase in individual numbers within a species can be seen in the crown fire plot. Table four shows how few species were common to the crown fire plot as well as the ground fire and unburned plots. The ground fire and unburned plots shared more common species.

Control plot two and the ground fire plot shared the most common species. Control plot two had large openings in the canopy and the available light may have caused the difference between control plot one and control plot two. Also, the exposure was slightly different. Control plot one sloped slightly to the north whereas control plot two sloped slightly to the southeast.

The crown fire plot shared relatively few species with the other sites. Two of these are annual composites and the other is the shrub oak.

Diversity and Equitability

Diversity is highest in terms of abundance in the ground fire plot (see table five). In terms of area it is

highest in the crown fire plot. Some of the plants in the crown fire plot were very large as individuals where others were able to occupy large areas by having dense growths of numerous individuals. In the ground fire plot and the control plots, the plants were widely separated and as individuals were often larger than those in the crown fire plot. Verbascum thapsus and Chenopodium album occupied large areas in the crown fire site, Verbascum with a large rosette of basal leaves and Chenopodium in terms of large numbers. Thus each has different morphologies. The dominance of Verbascum will only be apparent in the indices based on area.

When one species has many more individual members than the other species, it is dominant in terms of abundance. The more dominant a species is in a community, the less equitable the community becomes. Hence fewer members of other species can find available habitat and species richness decreases.

Figure 1 shows the relative abundance curve or dominance-diversity curve for the species found in the four study plots. A horizontal line on such a graph represents an equitable distribution of individuals among the species present. The heavy line representing the ground fire plot is most nearly horizontal, showing a greater equitability. The crown fire plot curve and the unburned plots' curves have similar slope. These three

plots exhibited dominance by a few species. The crown fire plot is colonized recently by adventive species, some of which colonized more successfully than others. With the available habitat nearing saturation, competitive interactions among these individuals intensifies.

Litter buildup and years of competitive displacement among the species may have led to a decrease in equitability in the unburned sites.

Interestingly, these curves of the crown fire plot and the unburned plots appear similar although the ecological conditions in the two communities are radically different. All three plots have a few species that are codominant in similar proportions to the many less-common species.

The difference between the area and abundance calculations is most marked in terms of the ground fire plot. The diversity here is greatest in terms of abundance because there are five co-dominant species in terms of abundance and these are all plants which occupy a small area as individuals. Thus the area diversity is lower.

Taking the trees into account, the indices increase the most both in terms of area and abundance.

The indices using area take in to account the habits of the species rather than their population alone. Thus some insight into competition is possible using area calculations. The superior or inferior ability of a species

to gain light and substrate will be apparent in the higher area values for that species although it may be relatively less abundant.

The plots all had similar numbers of species. The main difference is in the number of individuals. The ground fire plot has the most equitable distribution of individuals among species whereas the crown fire plot has the least equitable distribution. The ground fire plot is more similar to the control plots than it is to the crown fire plot.

Diversity in terms of abundance is highest in the ground fire plot when the trees and understory are taking into account. The crown fire plot has the lowest diversity in terms of abundance.

When examining diversity indices in terms of area, the highest diversity is found in the crown fire plot taking into account all living species. The ground fire plot has lower diversity than the other plots except when examining forbs and grasses only, in which case control plot two is lowest.

GENERAL DISCUSSION

Niche Dynamics

In communities, each species present has niche requirements that are fulfilled somewhat by the available

resources. Some plants have very narrow niche requirements and thus are found only where these needs are satisfied. Dominance often occurs when the species has broad niche requirements and is therefore adaptable and able to exclude those neighbors with narrower requirements. Adventives commonly have a broader niche than plants in more advanced stages of succession. A habitat may often have an extreme shortage of nutrients and the dominant species will be adapted to such stress. The ponderosa Pine is such a species. It is able to tolerate low nutrient soils and aridity found where it is prevalent (Connell 1977). The borders of the ponderosa's potential habitat are defined by the ecotones that surround the ponderosa forest.

A species that is dominant in a community will often over-exploit its niche, especially if it is an r-selected species (Price 1975; Colwell 1969). This occurs when a species uses up the nutrients that define its habitable niche or limits them to the point where it is no longer able to maintain a dominant population level. Often in so doing, a previously dominant species will alter the habitat in a way that makes it possible for a new species or group of species to become dominant. This is one of the mechanisms of succession, especially in terms of ruderal vegetation, that is adapted to exploit broad niches quickly with high levels of reproduction and hence

and the recovery rate is longer. Disturbances such as severe storms, crown fires, and clear cutting by man have then an obvious effect on dominance structure in communities (Connell 1978).

Richness

As a habitat is exploited through time, each species present within the community exerts an influence on the nutrient base of the habitat. Plants tie up nutrients in the organic and inorganic compounds of which they are composed. Ponderosa pine does this on a large scale. Symbionts on other plants such as members of the Leguminosae take free nitrogen in the soil and fix it into organic compounds thus increasing the amount of available nitrogen for current and later generations of vegetation. A legume found within my study plots is Robinia. Thus plants exert a dynamic influence on the niches where they are found (Krebs 1978).

