REGENERATION PATTERNS WITHIN CANOPY GAPS IN A GIANT SEQUOIA-MIXED CONIFER FOREST: IMPLICATIONS FOR FOREST RESTORATION

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A Thesis

Submitted in Partial Fulfillment

of the Requirements for the Degree of

Master of Science

in Forestry

Northern Arizona University

December 1995

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The Giant Forest grove of giant sequoia trees (*Sequoiadendron giganteum*) is one of the largest of this species' 75 extant groves, all of which are located on the western slope of the Sierra Nevada (Rundel 1971). Construction of lodging and other tourist facilities in the Giant Forest for the newly established Sequoia National Park began in the early part of the 20th Century and escalated throughout the 1930's. In recent years, the National Park Service has recognized the potential impacts of concentrating heavy visitor use in this area and has begun relocating these lodging facilities to another site. When the new construction is completed, projected for the year 1999, most of the buildings in Giant Forest will be removed and efforts will be made to restore the forest to a more natural condition.

The Giant Forest has been so influenced by both aboriginal and European humans that no clear definition exists of natural conditions (Bonnicksen and Stone 1981, 1982a). In species composition, density, and horizontal and vertical structure, the forest has been considerably altered from its presettlement state due to a century of fire suppression (Bonnicksen and Stone 1981, 1982a). The historic mosaic pattern of burns and reproduction, a critical horizontal structure for the dominance of giant sequoia (Parsons and DeBenedetti 1979), has become more uniformly dominated by mature trees in the absence of fire (Bonnicksen and Stone 1981). This increase in area dominated by patches of pole-sized and mature conifers has been accompanied by a decrease in area dominated by patches of saplings and seedlings, shrubs, grasses, and forbs (Bonnicksen and Stone 1982a). The vertical structure of the forest has become more complex, with the survival of one or more vertical layers of white fir (*Abies concolor*) beneath the dominant overstory of giant sequoia and pine (Bonnicksen and Stone 1982a). The managers of Sequoia National Park have used prescribed fire, with no explicit structural goal for the vegetation (i.e., a goal which includes desired species composition, age distribution, density, and spatial arrangement of trees), in an attempt to restore this natural process to Giant Forest. Whether this treatment will also restore a more natural structure to the forest has been questioned (Bonnicksen and Stone 1982b, Bonnicksen 1985, Bonnicksen and Stone 1985). In a recent workshop, scientists and managers acknowledged the importance of the interaction of the fire process with vegetation structure and the necessity of defining structural criteria for restoration (Parsons 1994).

The task of restoring Giant Forest thus includes two distinct problems: how to integrate, both ecologically and visually, formerly developed areas into the rest of Giant Forest; and how to document historical ranges of forest structure and restore the entire Giant Forest to a more natural state within this range. The standard approach of dating live trees and dead woody material to reconstruct a historic stand structure (Henry and Swan 1974, Oliver and Stephens 1977, Covington and Moore 1994) has been applied in giant sequoia groves of Sequoia National Park by Bonnicksen and Stone (1982b). However, Stephenson (1987) stated that this approach cannot be used without bias in the giant sequoia-mixed conifer type due to substantial decomposition of dead woody material, particularly white fir (Harmon and Cromack 1987), since presettlement time (circa 1890). The method has also been criticized for providing a static "snapshot in time," without addressing temporal variation in forest structure (Parsons et al. 1986). While temporal variation in disturbance regimes can be addressed through fire scar analysis (Swetnam 1993), it is more difficult to determine how temporally variable disturbance regimes affected forest structure.

As an alternative approach, I have studied tree recruitment within canopy gaps in response to gap size in an attempt to infer historic forest structures based on the predominant scale of the disturbance regime at various times in the past millennium. Specifically, this study analyzes how changes in the scale of disturbance affect spatial patterns of tree recruitment within canopy gaps in a giant sequoia-mixed conifer forest for the purposes of: (1) defining a conceptual model of species composition and spatial distribution of tree seedlings within disturbed patches in developed Giant Forest; and (2) determining how historical variation in climate and fire regime has affected forest structure (i.e., defining a past range of natural forest structure). I address three ancillary questions within this greater context. First, what are the community-level, spatial patterns of gaps presently within Giant Forest? Second, does woody species composition vary with gap size? Finally, what are the spatial patterns of regeneration within different-sized gaps? This study addresses several of the research needs defined by the scientists and managers of Sequoia National Park (Lee 1993, Parsons 1993), and contributes to the understanding of how the scale of disturbance controls forest structure.

This thesis is organized in a manuscript format, with a Literature Review chapter followed by a manuscript chapter. The manuscript chapter is intended for submission to the journal *Restoration Ecology*. Because the manuscript shares some common material with other chapters, there is some redundancy, which I have tried to keep to a minimum.

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CHAPTER 2

LITERATURE REVIEW

Introduction

The cyclic structure and processes of forests have long been of interest to ecologists. In particular, the characteristics of disturbance events (e.g., type, spatial scale, frequency, severity), the nature of the cohort of vegetation that establishes following disturbance, and the patch-like pattern created by repeated disturbance have long been topics of study. Most ecologists agree that disturbance phenomena, such as the formation of gaps by treefall and fire, drive forest development (sensu Oliver 1981) in nearly all forests (Watt 1947, Cooper 1961, Whitmore 1982, Pickett and White 1985, Whitmore 1989), and that certain species have developed specialized life-history characteristics to take advantage of gaps. These pioneer species tend to have numerous lightweight, well-dispersed seeds that are incapable of germinating or becoming established in shade, and tend to have rapid height growth. In contrast, climax species tend to have fewer, larger seeds which are capable of germinating and becoming established in shade (Whitmore 1989).

Ecologists have also recognized the importance of varying scales of disturbance in driving forest development (Drury and Nisbet 1973, Oliver 1981, Sousa 1984, Spies and Franklin 1989). A body of work investigating disturbance and patch dynamics has shown that the size of the gap in a forest canopy affects the light, moisture, temperature, and nutrient regimes in the forest floor beneath the gap (Forman and Godron 1981, Canham and Marks 1985, Runkle 1985). Different-sized gaps possess very different patterns of environmental gradients, and the vegetation should sort itself out along these gradients because of the differential growth, survival and dispersal of species adapted to grow at different points along stress gradients (Drury and Nisbet 1973, Whittaker and Levin 1977, Noble and Slatyer 1980, Sousa 1984, Thompson 1985). While mature individuals of different species may seem to occupy identical habitats, microenvironments within gaps may be especially important in determining species composition at the regeneration stage when species have more specific requirements, allowing niche differentiation (Grubb 1977). Thus, different-sized gaps may contain fundamentally different vegetation in a predictable manner.

The contents of this literature review are set within a theoretical context of disturbance and gap dynamics. I first discuss the gap environment, how it differs from the environment under an intact canopy and how resource gradients within gaps are formed. I then discuss life history and physiological characteristics of Sierra Nevada mixed conifer tree species and postulate how each might perform in a gap environment. Finally, I address landscape-scale processes and the influence of gap-level structures and events on larger scale phenomena.

A "canopy gap" is defined here as a site at which a canopy individual or individuals have died, resulting in a change in the surviving community (Christensen and Franklin 1987). "Patch" is defined as the resultant unit of vegetation arising within the gap (White and Pickett 1985).

The Gap Environment

When a canopy gap is formed by disturbance, the environment at that site is abruptly modified. The degree of microclimatological change produced by the gap generally increases with the size of the opening. Microclimate also varies within gaps; gradients are related to distance from the forest edge, the size of the opening, and its geometrical configuration (Lee 1978).

Light

Most studies of the gap environment have focused on the light regime, because light is so directly altered by the creation of an opening in the canopy. Light intensity and duration are greater in gaps than under an intact canopy (Brokaw 1985, Collins et al. 1985). Minckler and Woerheide (1965) found that as gap size (measured as a ratio of gap diameter to intact canopy height, or D:H) increased, light intensity also increased, from a minimum of 10% full sunlight under an intact canopy to a maximum of 65% to 90% full sunlight at a D:H of 2:1. Working in a southeastern hardwood forest, Phillips and Shure (1990) found that solar radiation, integrated over 24 hours, was 2 to 4 times higher in large (2.0 ha) than small (0.016 ha) canopy openings and increased from edge to center within each opening. Canham and others (1990) investigated light regimes beneath closed canopies and tree-fall gaps in five temperate and tropical forests using hemispherical photography. In the an old growth Douglas-fir (*Pseudotsuga menziesii*) - western hemlock (*Tsuga heterophylla*) forest in the Oregon Cascades, the understory in a single treefall gap received only slightly more photosynthetically active radiation (PAR) than beneath an intact canopy due to the extreme height of the surrounding canopy in relation to gap radius and the high latitude of the site. In four other forest types, small, single-tree gaps produced significant increases in understory PAR. In the northern latitude gaps, the highest intensity light occurred north of the center of the gap, and the light influence extended beyond the projected outline of the gap into the understory adjacent to the borders of the gap (Canham et al. 1990).

Light quality in gaps also differs from that beneath an intact canopy. Light which has been attenuated by passage through a forest canopy is depleted of red, blue, and green wavelengths due primarily to absorption by chlorophyll. Consequently, light reaching the forest floor is enriched in far-red radiation, which is not absorbed by leaves. While the red:far red (R:FR) ratio of sunlight is approximately 1.1, the R:FR ratio beneath a white pine canopy is 0.25 (Kozlowski et al. 1991). Thus, plants receiving direct, unattenuated light in gaps receive light of higher spectral quality than plants growing beneath an intact canopy.