The overall diversity of the community may gradually increase through niche specialization if there are species to match the requirements and constraints created by the influence of past inhabitants on the habitat. High diversity implies a finely adjusted accumulation of co-evolved species (Price 1975; Pielou 1975; Colwell 1969; Ricklefs 1978). Species present in low diversity situations are

co-evolved as well. The diversity of a community will continue to rise in this way until the niches become limited beyond the specialization of the available species (Pielou 1975). Successful colonization will be less and less frequent as time goes on and after a point the diversity may decrease as more and more species are excluded. Populations of particular species will certainly decline.

The species found in the ponderosa community in Bandelier must be adapted to stresses such as drought, low annual precipitation levels, relatively poor soils, and very low humidity levels. The "niche" is a concept inherent to the ecological dynamics of organisms and such stresses in part define the niche. In Bandelier the physical environment is harsh and the resources for which the species compete are often limited (Connell 1978).

As colonization in a habitat progresses, there is more and more overlap in resource use among species. There is a maximum degree of overlap of niche utilization before one of the species involved is forced to specialize beyond its intrinsic capability to do so and may be eliminated. Assuming there is no perturbation, the diversity of a community may only increase until the degree of specialization required of the species for survival is exceeded by the limiting factors or stresses acting upon those species. This is another factor in richness and diversity (Colwell 1969; Pielou 1975; Krebs 1978).

Competition, the process of a species being limited by its neighbors, has many pathways in the dynamics of a community (Krebs 1978). Resource competition involves species that are both seeking a resource that is in short supply. Interference competition occurs when species impair each others' ability to obtain a commonly needed resource. This involves adaptations such as lateral rootsystems, large leaves, or branching patterns that shade potential competitors (Ricklefs 1977).

One path of competition in communities is the differential ability of neighbors to utilize commonly needed resources as described above. This is done through various morphological and physiological adaptations on the part of the species in question. Species have evolved different features and mechanisms with which to exploit commonly needed resources such as sunlight or compounds in the substrate. For example, differing leaf shape in apparently co-evolved species show different evolutionary pathways that deal with water loss and photosynthetic needs. Similarly, members of the Leguminosae have evolved the potential for a symbiotic relationship with the soil bacteria Rhizobium which allows these species to fix free nitrogen in the soil and thus become adaptable to situations where fixed nitrogen is in short supply. There are countless such examples of evolution and speciation which consequently are important in the dynamics of community

ecology (Esau 1977).

Some plants have widespreading root systems which range far from the plant of their origin and crowd out root systems of other plants seeking water and nutrients in their immediate locale. This occurs in ponderosa communities as ponderosa pine has a shallow widespreading root system which ranges far for the scarce nutrients and water.

Shading is a similar type of competition. Plants often develop large leaves or habits which give them advantage in light gathering. Understory plants in forests are adapted to endure shading. As mentioned above, young trees are able to endure shading from the canopy better than mature trees of the same species. But the growth of conifer species is slowed considerably by the lack of light. When a break occurs in the canopy, these trees will accelerate their growth and eventually occupy the opening in the canopy. This ability has been especially noted in redwood (Sequoia sempervirens) forests (Viers 1972). In ponderosa forests the shading caused by the canopy is not as dark as that in redwood forests. But the same process occurs with understory conifers in the ponderosa forest.

There are at least two broad categories of competition types among organisms. R-selected plants are adventives or pioneer species which have reproductive

individuals and the ability of the species to maintain its position within the makeup of the community. Sexual reproduction is not emphasized by these plants as it is primarily in r-selected plants. These plants are adapted to pressures of prolonged resource competition and are always perennials, often with long life spans as in the case of overstory trees. There is interspecific competition among K-selected species whereas r-selected species are not adapted for this to the same degree.

Predation is a vitally important factor in the dynamics of community structure. Without predation, communities would have the potential for reaching equilibrium, assuming no disturbances occurred (Grime 1977; Huston 1979). Competitive pathways and individual growth patterns among species could continue with no interference and the diversity of the community would eventually stabilize.

Predation in the ponderosa community is vastly complex and to quantify and understand its effect on the plant community would require an extensive study. The dynamics of predation and competitive exclusion are closely intertwined (Grime 1977; Price 1975). Predators in many cases keep species' populations below levels where competitive exclusion takes place (Krebs 1978).

Forbs are browse for various ungulates in the Jemez Mountains, including mule and white tailed deer, elk, and

feral burrows. There are numerous rodents that prey upon the seeds of the forb species as well as pine nuts. I observed a ground chipmunk eating the seeds of umbel-bearing forbs. In a short time it had consumed hundreds of these seeds. Numerous species of ground and tree squirrels and other rodents in the ponderosa forests of the Jemez Mountains no doubt have a marked impact on the seed crops of many plants, thus affecting the future generations. Pines have adapted to having a large number of their seeds reduced in this way and the impact is slight due to their overall reproductive strategy. Pioneer species such as those found in the crown fire plot will be more affected by this type of predation, although adaptations that compensate for this type of predation most likely exist in these species.

Dominant species have a greater chance of becoming browse for mammals than do less dominant species; the frequency of encounter with a predator is greater than with rare species (Price 1975). Thus predation is variable with population sizes and is one of the factors imposing upper limits on population sizes. Also, different predator-prey relationships exist among different plant species, depending on the morphological and biochemical features of the particular plant and the co-evolved predators.