Lieberman and others (1989) argue against using a strict gap vs. non-gap dichotomy of classifying light regimes, citing the wide heterogeneity in light regimes found in "intact" canopies. They state that the entire range of conditions present, from dense shade to full sunlight, must be considered when asking how species respond to openings in the forest canopy, and that questions should be framed in terms of the continuum of light levels or canopy closure rather than in terms of gap characteristics. This conflict could perhaps be avoided if the discussion of gap phenomena is restricted to openings in the canopy caused by discrete disturbance events. In such cases, the borders of the disturbance should be definable. In addition, a disturbance event results in a dramatic change in a number of resources other than light (e.g., the formation of belowground gaps) (Pickett and White 1985).

Soil Moisture

Processes which affect the soil moisture regime in gaps include throughfall, evaporation, and transpiration. Due to the interception of a large fraction of rainfall by intact forest canopies, much more precipitation may reach the forest floor in gaps than beneath intact canopies (Collins et al. 1985). Less rainfall reaches the soil in smaller gaps because of interception of slanting rain by edge trees (Geiger 1957). Evaporation from the soil is greater in gaps than intact forests, and during dry periods moisture levels are lower at the surface. However, soil moisture at a few centimeters depth is usually greater in gaps than intact forests, where mature trees compete for available moisture (Lee 1978). Minckler and Woerheide (1965) report that available soil moisture in the top 46 cm of soil increased from 5% beneath an intact canopy to 10% at the edges of gaps and 20% near the center. In the northern hemisphere, the northern portions of gaps may be drier than other areas due to greater insolation and subsequently greater plant growth and transpiration (Collins et al. 1985).

In the Sierra Nevada, where most of the annual precipitation falls as snow during the winter months, snowfall dynamics greatly affect the soil moisture regime. The snowpack in gaps has a greater water content than the snowpack under intact canopy due to the following: (1) interception of snowfall by the forest canopy and its subsequent evaporation or sublimation, (2) heavier distribution of snowfall into gaps during snowstorms, due to local-scale wind patterns, and (3) redistribution of snow into gaps by wind after snowstorms. Snow in gaps also melts sooner and more quickly in large gaps than under an intact canopy (Stephenson 1988).

Temperature

Soil and air temperature can be much higher in gaps and fluctuate over a greater range (Brokaw 1985) than under an intact canopy. Within gaps, the exposure to direct solar radiation during the day and the lack of a canopy to reradiate longwave radiation at night cause higher maximum and lower minimum soil temperatures in gaps than in closed forests (Lee 1978). Patterns of air temperature are more dynamic and appear to depend on gap size, insolation, and wind patterns. Maximum temperatures increase with increasing gap size, until at some point increasing winds in large gaps cause maximum daytime temperatures to decrease and minimum nighttime temperatures to increase (Geiger 1957, Lee 1978, Collins et al. 1985); an intermediate gap size thus exists at which air temperature extremes are greatest (Lee 1978). Minimum temperature decreases with distance from gap edge, with the frequency and amount of dewfall and frost formation increasing with distance from edge (Lee 1978). Phillips and Shure (1990) found that both soil temperature and air temperature increased from edge to center of openings, especially in larger patches. Soil and air temperatures were higher in large than small openings.

Nitrogen

Several studies have documented increasing microbial activity and net nitrogen mineralization following vegetation removal (Vitousek and Melillo 1979, Matson and Vitousek 1981, Frazer et al. 1990), in treefall gaps (Mladenoff 1987), and following fire (Jorgensen and Wells 1971, St. John and Rundel 1976, Kutiel and Naveh 1987, Kutiel and Shaviv 1992). A pattern of total N loss during fire, followed by an immediate increase in ammonium and a delayed increase in nitrate, has been shown in both coniferous (Jorgensen and Wells 1971, St. John and Rundel 1976, Kutiel and Naveh 1987, Covington and Sackett 1992, Kutiel and Shaviv 1992) and deciduous (Kutiel and Shaviv 1992) forests. Laboratory results have shown that increasing moisture and temperature, as found in clearcuts, were the mechanisms underlying increasing decomposition rates (Moore 1986), but results of field studies are varied in showing what factor or interaction of factors actually controls net N mineralization and nitrification (Matson and Vitousek 1981). Edmonds (1979) suggests that while higher temperatures regulate litter decomposition in areas where rainfall is evenly distributed, moisture is the regulating factor where summer droughts predominate; moisture controlled decomposition rates in Douglas-fir clearcuts in western Washington (Edmonds 1979). Because the Sierra Nevada mixed conifer type is subject to summer droughts, one would expect moisture to regulate litter decomposition and N mineralization as well.

Mineral nitrogen has been shown to vary spatially within a burned patch as a result of the nature of the prior vegetation of the site (Covington and Sackett 1992, Kutiel and Shaviv 1992). Spatial variation in nitrogen at the microsite scale, as a result of litter type (generating species) and/or litter thickness has been shown in a Sierra Nevada mixed conifer forest (Stohlgren 1988a, 1988b), in other conifer forests (Mueller-Harvey et al. 1985, Lensi et al. 1991), and in deciduous forests (Boerner and Koslowsky 1989).

Biotic Response

Many studies report on gap light regimes or relate gap size and vegetation (Runkle 1982), but few attempt to correlate gap size, gap microenvironment, species composition or success, and within-patch patterns. Success is defined here as the probability that an individual seedling will reach canopy status; measures of success can include height, diameter, and growth rate. Many of the studies that do correlate these factors report varying species composition and success with gap size and with position within a gap, and report correlations of species composition with some aspect of the microenvironment. Minckler and Woerheide (1965), working in an Illinois mixed-hardwood forest, found that gaps with a D:H ratio of less than 1 contained predominantly hickory (*Carya* spp.), whereas gaps with a D:H ratio of 1 to 2 contained predominantly yellow-poplar (*Liriodendron tulipifera*). Gaps with a D:H ratio larger than 2 differed little in light and soil moisture from gaps with a D:H of 2, and were not expected to increase tree seedling growth. Within-gap patterns were also shown. Few trees in the shaded western, southern, and eastern portions of plots were more than 1.5 meters tall 10 years after the gaps were created, whereas the central and northern portions of plots contained many more trees greater than 1.5 meters. This effect was most pronounced in the shade intolerant species such as yellow-poplar and oaks (*Quercus* spp.). Minckler and Woerheide (1965) state that the reproduction in the central and northern portion of the openings will eventually dominate the openings. The effects of light and moisture regimes in gaps varied with aspect. Openings on northern aspects received the greatest intensity and duration of light in June, when soil moisture was high, whereas openings on southern aspects received the most light late in summer when soil moisture was at or near the plant permanent wilting point. The authors explain the predominance of rapidly growing yellow poplar in openings on northern aspects, which received less than 50% of full sunlight for the summer, by the co-occurrence of favorable light and moisture conditions.

Working in a southeastern hardwood forest, Phillips and Shure (1990) found that standing crop biomass and aboveground net primary production (ANPP) were consistently higher in large than small patches. This effect was mostly due to greater sprout productivity in large than small openings; advance regeneration was more important in small than large patches in the first growing season, and seedling production did not change significantly with patch size. Position (edge or interior) had little effect on tree ANPP. Species diversity increased with increasing patch size; black locust (*Robinia pseudoacacia*) was the only species to increase consistently in relative importance from small to large openings. Microenvironment (solar radiation and soil and air temperature) varied across the patch, but Phillips and Shure did not relate these gradients explicitly to within-gap patterns of species composition or success.

Poulson and Platt (1989) explain the success of species in different locations within canopy gaps in an eastern old-growth deciduous forest based on species architecture and the relationship of architecture and vertical growth to light regime. White ash (*Fraxinus americana*) is likely to attain canopy status in the brightest area in the north of the gap. Here, where the high insolation promotes rapid herb and shrub growth, ash succeeds through its ability to rapidly reposition large leaf areas from branches receiving low intensity light to branches receiving high intensity light (by varying the size, number, and position of terminal buds) and through rapid extension growth, enabling it to penetrate a growing tangle of herbs and shrubs. Yellow-poplar grows rapidly but lacks the architectural flexibility to adjust to severe crowding; it is thus likely to be found in areas of slightly lower light levels just south of the east-west gap axis where herbs and shrubs are sparse. American beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*), the two least light-demanding species, will attain canopy status along the edges of the gap. Thus, the authors note that the chance of a species reaching the canopy in large gaps is predicted by the microenvironment, growth rate, and architecture, but not by the overall frequency or density of the species. In other words, no matter its initial density across a gap, a species will only succeed in those areas within a gap for which its architecture and physiology are most adapted.

Spies and Franklin (1989) stress that a wide range of gap sizes and gap phenomena is important in the Pacific Northwest. Coarse-scale phenomena, such as large gaps created by fire, wind, and volcanic eruption, result in large, closed patches of nearly pure Douglas-fir. These large patches are then broken up into a mosaic pattern by fine-scale phenomena such as the death of a single tree or several trees due to windbreak or pests. These small patches are occupied by the more shade tolerant species such as western hemlock and western red cedar (*Thuja plicata*). Spies and others (1990) further found that within the smaller patches, factors such as gap age, surrounding forest structure, and the nature and severity of the disturbance must be included in addition to gap size in order to explain vegetation response to disturbance.