Equilibrium and Stability

Equilibrium is an ecological concept that has been reconsidered by recent workers (Connell 1978; Ricklefs 1978; Price 1975; Huston 1979). In the early days of quantitative ecology, workers such as Lotka and Volterra (1925) designed mathematical models that assumed a stabilization point (equilibrium) was possible in ecological systems. A great deal of work was done through the years using models such as these where theory was devised around convenient mathematical models (Huston 1979). Workers such as Robert MacArthur began to sense the shortcomings of this approach but in many cases based their work on equilibrium models. The concept of stability is analogous to equilibrium. The idea that "diversity leads to stability" is still common in elementary ecology and is a premise for many management techniques in use by land managers today.

In order for there to be equilibrium in a community system, all of the factors such as predation and the various forms of competition discussed earlier would have to stabilize so that they were no longer causing significant fluctuations in specific populations. Huston (1979) points out that the process of stabilization of a community ecosystem would take a very long time for a number of reasons. Each species has a different competitive ability

relative to the other species around it in the community. Species have individual growth rates and thus the process of competitive exclusion will take a long time to complete and stabilize the various specific populations. Even when the community appears to have stabilized, there will still be some species whose populations are still changing and their influence on the other species and on the niches is not yet fully expressed. This is, in short, the rate of approach to competitive equilibrium.

In most communities, predation and perturbation prevent the growth structure of the community from ever resolving itself. These factors are variable and in wilderness situations would keep most communities in a recurring state of flux. Thus succession would be a cyclical process instead of a conclusive process. It can be disrupted at any point and the duration of the overall cycle will be longer or shorter accordingly. Many perturbations only occur when the victim population is vulnerable. For example, even aged stands of ponderosa pine are often attacked by the western pine beetle (Dendroctonus brevicomis) which weakens the trees and often causes death. Thus the forest attains an uneven age structure which is the way it occurs in totally unmanaged wilderness situations (Weaver 1974). Fire is a similar perturbation. When a stand of ponderosa becomes too dense or accumulates too much litter it is vulnerable to fire. The fire may be a

low ground fire or a crown fire, depending on the condition of the community. My observation is that ponderosa communities are never in a state of equilibrium due to their dependence on fire. If an artificial equilibrium is imposed on a ponderosa forest through the suppression of fires, the result is an unhealthy tangle of malnourished ponderosas and the exclusion of most other species. Importantly, the potential for crown fire in this situation increases as suppression efforts are continued (Weaver 1974; Gartner and Thompson 1972; Biswell 1972). Thus when such an equilibrium is imposed on the forest, the potential for perturbation increases.

It is common for a community to have a dominant species if there are excesses of a resource present (Price 1975). For example, a plant that is adapted to high levels of Potassium in the soil will have an advantage over plants that may find the same levels toxic or restricting. In the crown fire plot there is an excess of many resources such as sunlight and space. After the fire, the potential for colonization here was very high; all the previous vegetation had been cleared and the soil was enriched by the breakdown of organic compounds previously tied up in vegetation (Biswell 1972). Although in my sites the levels of many important nutrients decreased with the intensity of burning, other workers have found higher levels of necessary soil nutrients in sites affected by

ground fire (Dickson 1976; Biswell 1972; Gartner and Thompson 1972; Viers 1972). Once again the time lapse between burning and soil nutrient measurement may be an important factor in the decline of many of the nutrient amounts.

CONCLUSIONS

The diversity of the sites studied here which experienced light ground fire in the La Mesa fire of 1977 was higher than either the sites which experienced intense crown fire or which had experienced no fire for seventy years. There are only slight differences in the number of species found at the four different sites. The major factor in the variation of diversity is the evenness of the population distribution among the species present. The ground fire site has a more equitable distribution of individuals among the thirteen species found there than does the crown fire site or the control plots. The equitability of the ground fire site is markedly higher than that of the control sites which in turn was higher than the crown fire site. The many ecological events which potentially cause the differences in equitability are discussed in chapter three. These include various competition pathways, predation, and physical factors such as nutrient levels, litter buildups, and light availability.

Contrary to the findings of other workers such as Biswell and Weaver, I found that nutrient compound levels in the sites that had experienced ground fire are lower than the nutrient levels in the unburned sites. Exceptions include the ions sulphate, chloride potassium and phosphorus. These increased with the intensity of the burn as they were markedly higher in the crown fire site. Ion levels in the soil immediately after the fire may have been drastically different than those found here two years after the actual burning.

In its uninterfered-with wilderness state, the ponderosa pine community is continually experiencing ground fires (Foxy 1978; Weaver 1974). Fires are frequent and low key (Foxy 1978; Biswell 1972). Fires are one of the major ecological factors maintaining the diversity of the ponderosa community. This is exemplified by the changes that occur in the community when fire is eliminated and by the evidence that suggests that ponderosa pine is fire adapted. If fire is considered an intrinsic part of the ecological processes that regulate the ponderosa community, if one looks at a community where ground fire is somewhat regular over an extended period of time (100-200 years), then the community may be said to be in a state of equilibrium. This view is valid if ground fire is not classified as a perturbation; the species present in the community over extended ecological time will vary only

slightly.

A ponderosa forest where natural ground fires occur at thirteen to twenty year intervals is in a state of continuous change; fire eliminates the foliage but the roots of the perennials remain alive. Local populations of annuals will be reduced considerably if their sexual or asexual propagules are destroyed. Annual plant populations in large, intensely burned areas will be slower to recolonize; colonization will depend largely on off-site propagules (Foxy 1978). In areas that experience ground fires at natural intervals, there will be a "micro-succession" process between fires always occurring. The diversity of the understory species will be low immediately following a fire but will increase until the niches available are filled. Diversity in terms of understory species will decline as competitive pressures among species increase and soil nutrients are exhausted. Many perennials survive ground fire and will reestablish themselves from living root systems soon after the burn (Foxy 1978; Weaver 1974; Gartner 1972). It is possible that within the interval between naturally occurring ground fires diversity may not decline very noticeable. Further study on this question is needed. If many annual pioneer species colonize an area following a ground fire, their decline during the interval between ground fires will reduce the species richness. The existing perennials will

expand their populations and eliminate many annuals through competitive displacement.

If fires are eliminated altogether from an area, the richness and equitability of an area will decline as litter buildup increases and as the selective force of fire ceases to eliminate the overabundant ponderosa seedlings in the understory. The eventual result is a "doghair thicket" monoculture of ponderosa pine. The vulnerability of such an area to crown fire is very high (Weaver 1974; Biswell 1972).

The crown fire area has been set back to pre-grassland succession as evidenced by the annuals found there. In the arid climate of New Mexico its return to fully established forest land will be slow.

Health is a subjective term. When referring to community ecology, there are many elements on which workers are not in complete agreement. Application of the concept of "health" to community ecology becomes more difficult and ambiguous. However, a diverse community having more species has more genetic pathways on which selective forces may act. A diverse community may be more resilient to changes such as climate variation and pollution (Huston 1979; Krebs 1978).

The sites that have experienced no natural fires over an extended period of time are less diverse and are extremely prone to crown fire which can alter the forest

community completely. In terms of ponderosa community, this condition may be said to be "unhealthy" as it threatens to destroy the forest completely. Also, the nutrients of the system are tied up in slow growing and decaying plant structures when fire is suppressed.

The elimination of natural ground fire from the ponderosa community is a questionable management practice. The extensive wildfires which have plagued western forests, including ponderosa communities in the last few summers, can be traced in cause to the suppression of fires. The La Mesa fire in Bandelier National Monument during the summer of 1977 was only one of eight wild fires during that summer in Arizona and New Mexico. Concurrently in California the highly destructive "Marble Cone" fire in the Big Sur Mountains raged.

Fire is a natural, intrinsic part of many ecosystems and can be used to great advantage by wilderness "managers." The buildup of fuels in forests due to prolonged fire suppression is creating an ever increasing problem for forest managers. The National Park Service has in many areas come to realize the importance of fire in wild ecosystems and is successfully using it as a wilderness maintenance tool.

Today there is a wide body of ecological knowledge generated in laboratories and universities around the world. Yet the management techniques used by industry and

government agencies on forest land most often reflect ignorance or arrogance to current ecological knowledge. If the productivity or wilderness quality of our forest land is to be maintained, the gap between knowledge and practice must be bridged; ecological research is not just an intellectual novelty.

TABLES AND PHCTOGRAPHS

TABLE 1

Percentage of Various Types of Ground Cover

	Pine Litter*	Living Plant Matter	Bare Ground	Dead Forbs	Rock
C P 1	93	6.6	-	-	-
C P 2	93.3	3.3	-	-	3.3
G F P	70	16	13	-	-
C F P	3.3**	40	53	3.3	-

* This includes pine needles, fallen branches, and fallen logs.

** In the crown fire area there were no needles left after the fire. This percentage was entirely trunks of trees killed by the fire and felled by boring insects.

TABLE 2

Depth of Pine Needles at the Four Study Plots

	Depth, cm
Control Plct 1	2.85
Control Plot 2	2.90
Ground Fire Plot	0.50
Crown Fire Plot	0.00

TABLE 3

Abundance of Plant Species in the Four Study Plots

Species Name	Individuals
Control Plot 1	
<u>Erigeron</u> sp.	166
<u>Solidago decumbens</u>	53
<u>Penstemon bridgesii</u>	8
<u>Thalictrum fendleri</u>	5
<u>Quercus gambelii</u>	4
<u>Rosa fendleri</u>	3
<u>Solidago</u> sp.	2
<u>Robinia neomexicana</u>	1
TOTAL	243
Control Plot 2	
<u>Townsendia exscapa</u>	56
<u>Solidago</u> sp.	31
<u>Erigeron macranthus</u>	14
<u>Aster integrifolius</u>	11
<u>Rosa fendleri</u>	2
<u>Juniperus scopulorum</u>	1
<u>Quercus gambelii</u>	1
<u>Robinia neomexicana</u>	1
<u>Lithospermum multiflorum</u>	1
<u>Fragaria ovalis</u>	1
TOTAL	119
Ground Fire Plot	
<u>Townsendia exscapa</u>	34
<u>Solidago</u> sp.	30
<u>Aster integrifolius</u>	23
<u>Robinia neomexicana</u>	22
<u>Allium cernuum</u>	22
<u>Gilia texana</u>	6
<u>Geranium caespitosum</u>	6
<u>Ceanothus fendleri</u>	5
<u>Lithospermum multiflorum</u>	5
<u>Erigeron macranthus</u>	4
<u>Rosa fendleri</u>	4
<u>Penstemon bridgesii</u>	2
<u>Taraxacum officinale</u>	1
TOTAL	164