Gray (1995) further investigated the role of these fine-scale gaps in tree seedling establishment and growth in mature, mesic Douglas-fir forests of the western Cascade Range of Washington and Oregon. In experimentally-created, circular gaps with D:H ratios from 0.2 to 1.0, Gray studied seedling establishment and growth as a function of stand structure (mature or old-growth), gap size, within-gap position, substrate, understory shade, understory competition, and resource gradients. This study is unusual in that it considered factors at several hierarchical levels, including the stand, gap, and microsite. Establishment of Pacific silver fir (*Abies amabilis*), western hemlock, and Douglas-fir was significantly greater in gaps than in closed-canopy areas, but predictions of establishment success in different gap sizes based on shade tolerance were not supported. Rather, Gray's data suggested that below-ground controls on seedling establishment may be more important than light levels in gaps. Seedling growth increased with gap size, and was greater at centers than edges of gaps. Microsite considerations, such as substrate, coarse woody debris, and understory shade, did not simply modify the effect of gap size and within-gap gradients, but allowed species to "transcend the constraints of those environments." For example, given a forest with sufficient microsite heterogeneity, western hemlock was able to establish in both dry, low-light, closed-canopy forest as well as in high-light areas of gaps prone to environmental extremes. Stand-level considerations affected establishment and growth in gaps due to different soil moisture environments (old-growth stands had higher soil moisture content than mature stands) and seed availability (seed rain of western hemlock was rare in mature stands and abundant in old-growth stands). Finally, Gray compared the gap-size classification approach to the resource-gradient approach, and concluded that the gap-size classification approach accounted for greater portions of the variability in seedling establishment. Gray explained the lack of stronger relationships in regressions of seedlings establishment with light, moisture, and surface temperature by possibly-inappropriate spatial and temporal scales of measurement, as well as by missing variables that are important for plant growth (e.g. nitrogen availability). Gray concludes that because it is difficult and time-consuming to measure all relevant resource gradients at spatial and temporal scales appropriate for plant survival and growth, gap-level descriptions may capture important patterns that are not reflected by measurements of a few environmental variables alone (Gray 1995).

Physiology of the Sierra Nevada Mixed Conifer Species

The giant sequoia-mixed conifer forest is a mesic segregate of the white fir-mixed conifer forest community in the lower montane zone of the western Sierra Nevada, at elevations from 1400 m to 2450 m. Although white fir is the dominant species, up to six species of conifers may be present in individual stands. Important associates of white fir include sugar pine *(Pinus lambertiana)*, incense cedar (*Calocedrus decurrens*), jeffrey pine (*Pinus jeffreyi*), and giant sequoia. Douglas-fir (*Pseudotsuga menziesii*) becomes dominant in the northern end of the range. At lower elevations and drier sites, incense cedar becomes dominant and ponderosa pine (*Pinus ponderosa*) and black oak (*Quercus kelloggii*) are important associates. At higher elevations, white fir mixes with red fir (*Abies magnifica*) in the transition to red fir forest communities (Rundel et al. 1977). This section will examine the light, moisture, and temperature requirements and tolerances of these giant sequoia-mixed conifer zone species.

Red Fir and White Fir

White fir is the most shade tolerant species in the mixed conifer forest, followed by red fir, Douglas-fir, incense cedar, sugar pine, ponderosa pine, and giant sequoia, considered the most shade intolerant species (Oliver and Dolph 1992, Barbour et al. 1990, Stark 1968a). The ecotone between white fir-dominated forest at lower elevations and red fir-dominated forest at higher elevations has been studied extensively to try to deduce the physiological and ecological differences between the two species (Parker 1986, Barbour et al. 1990, Pavlik and Barbour 1991). Parker (1986) found that both species regenerate successfully on similar sites. However, red fir reproduces in greater numbers and on a wider variety of sites, and is able to dominate on nutrient-poor and disturbed sites under a more open canopy than white fir. Microhabitat differences between sites that favor white fir and sites that favor red fir along an elevational gradient were investigated by Barbour and others (1990). The authors concluded that first-year seedling mortality can partially explain the forest transition between white and red fir dominance along an elevational gradient. At high elevations and open, mesic microhabitats, red fir seedlings outperform white fir, whereas at lower elevations and open, xeric microhabitats, white fir seedlings outperform red fir. The prevalence of shade along the elevational gradient modified or negated differences between the species, with red fir more negatively affected by shade than white fir. The corresponding hypothesis that white fir has adapted to a more arid zone by faster root growth and higher allocation of photosynthate to roots during the first 6 months of life was not borne out in their experiments. Results showed that white fir seedlings invested more photosynthate in the shoot and less in the root than red fir seedlings. Other anatomical and morphological traits were very similar between the species, suggesting that physiological differences more likely account for the differential survival of the seedlings. The authors hypothesized that gas exchange patterns, seasonal patterns of xylem water potential, and the phenology of bud break and stem growth differ between saplings of the two species (Barbour et al. 1990). White fir would be likely to maintain higher leaf conductances at lower water potentials than red fir, allowing white fir to maintain a higher photosynthetic rate than red fir as soil drought progresses through the summer. Results of a later study (Pavlik and Barbour 1991) showed that white fir and red fir saplings photosynthesized at similar rates, and that rates changed in similar ways with respect to xylem water potential and leaf temperature. However, differences in growth phenology between red and white fir saplings were large and distinctive. White fir had an extended season for bud break, height growth, and diameter growth relative to red fir, but these phenological differences did not vary with elevation. Regardless of microclimatic variability, white fir buds broke 2 weeks earlier than those of red fir, leading the authors to conclude that bud break is under strong photoperiod control. None of these factors fully explain the transition from white to red fir on an elevational gradient. The authors further suggest that factors influencing seedling survival over winter, such as snow shedding or resistance to snow breakage, may provide clues to explain the altitudinal zonation of red and white fir.

Specific microsites within the Sierra Nevada mixed conifer forest were shown by Tappeiner and Helms (1971) to favor white fir and Douglas-fir regeneration on exposed, south to west-facing slopes. The establishment of both species was favored in partial-shade sites and in full-sun sites where a cover of squaw carpet (*Ceanothus prostratus*) was present. This success was specific to squaw carpet, since in full-sun sites where a cover of bear clover (*Chamaebatia foliolosa*) was present, there was high conifer mortality due to heat and drought. The authors attributed the high conifer survival associated with squaw carpet ground cover to the significantly greater soil moisture from 0-7 cm in depth and the lower potential evaporation at seedling height. There was little seedling establishment in the full-shade site, probably due to insufficient light intensity, greater depth of forest floor, and burial by large quantities of litter which become compacted by snow. In all sites, soil moisture throughout the profile from 0 to 55 cm was at a minimum of 1.5 MPa by the end of the summer. The authors observed that surviving seedlings were able to develop a dormancy in response to this drying pattern. Evidence of dormancy included cessation of top growth, development of prominent terminal buds, cessation of root growth, and the hardening of hypocotyls as early as mid-July. The almost total lack of mortality after early August, despite the continuation of summer drought conditions for an additional 2 months, is further evidence of this dormancy.

The patchy distribution shown by red fir is explained by Ustin and others (1984) as a response to the distribution of sunflecks throughout the day. Red fir seedlings exhibited low survival under large canopy gaps on south-facing slopes where there was a long interval at midday during which full-intensity, direct solar irradiance penetrated to the forest floor. Red fir seedlings exhibited high survival under smaller canopy gaps where sunflecks lasted no longer than a few minutes. On north-facing slopes, red fir seedling survival remained high under larger gaps than on south-facing slopes. The authors suggest that the mechanism for this response is that high midday irradiance has the most severe effect on water relations by inducing early stomatal closure and high leaf temperatures, consequently reducing carbon gain. This mechanism is supported by the finding that midday temperatures above, at, and below the soil surface were all significantly higher in plots with few seedlings, indicating higher levels of thermal stress (Ustin et al. 1984). These results were confirmed by Selter and others (1986), who found that patches of young established Shasta red fir (*Abies magnifica* var. *shastensis*) seedlings with high first-year survival had more midday shade, shorter periods of direct sunlight, and lower surface temperatures from midsummer to mid-September than did patches in which most new seedlings died. No soil or litter characteristics were found to correlate with the differential seedling survival. Direct heat injury (girdling) was not found to be a cause of seedling mortality; rather, high temperatures were thought to act indirectly, by affecting seedling water relations. Higher transpirational demand superimposed upon lower soil moisture availability in more sunny sites was likely responsible for the observed increased mortality from desiccation in low survival plots (Selter et al. 1986).

Incense Cedar

Incense cedar is of intermediate shade tolerance, generally considered more tolerant than ponderosa pine and sugar pine but less tolerant than white fir. Seedlings of incense cedar can endure deep shade and may require partial shade, but more light is required for their development to saplings and mature trees (Schubert 1957). Suppressed seedlings are capable of rapid height growth when released (Schubert 1957). Shade tolerance of incense cedar has been shown to vary with temperature. In laboratory experiments, incense cedar seedlings showed lower survival and growth in warm, very low light environments than in cool, very low light environments (Minore 1988). Incense cedar is listed as less drought tolerant than ponderosa and Jeffrey pines but more drought tolerant than white fir, red fir, Douglas-fir, and sugar pine. The growth rate of seedling roots is slower than ponderosa pine and sugar pine, but faster than Douglas-fir. The yearly shoot growth period of incense cedar is listed as the longest of all the mixed conifer species (Minore 1979), although the shoots grow relatively slowly, often taking 3 to 5 years to grow 6 inches in height (Schubert 1957).