TABLE 5

Diversity Indices (H) Based on Abundance

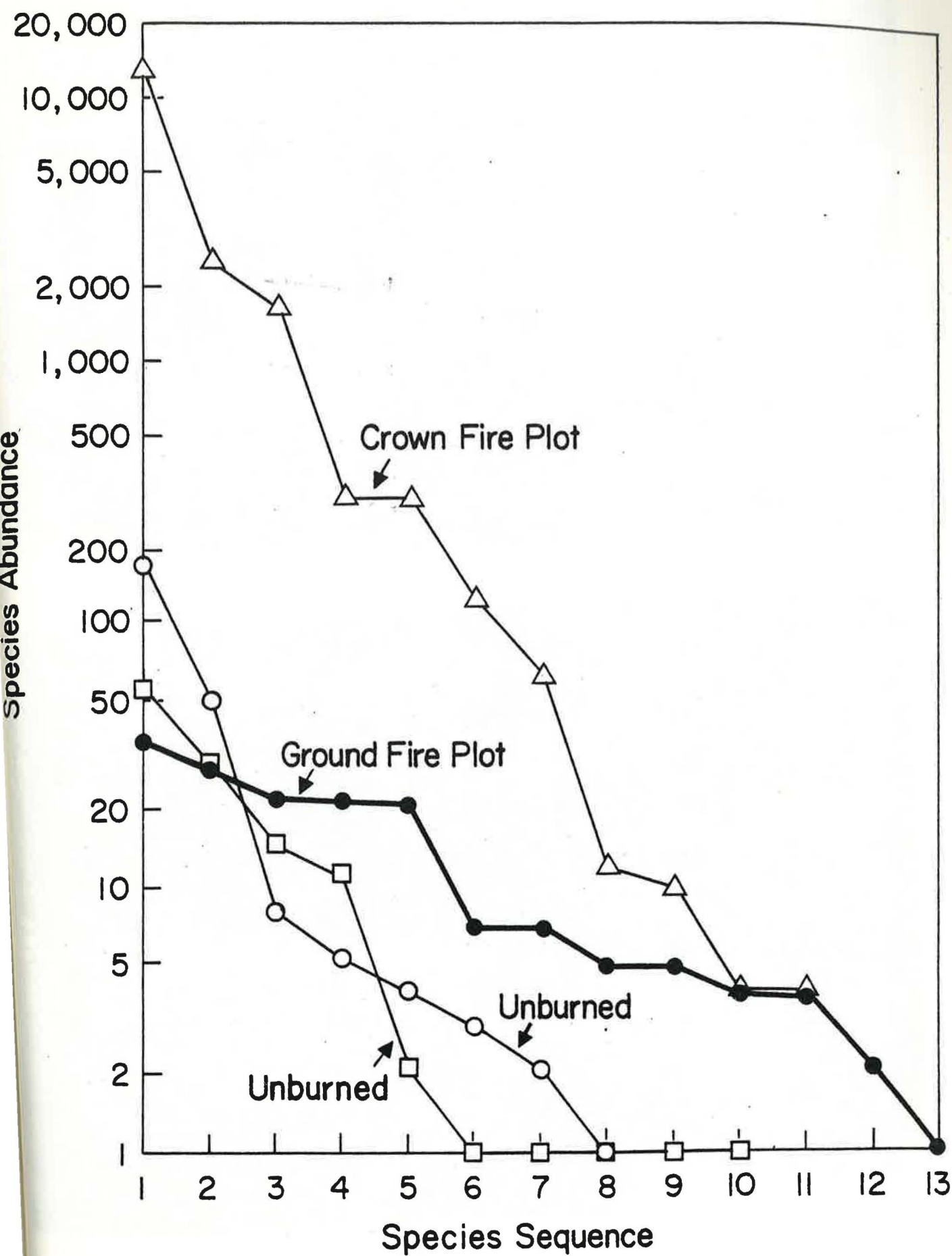
	Understory	Canopy, Understory
Control Plot 1	1.528	1.695
Control Plot 2	2.099	2.392
Ground Fire Plct	3.169	3.314
Crown Fire Plot	1.360	1.360

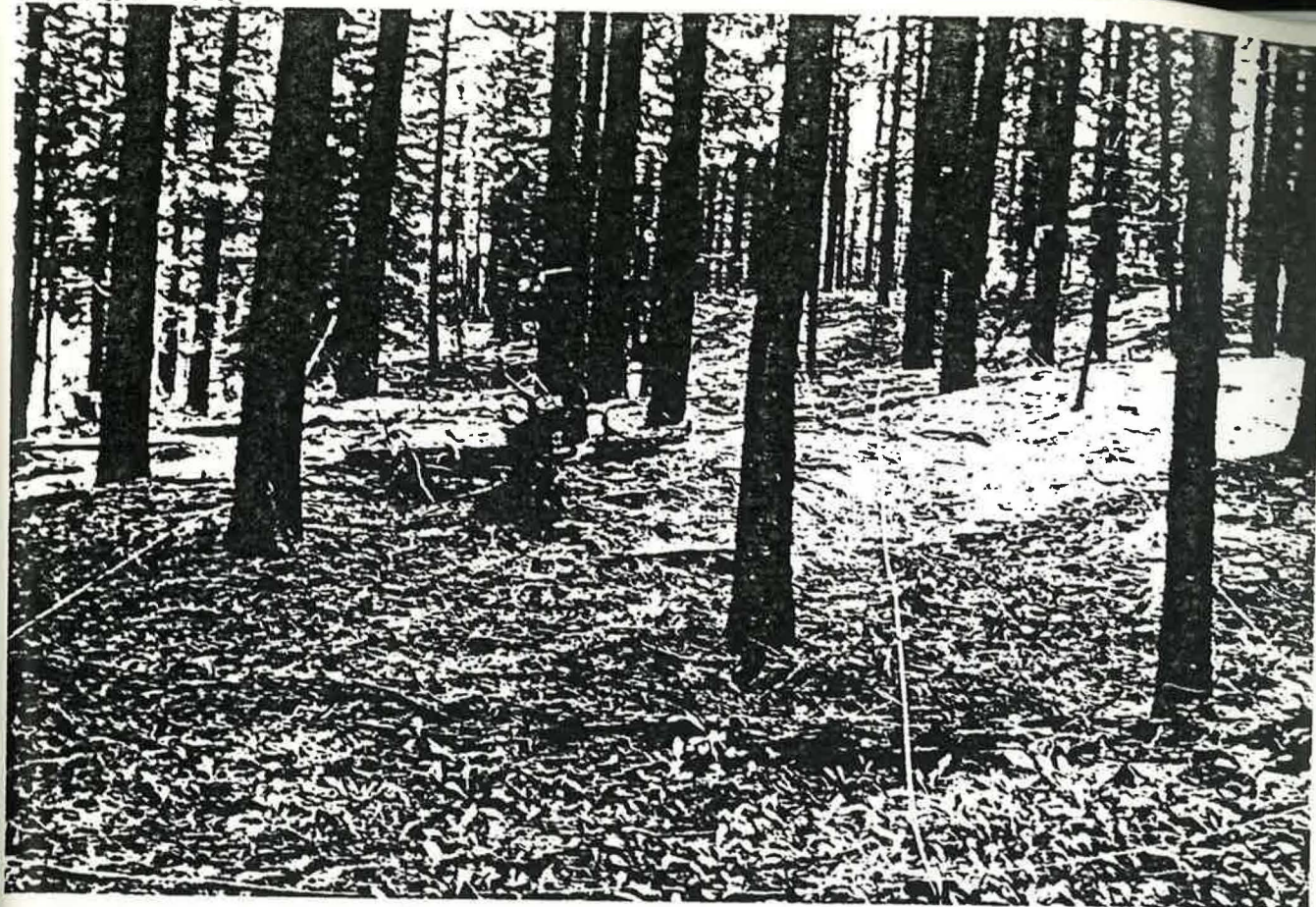
TABLE 6

Equitability Indices Based on Abundance

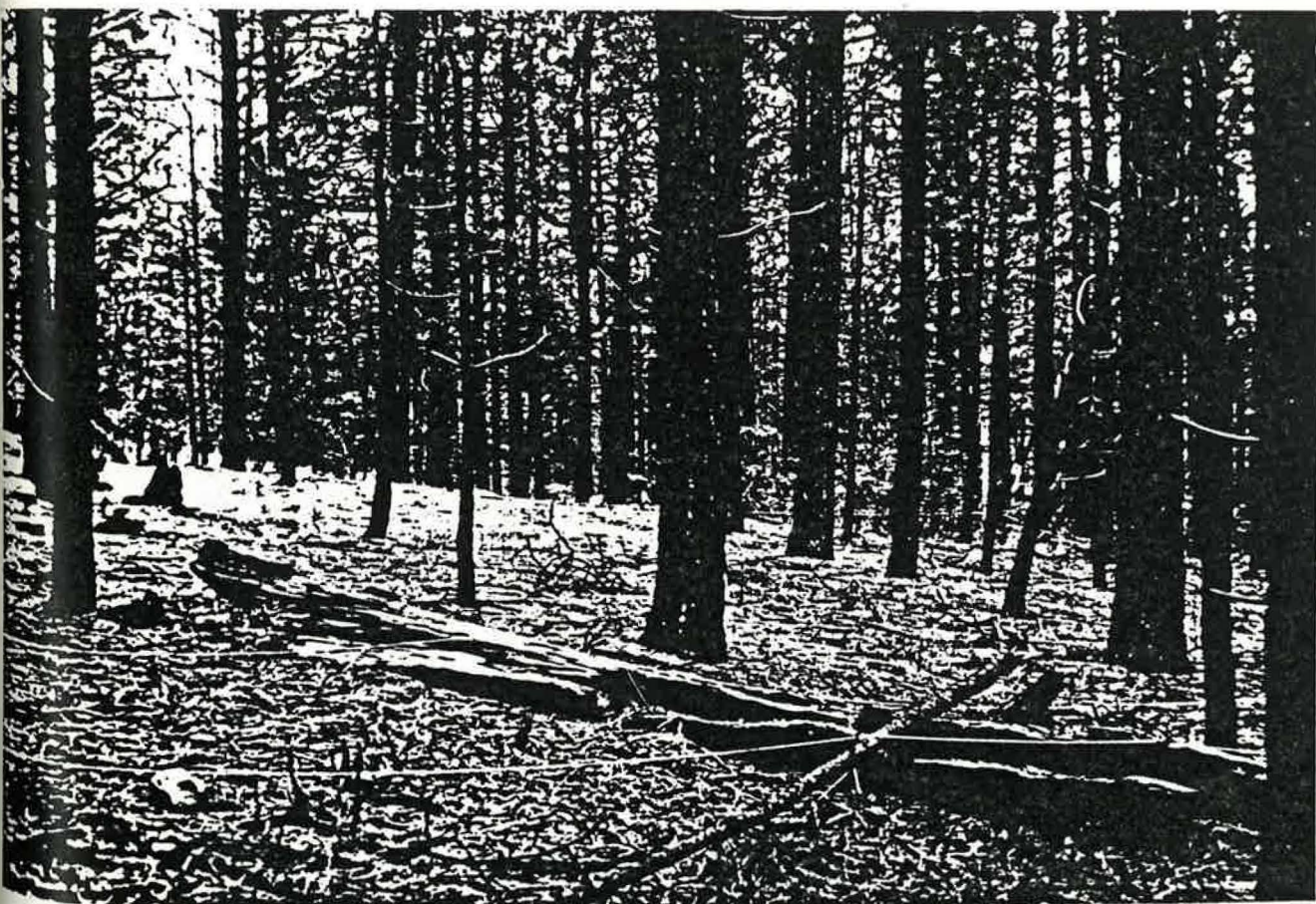
	Understory	Canopy, Understory
Control Plot 1	0.4807	0.5103
Control Plot 1	0.588	0.670
Ground Fire Plct	0.832	0.8181
Crown Fire Plot	0.367	0.367