Sugar Pine

The shade tolerance of sugar pine has been described as "problematical," and its ability to maintain itself in the mixed conifer type as "something of an enigma" by Oliver and Dolph (1992), who conducted a study of the relative shade tolerances of seedlings of the mixed conifer species under three densities of thinning (9, 23, and 36 m^2 basal area per ha). Five-year height growth was greater with increasing solar radiation, expressed as percent of full sunlight (PFS), which was 15% under the 36 m^2 BA plot, 34% under the 23 m^2 plot, and 58% under the 9 m^2 plot. The resulting shade tolerance ranking--white fir as most tolerant, Douglas-fir and incense cedar similar and somewhat less tolerant than white fir, and ponderosa pine least tolerant of the five--was in agreement with generally accepted shade tolerance rankings (Minore 1979). Sugar pine, at the lowest light intensities of 15% and 34% full sun, showed (like ponderosa pine) poor height growth. At 58% full sun, however, sugar pine's growth was similar to that of incense-cedar and Douglas-fir, suggesting that sugar pine may have a greater ability to respond to additional light than do its associates. The authors suggest that this ability to quickly exploit the added light of canopy openings and grow beneath thin canopies as rapidly as its more tolerant associates accounts for sugar pine's ability to maintain itself in the type (Oliver and Dolph 1992).

Sugar pine typically grows on many different soils and thrives over a broad range of elevations (Harry et al. 1983). Growth rates and reproductive potentials of three populations of sugar pine along an elevational gradient were studied by Yeaton (1984). Soil moisture and growth rates of seedlings and saplings increased with increasing elevation, while cone production was higher at the lower two populations. Effects of seed predation, however, tended to compensate for differences in cone and seed production. The low and middle elevation sites, in the white fir-incense cedar association, had relatively high light levels, while the high-elevation site, in the red fir association, had significantly lower light (2% to 15% full sunlight). The further finding that there were more individuals in the smaller size classes at the lower two populations suggests that favorable light conditions allow high initial establishment. However, this early stage is followed by reduced survivorship due to moisture stress produced by low soil moisture levels and high temperatures in late summer. At higher elevations, fewer seedlings become established due to lower light levels, but survivorship and growth rates are higher due to greater soil moisture. The relative impact of these factors is to produce equivalent numbers of canopy trees of sugar pine at each elevation (Yeaton 1984).

Possible genetic differences between populations of sugar pine at different elevations were investigated by Harry and others (1983) by using controlled sowing experiments at a single location with seed from five elevations. Both seed weight and seedling growth were negatively correlated with elevation of the seed parents. Decreases in seedling height with increase in parent stand elevation were evident after one growing season, and were even more obvious in the following seasons. These elevational patterns indicate strong adaptation to temperature and moisture gradients, which coincide with elevational gradients.

Ponderosa and Jeffrey Pines

In a study of the competitive ability of ponderosa pine in a replacement series with greenleaf manzanita (*Arctostaphylos patula*), Shainsky and Radosevich (1986) found that ponderosa pine grown with mixtures of manzanita had lower relative canopy growth rates than ponderosa pine growing in monoculture. This reduction was shown to be mainly a response to increased depletion of soil moisture when growing with manzanita; this moisture depletion increased as the summer progressed. Mechanisms of manzanita's superior competitive ability were hypothesized to be earlier colonization of the site, the disproportionate use of a limiting resource (water), and ability to tolerate stress associated with depleted resources. While moisture appears to be limiting pine growth in the seedling stage of development, nutrients or light may become limiting at later stages, perhaps changing the relative competitive abilities of the two species.

An inhibitory effect of ponderosa pine seed trees on ponderosa pine seedlings was found by McDonald (1976) in a Sierra Nevada mixed conifer forest. Seedling height growth decreased with increasing proximity to seed trees, and there were indications that this effect was due to soil moisture depletion in the vicinity of the seed trees. However, once seed trees were removed, seedlings did not react rapidly in regaining height growth. Nutrient depletion, release of allelopathic chemicals by seed trees, and a cumulative weakening effect on seedlings (fewer feeder roots becoming developed on inhibited seedlings) are additional possibilities to explain the inhibitory effect.

In northern Arizona ponderosa pine forests, moisture stress is the major cause of seedling mortality (Elliott and White 1987). Competition which further reduces moisture available to ponderosa and jeffrey pines appears to be a major limiting factor to seedling growth and survival in the Sierra Nevada as well, as indicated by these and other studies (Parker and Yoder-Williams 1989).

In a 5-year study in the Sierra Nevada, seedling survival for ponderosa pine was found to be poorest under a dense white fir-sugar pine stnad on a north facing slope and highest on an open south facing slope. No ponderosa pine seedlings survived for 5 years in heavily timbered areas (Fowells and Stark 1965).

Giant Sequoia

Much work has been done on the environmental requirements and tolerances of giant sequoia. Rundel (1972) concluded that expansion of the Giant Forest grove is limited by moisture, since measurements of soil-moisture stress and water-potential of coniferous species inside and outside the grove boundaries indicated that conditions of water availability for plant growth are more favorable inside the grove than out. The author suggests that high levels of soil moisture are maintained in the grove throughout the summer months by the input of ground water originating in summer thunderstorms in the High Sierra Nevada.

Stark (1968a, 1968b) studied the seed and seedling ecology of giant sequoia. Seed germination tests resulted in the following conclusions: (1) seeds germinate best at constant temperatures between 10° and 20° C; (2) germination under natural fluctuating air temperatures and adequate soil moisture is best between -2° and +34° C (occurring in April, May, and sometimes September, with October and November seeding providing good spring germination); (3) seeds will germinate on moist surfaces but not under water; (4) seeds germinate best in half of full light; (5) healthy seedlings and good growth result from seeds germinated at pH 6, 7, and 8; (6) seeds decrease in viability by 32% in 20 years; (7) the radicle of germinated seeds seldom breaks the soil surface if seeds are germinated below 2.4 to 3.6 cm in the soil, depending on the degree of compaction; (8) no allelopathic inhibition of germination by litter extracts or cone extracts was found; (9) larger seeds germinate better than small seeds; (10) partially burned litter can hold up to 273% more available water by weight than unburned litter, forming a good seedbed; and (11) seed-eaters prefer seeds of sugar pine and the acorns of many oaks over giant sequoia seed (Stark 1968b).

Tests of the response of giant sequoia seedlings to variations in a number of environmental conditions led to the following conclusions: (1) infection by high temperature root rot such as *Sclerotium bataticola* slows growth initiation and limits growth and survival (litter on the soil surface reduces damage from heat canker and root rot); (2) shade in winter prevents the darkening and purpling of seedlings; (3) seedlings survive well but grow poorly in dense shade (color, growth form, and roots develop abnormally in less than 25% full sun); (4) optimum height growth occurs at pH 6; (5) seedling height growth and survival decreases as soil mass water content in the root zone drops from 16% to 5%; (6) saturating watering frequencies of 2 to 4 days provide the optimum balance between soil moisture and aeration; (7) once the seedlings extend taproots into zones of permanent and adequate moisture, growth is rapid; and (8) giant sequoia can develop a two-storied root system well suited to summer drought (Stark 1968a).

The primary cause of giant sequoia seedling mortality appears to be desiccation. Harvey and others (1980) found a mortality rate of nearly 75% from July to October following a spring prescribed burn. Nearly 90% of the mortality rate was attributed to desiccation. From mortality data collected during the 10 years following the fire, Harvey and others (1980) concluded that sequoias generally become established in the first 3 years after a fire, with little latent establishment. On the same site, Harvey and Shellhammer (1991) concluded that seedlings which become established on burn pile soils survive better than those on other substrates, including a scarified surface, during the first few years. Their results also showed that the hottest fires bring about soil conditions that are most favorable to the survival and growth of giant sequoia seedlings. Increased germination and survival following a hot fire is attributed to increased wettability and friability of heated soils, the killing of soil pathogens and seeds of competing species, and the seed rain induced by the heating of the serotinous cones of giant sequoia. Another potential factor affecting seedling survival on burn piles is that burn piles were placed in openings to reduce potential damage to mature trees; thus seedlings growing on burn pile soils received considerably more sunlight than other environments (Hartesveldt et al. 1975).

The Performance of the Sierra Nevada Mixed Conifer Species in a Gap Environment

Given the environmental requirements and tolerances of these Sierra Nevada mixed conifer species, how might one expect them to perform in different sized gaps and in different areas of a single gap? The most light-demanding species, giant sequoia, would probably require the largest gaps for regeneration. Work by Stephenson and others (1991) and Stephenson (1994) indicates that giant sequoia requires a minimum opening on the order of 0.1 ha. Due to its rapid growth rate, characteristic of a pioneer species, giant sequoia would most likely dominate in the central to northern areas of a large gap. The fastest growing individuals would likely be found in areas of lower stem density, higher soil moisture, and better soil nutrient status. It has been hypothesized, from observations of large giant sequoia seedlings growing within clumps of *Ceanothus* spp., that these nitrogen-fixing shrubs might increase the growth of giant sequoia seedlings due to nitrogen fertilization (Nate

Stephenson, National Biological Service Research Scientist, personal communication, 1995). Thus, rapidly growing sequoia individuals might also be found in association with *Ceanothus* species. How these factors might manifest in spatial pattern of fast-growing individuals is difficult to predict, but may be controlled by root competition with mature trees on the gap edge and with other seedlings in areas of dense establishment.

Ponderosa and Jeffrey pines, the next most light-demanding species, would probably also require large gaps, on the same scale as giant sequoia or slightly smaller, for successful recruitment. Within a large gap, these pines might be found interspersed with sequoia in the central to northern areas of the gap, probably at much lower densities since they lack the heat-induced seed rain of giant sequoia. The inhibition of ponderosa pine seedling growth by mature trees (McDonald 1976) also suggests that seedlings might grow most rapidly in the center of gaps.