FIGURE 1

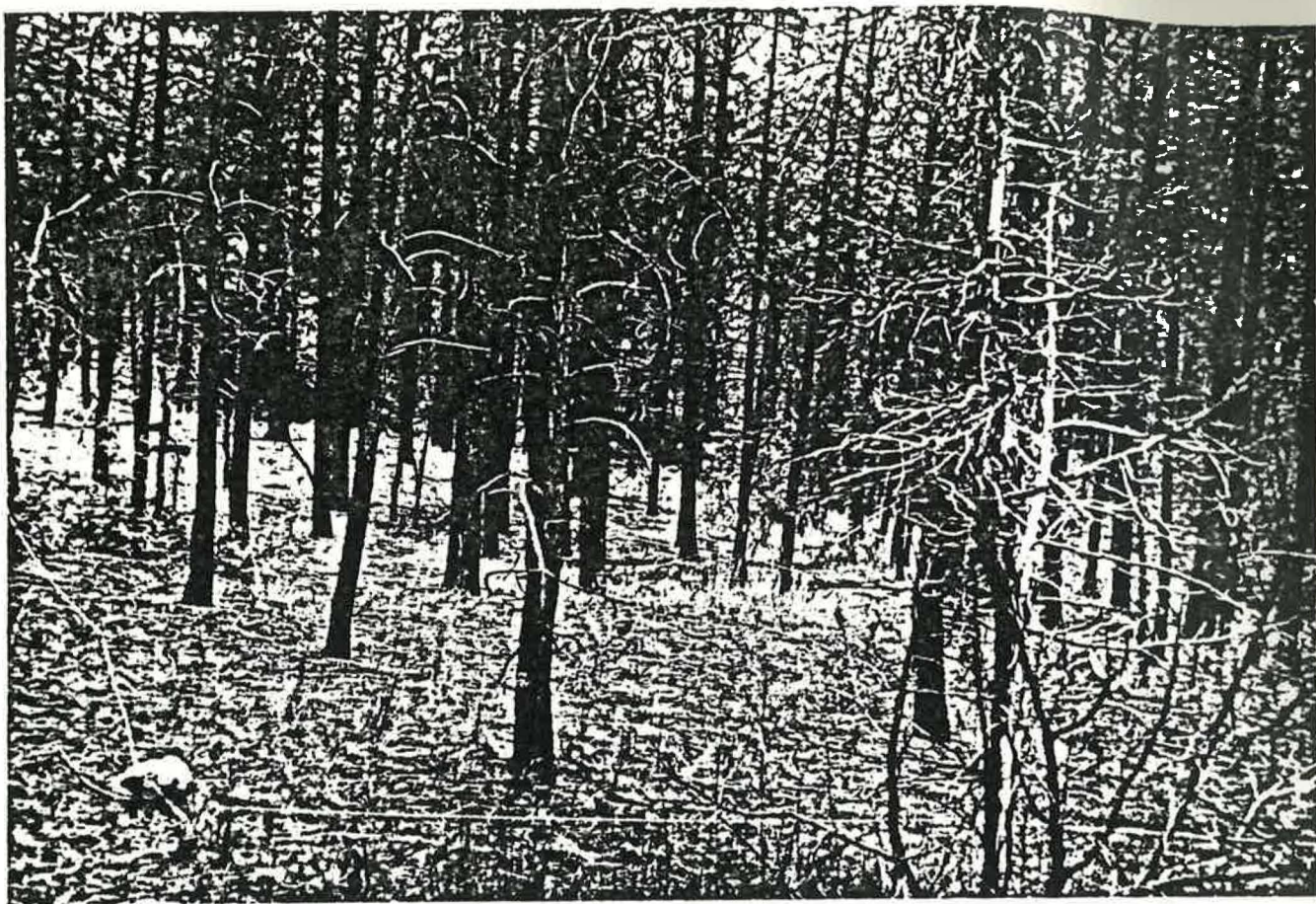




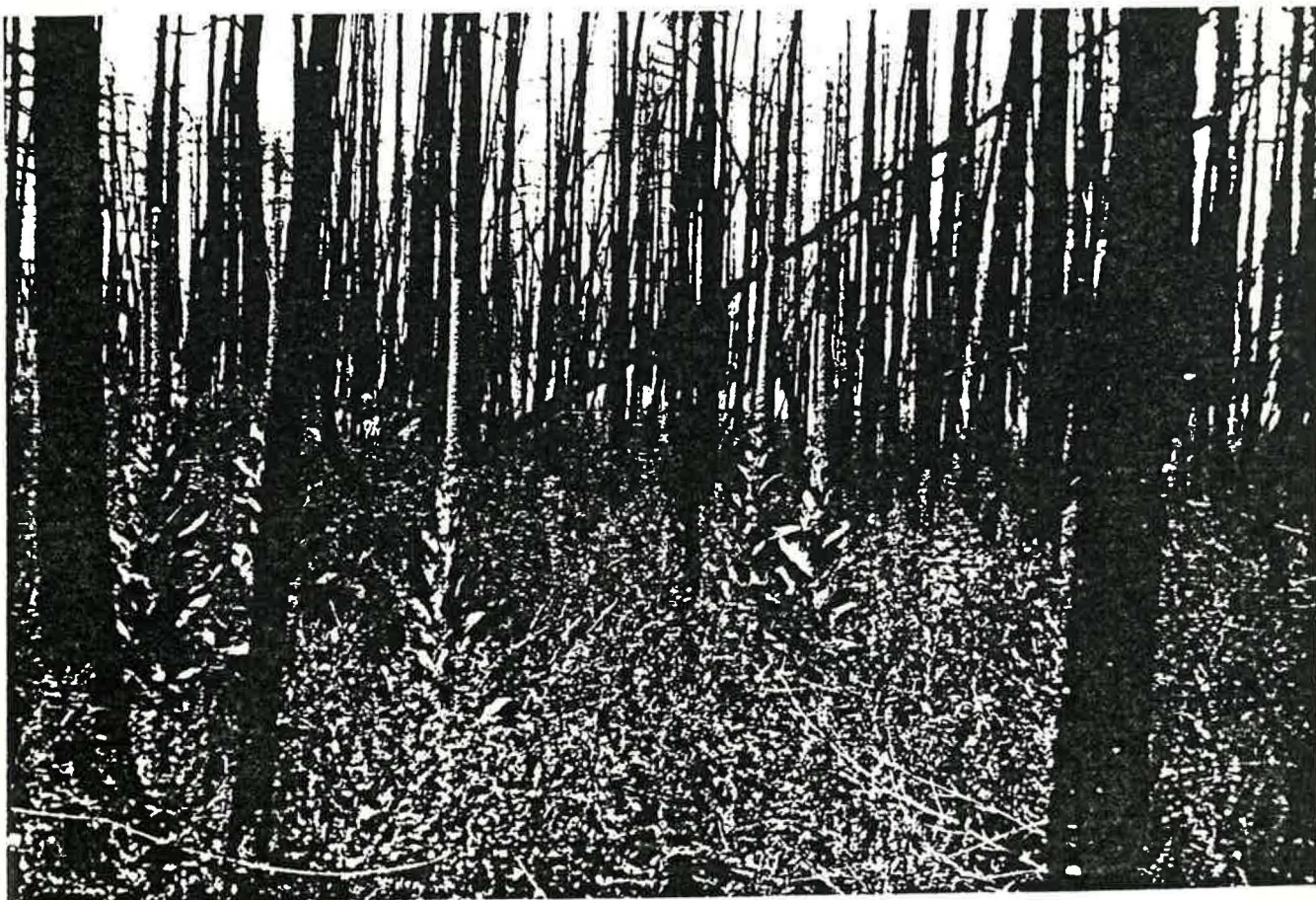
Control Plot 1



Control plot 2



Ground Fire Plot



Crown Fire Plot

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