Sugar pine is of intermediate tolerance and has the ability to grow beneath thin canopies as well as to exploit the added light of canopy openings, hence it might be able to reproduce in smaller gaps than sequoia, Jeffrey pine, and ponderosa pine. With relatively large, heavy seeds and long seed longevity (Minore 1979), sugar pine may be able to regenerate in a large treefall gap as well as in fire-caused gaps. Sugar pine might be found in the central to southern areas of large gaps, and perhaps along the edges.

Incense cedar, of intermediate shade tolerance but considered more tolerant than sugar pine, might be found in intermediate and large treefall gaps. Within a large fire-caused gap, incense cedar might be found in the center-south areas of the gap.

Red fir and white fir, the most shade-tolerant species, would both likely be found in all size treefall gaps within their elevation range. Red fir might be slightly more successful in the larger gaps than white fir because red fir is considered slightly more demanding of light and tolerant of low-nutrient and disturbed sites. In large gaps, these species might be found along southern edges and in areas of high moisture and low light intensity.

Patch Dynamics and Landscape Processes

In a previous section I discussed how the environment within canopy gaps is different from the environment under an intact canopy, and how patterns of regeneration can vary within different-sized gaps. In this section I will discuss how these gaps and mature forest patches are arranged in the forest (i.e., the horizontal and vertical structure).

Many authors have proposed that the structure of the vegetation affects how natural processes, such as fire, operate in the forest (e.g., Sousa 1984). It is difficult to tease apart which is the controlling factor -- structure or process. Rather, there is a feedback where the frequency and intensity of disturbance affect the pattern of species recruitment, survival, and structure of a community; and the composition and structure of the community may in turn affect its susceptibility to, and frequency of, disturbance (Whittaker and Levin 1977). For example, a heterogenous landscape of patches of different ages, species, and fuel loading (a mosaic structure) causes fire to burn unevenly through the forest (i.e., very hot in mature patches with heavy fuel loading, and very lightly or not at all in young patches of seedlings or saplings with light fuel loading). Fire which burns unevenly perpetuates this patchy mosaic structure. The importance of the scale of disturbance and the implications of artificially altering the scale of the patch mosaic structure are not well understood.

Changes in Forest Structure Since European Settlement

Bonnicksen and Stone (1981, 1982a) suggest that in giant sequoia groves of Sequoia National Park, the patch mosaic pattern of burns and reproduction has become more uniform and the horizontal and vertical structure of the vegetation within the patch has been altered by a century of fire exclusion. The main structural changes, as summarized by Kilgore (1981), were the following: (1) a large increase in the younger age classes of shade tolerant white fir with a corresponding decrease in young, fire-dependent ponderosa pine, black oak, and giant sequoia; (2) a smaller increase in young sugar pine; (3) the survival of one or more vertical layers or tiers of white fir beneath, or adjacent to, the overstory canopy of giant sequoia and pine; (4) a denser forest generally, particularly of white fir; and (5) a blending of what had been discrete patchy units into a more uniform forest.

The Bonnicksen and Stone studies (1981, 1982a) generated much debate, partially because the validity of their methods were questioned (Stephenson 1987), but mainly because their recommendations were considered too radical to the Park's scientists and managers at the time. Bonnicksen and Stone recommended mechanical removal of the dense understory of pole-size, 41 to 60 year-old white fir in order to return the forest to the pattern characteristic of the presettlement state before allowing fires to burn through the forest, arguing that prescribed burning in an unnatural forest structure will not produce a natural result. They recommended that a quantitative goal be defined, within which the forest has historically fallen, before burning commenced. Doing otherwise would insert the manager's biases, however inadvertently, into the resulting system (Bonnicksen and Stone 1982b, Bonnicksen 1985, Bonnicksen and Stone 1985).

The scientists and managers of Sequoia National Park, however, argued that a more conservative approach was warranted. While they recognized the importance of establishing a restoration goal, they believed that the present structure was not necessarily unnatural when structural variations over time were considered; therefore, they did not consider it appropriate to manipulate vegetation to what they considered a "snapshot in time." To do so would be to insert the biases of the manager into the forest system (Bancroft et al. 1985). Instead, their stated goal was "to allow natural ecological processes to dictate the character" of the environment (Parsons et al. 1985), and to "permit process-structure interactions to reequilibrate on their own after one or more prescribed fires" (Parsons et al. 1986). They maintained that a half-century of fire suppression had not caused significant changes outside normal variance in ecological time, and that restoring the natural fire regime and allowing the structure and function to return to equilibrium was sufficient for restoring naturalness (Bancroft et al. 1985, Parsons et al. 1986, Parsons and Nichols 1986).

More recently, these same scientists and managers have more explicitly recognized the necessity of defining a structural goal state for the forest. During a fire effects and prescribed fire workshop held in Sequoia and Kings Canyon National

Parks in 1993, participants recognized the need to move beyond restoring fire as a singular, process-oriented goal. The importance of interactions between fuel, fire, and vegetation structure were explicitly addressed, and a rewording of the goal for the prescribed fire program was agreed to be: "to restore and perpetuate the fire regime and the vegetation structure (or range of structural variability) that would have existed today had Europeans not come on the scene." In order to evaluate the success of the program, it was recognized that structural criteria (i.e., the range of desired vegetation structure) must be determined (Parsons 1994).

Recognition of structure, composition, and function in defining quantifiable objectives for the desired future condition of an ecosystem has been made explicit in a discussion draft of ecosystem management in the National Park Service (National Park Service, 1994). This document emphasizes that both passive and active management are appropriate for ecosystem management in National Parks, and that "letting nature take its course" may not often be a desired goal.

Fire History

Recent evidence has shown that the fire regime has varied widely in response to climate in the past two millennia, which has probably resulted in wide variations in the scale and pattern of the forest mosaic. Swetnam and others (1992) reconstructed the fire record back to about A.D. 500 from fire-scarred giant sequoias in five groves. Maximum fire frequencies within sampled areas of the groves were as high as 3 to 4 fires per decade, whereas lower fire occurrence periods had 1 or fewer fires per decade. Occasional fire-free intervals lasted 20 to 30 years. Generally, centennial maximum and minimum fire frequencies since A.D. 500 differed by a factor of 2 to 3 (Swetnam et al. 1992).

Because of these relatively high fire frequencies, most fires were probably low intensity surface fires and fuel loadings were usually low. Swetnam and others (1992) speculate that the very frequent fires (i.e., 1 to 3 year mean fire intervals) may have been supported by different fuel production rates or different types of fuels than found today. Grasses, for example, may have been a much larger component of pre-settlement understories than current understories. Occasional higher intensity surface fires and localized crown fires may have occurred after extended periods (greater than 10 years) without fire. These are the localized "hot spots," resulting in even-aged clumps of giant sequoia recruitment (Stephenson et al. 1991, Stephenson 1994).

Very rarely, large, high-intensity fires may have burned through giant sequoia groves. An A.D. 1297 fire in the Mountain Home Grove was recorded on all sample trees, and all these trees showed a large and sustained increase in growth in the following years (Swetnam et al. 1992, Caprio et al. 1994). This event was likely an intense fire in a fairly dense stand of trees which killed a large proportion of understory trees and possibly some larger giant sequoias as well. The spatial distribution of sample trees which recorded a growth release following the fire suggested that the fire was severe and had an impact over a relatively large area, from 16 ha to several square kilometers in size (Caprio et al. 1994). Additionally, age structure evidence suggests than an unusually large cohort of sequoias established shortly following this event (Swetnam et al. 1992, Caprio et al. 1994).

Swetnam and others (1992) also presented evidence to verify the assumption among disturbance ecologists (Pickett and White 1985) of an inverse relationship between fire frequency and fire size (within a single vegetation type over time). A simple analysis of fire size (percentage of trees recording fires) showed that higher frequency periods were dominated by smaller fires and that lower frequency periods had more widespread fires (Swetnam et al. 1992). How the variable frequency (and thus variable size and intensity) of fires was manifested in the structure of the forest is not known. By detecting variations of vegetation structure with gap size (a result of fire size and intensity) and extrapolating these structures over the landscape, a clearer understanding can be obtained of how the forest structure varied with fire regime.

Giant Sequoia Demography

A recent demography study (Stephenson 1994) has documented that far fewer giant sequoias have become established in this century than in the preceding century in groves protected from fire. Because sequoia populations were near equilibrium or increasing before European settlement, current reproduction is not sufficient to maintain giant sequoia populations. Stephenson (1994) has suggested that while surface fire is sufficient to allow *establishment* (successful seed germination, rooting of the seedling, and survival for the first few summers) of giant sequoias, it is not sufficient for their *recruitment* (growth of the seedling into a mature, reproducing tree). For recruitment to occur, a fire intense enough to kill the forest canopy locally, perhaps followed by one or more wet summers, may be required. The importance of locally intense fire is supported by three types of evidence (Stephenson

1994): (1) fires intense enough to kill the forest canopy locally did indeed occur in giant sequoia groves before forest structure and fuel loads were significantly altered by Europeans; (2) post-fire giant sequoia seed dispersal, seedling establishment, growth, and survival are highest where fires have burned most intensely; and (3) most living giant sequoias today occur in even-aged clumps that likely correspond to hot spots that killed the forest canopy in past fires. These even-aged patches range from less than 0.03 ha to more than 0.4 ha, suggesting that the minimum size of forest gaps leading to significant giant sequoia recruitment is on the order of 0.1 ha. This estimate is probably low, because observations suggest that successful giant sequoia recruitment often is limited to only a portion of a given gap, producing an even-aged patch of giant sequoias that was smaller than the gap itself (Stephenson 1994).

These advances in our knowledge of giant sequoia-mixed conifer forest demography and fire history suggest intriguing new questions as to how vegetation responds to large-scale changes (such as climate change and human intervention which changes the fire disturbance regime) which alter the gap size and the patch mosaic pattern. Development of buildings and pavement is another of these changes. The effects of development on the forest and the forest's subsequent recovery can be viewed, ecologically, as a disturbance phenomenon which can be compared to other historical disturbance regimes. This proposed approach to the Giant Forest restoration should supply us with a result that is ecologically sound.

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CHAPTER 3

REGENERATION PATTERNS WITHIN CANOPY GAPS IN A GIANT SEQUOIA-MIXED CONIFER FOREST: IMPLICATIONS FOR FOREST RESTORATION

Abstract

The structure of a giant sequoia-mixed conifer forest in Sequoia National Park, California, had been altered by a century of fire exclusion and the development of visitor facilities. The ecological restoration of this forest includes two distinct problems: how to integrate, both ecologically and visually, formerly developed areas into the forest; and how to document historic ranges of forest structure and restore the entire forest to a more natural state within this range. The purpose of this study was to estimate the range of historic variability in forest structure and to provide a model for restoration of previously-developed sites by studying regeneration within different sizes of fire-caused gaps. Woody vegetation was mapped in 6 gaps in each of 3 size categories: (1) small (0.05 to 0.1 ha), (2) medium (0.1 to 0.3 ha), and (3) large (0.3 to 1.2 ha). Results showed both differences in species composition among the three gap sizes and differences in spatial patterns of growth within gaps. Several pioneer-type tree (*Sequoiadendron giganteum* and *Pinus jeffreyi*) and shrub (*Ceanothus cordulatus*, *Arctostaphylos patula*, and *Ribes roezlii*) species grew with significantly higher density in large gaps. These pioneer-type species also grew most rapidly in

gap centers, suggesting that increased moisture availability in gap centers where root competition from mature trees is presumably lower may be an important mechanism in regulating growth in these gaps. Other species also tended to occupy microhabitats within gaps which increased their growth. A hierarchical model is presented to show how a variable fire regime, which alters the predominant gap size, can cause changes in forest structure at the landscape scale. A process for restoring previously-developed sites using these results is also presented.

Introduction

The cyclic structure and processes of forests have long been of interest to ecologists. In particular, the characteristics of disturbance events (e.g., type, spatial scale, frequency, severity), the nature of the cohort of vegetation that establishes following disturbance, and the patch-like pattern created by repeated disturbance have long been topics of study for several decades. Most ecologists agree that disturbance phenomena, such as the formation of gaps by treefall and fire, drive forest development (sensu Oliver 1981) in nearly all forests (Watt 1947, Cooper 1961, Whitmore 1982, Pickett and White 1985, Whitmore 1989), and that certain species have developed specialized life-history characteristics to take advantage of gaps. These pioneer species tend to have numerous lightweight, well-dispersed seeds that are incapable of germinating or becoming established in shade, and tend to have rapid height growth. In contrast, climax species tend to have fewer larger, poorly-dispersed seeds which are capable of germinating and becoming established in shade (Whitmore 1989).

Ecologists have also recognized the importance of varying scales of disturbance in driving forest development (Drury and Nisbet 1973, Oliver 1981, Sousa 1984, Spies and Franklin 1989). A body of work investigating disturbance and patch dynamics has shown that the size of the gap in a forest canopy affects the light, moisture, temperature, and nutrient regimes in the forest floor beneath the gap (Forman and Godron 1981, Canham and Marks 1985, Runkle 1985, Gray 1995). Different sized gaps possess very different patterns of environmental gradients, and the vegetation should sort itself out along these gradients because of the differential growth, survival and dispersal of species adapted to grow at different points along stress gradients (Drury and Nisbet 1973, Whittaker and Levin 1977, Noble and Slatyer 1980, Sousa 1984, Thompson 1985). While mature individuals of different species may seem to occupy identical habitats, microenvironments within gaps may be especially important in determining species composition at the regeneration stage when species have more specific requirements, allowing niche differentiation (Grubb 1977). Thus, different sized gaps may contain fundamentally different vegetation in a predictable manner.

With the scale dependence of gap-phase regeneration as my focus, I have investigated two problems relevant to the restoration of giant sequoia-mixed conifer forests of Sequoia National Park, California. The first problem, of a more theoretical nature, concerns the estimation of a historic range of variability in forest structure at several scales. Such an estimate will help managers determine if the restoration of fire to these forests after a century of fire exclusion is producing a forest structure that is within this range. The second, of a more localized and applied nature, concerns the ecological restoration of sites, in one of the Park's largest giant sequoia (*Sequoiadendron giganteum*) groves, from which visitor facilities (buildings, parking lots) are slated for removal.

Historic Range of Forest Variability

Many studies have examined the variability of forest disturbance regimes with time, but few have suggested how forest composition and structure have responded to this variability (Cattelino et al. 1979). Temporally variable disturbance regimes in a community, resulting in temporally variable scales of gaps and patches on the landscape, have likely produced substantially different forest structure, composition, and function through time. Fire history studies in giant sequoia groves (Swetnam et al. 1992, Swetnam 1993) have shown that fire frequency has varied in the past millenia in response to climate, from minimum frequencies of 1 to 2 fires per decade before A.D. 800, to maximum frequencies of 3 to 4 fires per decade during the medieval warming period of A.D. 1000 to 1300. Swetnam (1993) and Swetnam and others (1992) also presented evidence to show that fewer trees recorded fires during periods of high fire frequency, and more trees recorded fires during periods of low fire frequency, supporting the assumption among disturbance ecologists (Pickett and White 1985) of an inverse relationship between fire frequency and fire size within a single vegetation type over time. Fire behavior thus ranged from frequent, small, low intensity surface fires to less frequent, large, higher intensity surface fires with localized crown fire (Stephenson et al. 1991). How this variability affected forest structure and composition is unknown.

The giant sequoia-mixed conifer forests of Sequoia and Kings Canyon National Parks have been the subject of considerable dialogue in the literature concerning the importance of interactions between forest disturbance processes and forest structure, as well as appropriate management actions for restoring fire as a natural process after long periods of fire exclusion and consequent changes in forest structure (Bonnicksen and Stone 1981, Bonnicksen and Stone 1982a, Bonnicksen and Stone 1982b, Bancroft et al. 1985, Bonnicksen 1985, Bonnicksen and Stone 1985, Parsons et al. 1985, Parsons et al. 1986, Parsons and Nichols 1986, Stephenson 1987). While previously adhering to a policy of restoring the fire process and accepting the forest structure which results, scientists and managers of Sequoia National Park have more recently acknowledged the importance of the interaction of the fire process with vegetation structure and the necessity of defining structural criteria for forest restoration, which include an estimate of historic ranges of forest structure (Parsons 1994).

In order to begin to estimate this historic range of variability in forest structure, I investigated how woody vegetation responds to gap size. As suggested by Swetnam (1993), historic variation in disturbance regimes likely resulted in the predominance of different gap sizes at different periods in time (Figure 1). In giant sequoia-mixed conifer forest, a regime of frequent, low intensity surface fires likely produced a mosaic of small gaps within a low-density matrix of mature trees. Favored tree species for gap-phase regeneration may have been those with high to intermediate shade tolerance, such as white fir *(Abies concolor*), red fir (*Abies magnifica*), incense cedar (*Calocedrus decurrens*), and sugar pine (*Pinus lambertiana*). A fire regime of less frequent,higher intensity surface fires with localized crown fires

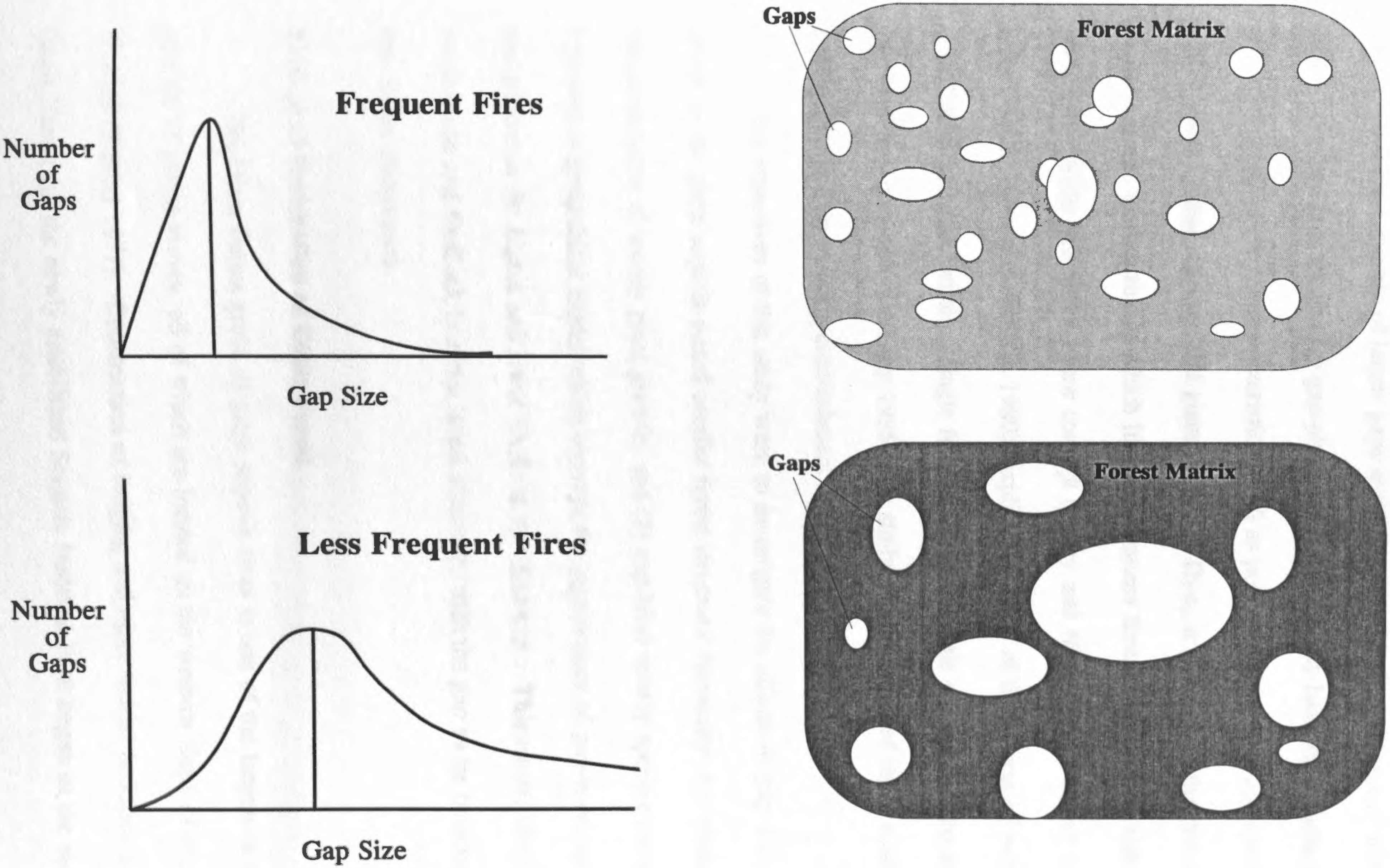

Figure 1. Hypothetical gap size distribution for periods with frequent fires and periods with less frequent fires.

likely produced a mosaic of larger gaps within a higher-density matrix of mature trees. Favored tree species for gap-phase regeneration may have been those with pioneer, shade intolerant characteristics, such as ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), and giant sequoia. Thus, it is not only the presence, but also the scale, of disturbance which likely determines forest composition and structure. While this is not a new concept (Drury and Nisbet 1973, Oliver 1981, Sousa 1984, Spies and Franklin 1989), explicit synthesis of the effects of variable scales of disturbance within a single forest type on multiple scales of forest structure has been less common (see Gray 1995 for a study of the effects of three scales of forest structure on seedling establishment and growth in gaps).

The objectives of this study were to investigate the effects of gap size on two levels in the giant sequoia-mixed conifer forest structural hierarchy: (1) within-gap spatial patterns of woody plant growth, and (2) gap-level woody species composition. I present a hierarchical model which conveys the significance of gap-level structures and processes for higher and lower levels in the hierarchy. This model clarifies the interactions and feedback between forest structure, with the gap as its building-block, and forest disturbance.

Ecological Restoration of Giant Forest

The Giant Forest grove of giant sequoia trees is one of the largest of this species 75 extant groves, all of which are located on the western slope of the Sierra Nevada (Rundel 1971). Construction of lodging and other tourist facilities in the Giant Forest for the newly established Sequoia National Park began in the early part of the 20th Century and escalated throughout the 1930's. For decades, the National Park Service has recognized the potential impacts of concentrating heavy visitor use in this area, but has only recently begun relocating these lodging facilities to another site. When the new construction is completed, projected for the year 1999, most of the buildings in Giant Forest will be removed and efforts will be made to restore the forest to a more natural condition.

Recognizing that sound management in the National Parks requires the integration of "scientific knowledge of ecological relationships with resource stewardship practices" (NPS 1994), the National Park Service has chosen a goal of ecological restoration for Giant Forest: "to create a structure and composition of vegetation at the restoration sites within the range of natural variability if development had not taken place and if fire had not been suppressed" (NPS 1995). One approach for achieving this goal is to look to the relatively natural surrounding ecosystem for a condition which resembles the condition of the disturbed target site; the species composition, density, and spatial pattern of vegetation in these sites can then be used as a model for restoration efforts in Giant Forest Village.

Relative to many human-impacted areas on public land, the Giant Forest developed area is not a heavily disturbed site, but one which has been altered structurally and compositionally and for which there is a relatively intact model in surrounding areas. Following the removal of buildings and pavement, there will be several large (several tenths of a hectare) patches of disturbed ground where major parking lots, large buildings, and close clusters of buildings once stood. These large patches will have no overhanging canopy, little or no ground vegetation, and will be very open, sunny sites. There will be many smaller patches (around 0.1 ha) of disturbed ground where single cabins or buildings stood. These smaller patches will have a sparse or no overhanging canopy and possibly some ground vegetation, but will be less open and sunny than the large patches. Finally, there will be areas where there has been ground disturbance but a canopy is present; these will be closed and shady.

Similar canopy-opening disturbances can be seen in the Giant Forest Grove where prescribed fires have been conducted during the last 16 years. These disturbance sites, or gaps, have an important ecological role. Like most forests, sequoia groves consist of mosaics of groups of trees that originated in forest gaps created by disturbance (Henry and Swan 1974, Oliver and Stephens 1977). In sequoia groves, fire was the most common source of disturbance (Swetnam et al. 1992), providing favorable regeneration sites for sequoia and other pioneer species. However, fire can be highly variable in its effects on vegetation, and the subsequent recolonization of burned areas can vary depending on many factors. One of the most important factors is the *size* of the gap created by disturbance. The size of the gap in a forest canopy affects the light, moisture, temperature, and nutrient regimes in the forest floor beneath the gap (Forman and Godron 1981, Canham and Marks 1985, Runkle 1985, Gray 1995). Different species will respond differently to these varying environmental regimes, causing different-sized gaps to contain different species, plant densities, and spatial patterns of regeneration (Drury and Nisbet 1973, Whittaker and Levin 1977, Noble and Slatyer 1980, Sousa 1984, Thompson 1985, Gray 1995). Thus, to use fire-caused gaps as a model for restoration in potential gaps in Giant

Forest Village, it is important that the vegetation in a range of gap sizes in Giant Forest Grove be carefully documented. This study addresses only the vegetation model for the restoration; other impacts of human use of Giant Forest Village, such as soil compaction, are discussed in Demetry and Duriscoe (1995).

Study Area

Giant Forest is located on a plateau in the mixed-conifer zone of the middle elevations (between about 1950 m and 2320 m) of the southern Sierra Nevada and covers an area of approximately 1012 ha (Figure 2). The most common tree species are white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), and giant sequoia (*Sequoiadendron giganteum*). The average annual precipitation, which falls mostly as snow during the winter months, is 113 cm. Average minimum air temperatures range from -6.7°C in February to 11.8°C in August. Average maximum air temperatures range from 3.4°C in December and January to 27.4°C in August. The soils in the Giant Forest Grove of Sequoia National Park are predominantly Pachic Xerumbrepts that are 0.5-1.5 m deep, well drained, acid soils formed in granitic rock residuum (Huntington and Akeson 1987). Typically, the soils are coarse sandy loams with an O horizon $\geq$10 cm thick (Stohlgren et al. 1991).

Prescribed fires have been conducted in Giant Forest since 1979 and have been accompanied by a standardized monitoring program. Consequently, fire dates and boundaries are well documented. The sites sampled in this study burned between 1979 and 1987.

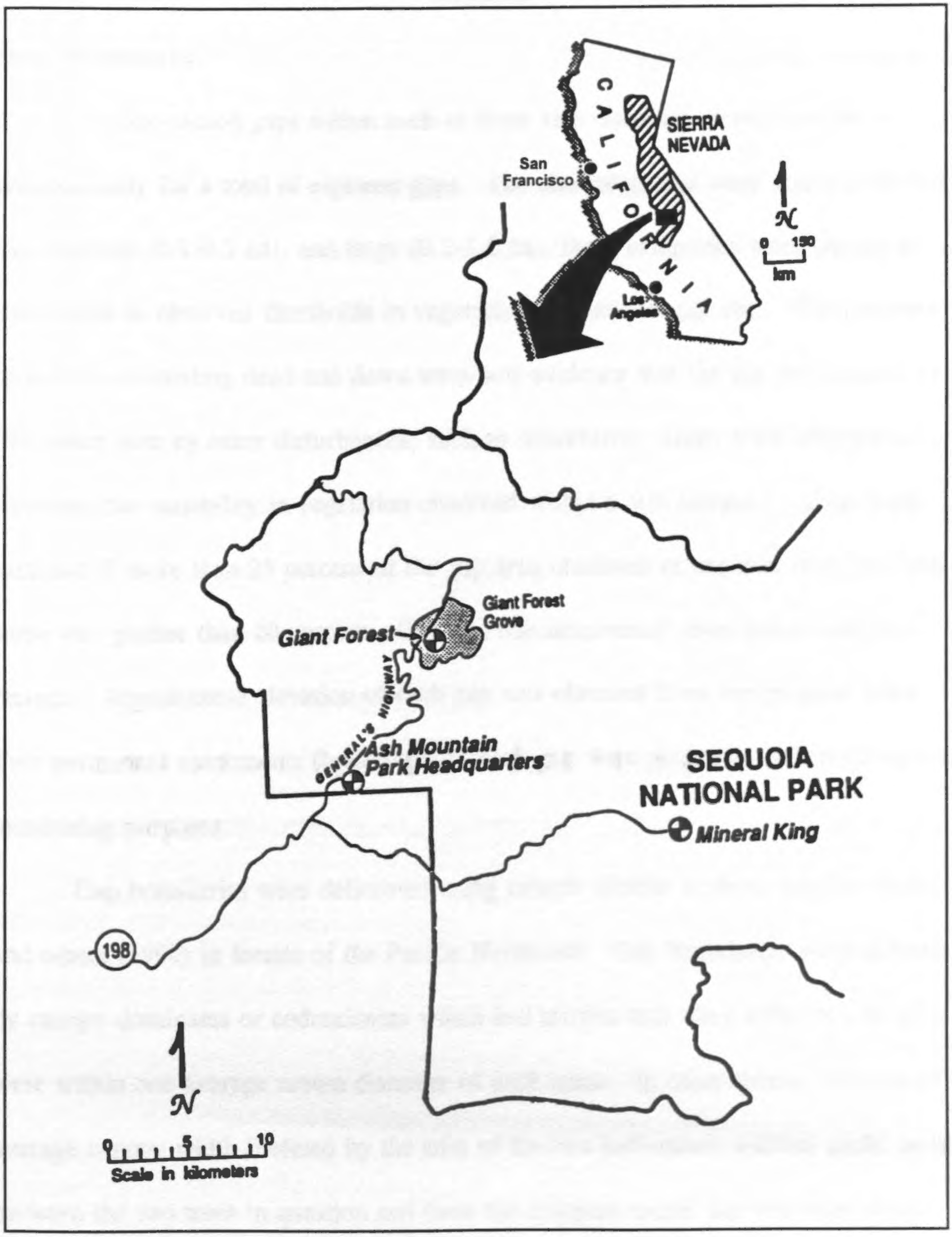

Figure 2. Study site. Figure adapted from Stohlgren et al. (1993).

Methods

Field Procedures

Six fire-caused gaps within each of three size categories were selected systematically for a total of eighteen gaps. The size categories were small (0.05-0.1 ha), medium (0.1-0.3 ha), and large (0.3-1.2 ha); these categories were chosen to correspond to observed thresholds in vegetation response to gap size. The presence of scorch on standing dead and down trees was evidence that the gap was caused by fire rather than by other disturbances, such as windthrow. Gaps were selected to represent the variability in vegetation observed within a size category. Gaps were excluded if more than 25 percent of the gap area consisted of exposed rock or if the slope was greater than 20 percent. Gap age was determined from prescribed fire records. Approximate elevation of each gap was obtained from topographic maps. Two permanent monuments (brass tags) in each gap were placed in rock for long-term monitoring purposes.

Gap boundaries were delineated using criteria similar to those used by Spies and others (1990) in forests of the Pacific Northwest. Gap boundaries were defined by canopy dominants or codominants which had crowns that were either touching or were within one average crown diameter of each other. In other words, if a tree of average canopy width (defined by the sum of the two half-crown widths) could be fit between the two trees in question and have the canopies touch, the two trees were considered boundary trees. A mature tree that was farther than one average crown diameter from a neighboring tree was considered part of the gap vegetation and not a boundary tree.

Woody plants within each gap were mapped by obtaining their exact x,y,z coordinates using a Topcon CTS-2 total station, which has sub-centimeter accuracy. All tree seedlings greater than 0.1 meters height were mapped, with the exception of red and white fir, which were mapped if greater than 0.2 meters height. This exception was necessary because of the establishment of high densities of fir seedlings following a mast year in 1991, accompanied by favorable climatic conditions. Heights of all mapped seedlings were measured, and nodes of all pines were counted to estimate their age. For three of the large gaps and one of the medium gaps, some sequoia seedlings were not mapped individually because of time constraints. In these gaps, high density clumps of sequoia seedlings no larger than 1 meter square, within which the stems appeared randomly distributed, were mapped as ellipses; the number of seedlings within the ellipse and their heights were recorded. Surrogate x, y coordinates were later generated using a random number generator within the bounds of the ellipse. Boundary trees and mature trees within the gap were mapped and their diameters and heights measured.

All shrubs with canopy dimensions at least 0.1 by 0.1 meter were mapped. Because shrub stems, or individuals, could not always be readily differentiated, shrubs were mapped as elliptic clumps, and the length and width of the ellipse was measured as well as the height of the clump. When a continuous group of a shrub species was encountered which was not roughly elliptical, the perimeter of the shrub polygon was mapped. Shrub cover was later generated by calculating the area of the ellipse or obtaining the area of the polygon from the AutoCAD map.

Analysis

Two main questions were investigated from the field data. The first question concerns the central level in the hierarchy, the gap: does species composition vary with gap size? Do the most rapidly growing individuals grow mostly in a certain gap size? The second question concerns the lower level in the hierarchy, within-gap aggregations: what are the spatial patterns of recruitment for a species within each gap size? More specifically, (1) Does the distance from gap edge influence where in a gap a species tends to grow, and where in a gap the fastest growing individuals tend to grow? (2) Do more specific microclimates (e.g. north edge, south center) influence where in a gap a species tends to grow, and where in a gap the fastest growing individuals tend to grow? (3) Does a species tend to grow in a uniform, random, or aggregated (clumped) spatial pattern? The following sections describe the data manipulation and statistical analyses used to address these questions.

Differences in species composition with gap size. The null hypothesis for each species found in more than two gaps was that the mean tree density (seedlings/ha) or mean shrub cover (m^2/ha) is the same in small, medium, and large gaps. The hypothesis was tested using Analysis of Covariance (ANCOVA) with tree density (or shrub cover) as the dependent variable, gap size as the treatment factor, and gap age as the covariate. Because of the small sample size and consequently the low power of these tests, the null hypothesis was rejected if the p-value was equal to or less than 0.10. Tree densities and shrub covers were logarithmically transformed to equalize the variance among treatments; the equal variance and normality assumptions were checked by plotting residuals vs. estimates, and by normal probability plots of the residuals. The "homogeneity of slopes" assumption of ANCOVA (Neter et al. 1990), or the assumption of no significant interaction between the covariate and the treatment, was tested by running an ANCOVA with the interaction term included; the null hypothesis of no significant interaction was rejected if $p \leq 0.10$. No violations of the homogeneity of slopes assumption were found. When the ANCOVA showed differences in mean tree density or mean shrub cover among gap sizes (the null hypothesis was rejected), I used Fisher's Least Significant Difference (LSD) procedure to test for pairwise differences. Although Fisher's LSD does not offer protection against finding a significant difference by chance alone in a family of comparisons (i.e., it presents an inflated α-level for the family of comparisons), I desired the more powerful tool of the Fisher's LSD to detect pairwise differences once differences were detected in the ANCOVA. The same analysis was performed for mean density of trees greater than one meter height to test if the most rapidly-growing seedlings of a species tended to grow in a particular gap size.

If the assumptions of the ANCOVA model were violated, as in the case of an infrequent shrub species being present in only a few of the gaps, the non-parametric Kruskal-Wallis test was used to test if the plant densities sampled from small, medium, and large gaps came from identically distributed populations. The null hypothesis of no difference in population distributions was rejected if the p-value was equal to or less than 0.10.

Within-gap spatial patterns: distance from edge. For each tree seedling, the shortest distance to the gap boundary was computed. If a shrub was mapped as an ellipse, the shortest distance from the center of the ellipse to the gap boundary was computed and the shrub cover for that ellipse assigned to the distance. If a shrub was mapped as a polygon, the polygon was divided into 0.5 meter by 0.5 meter grid cells and the distance from the center of each cell to the gap boundary computed; 0.25 m^2 of shrub cover was assigned to the cell's distance. Each gap was divided into a series of concentric, irregular "rings" in 2 meter increments. The total area within each ring was calculated by dividing the entire gap into 1 meter by 1 meter grid cells, calculating the distance from the center of each grid cell to the gap boundary, assigning 1 m^2 of area to its distance category, and summing the number of cells in each distance category. The density by species and 2 meter-distance category was then calculated as number of stems per hectare for trees and m^2 cover per hectare for shrubs. The mean height of each tree species within each 2 meter-distance category was also calculated. Because only frequent and dense species will produce meaningful results in this type of analysis, I included only tree and shrub species that were present in 10 or more gaps.

Within-gap spatial patterns: position within gap. Each tree and shrub was also categorized by its position in the gap: north edge, south edge, east edge, west edge, north center, south center, east center, or west center. The division between edge and center was made at half the maximum distance from edge. The north, south, east, and west divisions were made with offset quadrant axes through the centroid of the gap. Density of tree species (trees/ha), mean height by tree species (m), and cover of shrub species (m^2/ha) were calculated for each position category. The total area in the category was estimated by categorizing each of the 1 m^2 grid cells into one of the above positions and summing the number of cells in each category.

The null hypotheses (tested separately for each species in each gap size category) were: (1) mean tree density (seedlings/ha), mean tree height (m), or mean shrub cover (m^2/ha) is the same in the north, south, east, and west quadrants of gaps; and (2) mean tree density (seedlings/ha), mean tree height (m), or mean shrub cover (m^2/ha) is the same in the edge and center positions of gaps. While this is strictly a split-plot design with gap size as the whole-plot treatment and within-gap position as the split-plot treatment, I was unable to conduct a split-plot analysis of covariance because of software limitations. Rather, the hypotheses were tested using two-way ANCOVA, with tree density (or shrub cover or mean tree height) as the dependent variable, compass position and edge-center position as the two treatment factors, and gap age as the covariate; again, the significance level was set at $\alpha=0.10$. Tree density, shrub cover, and mean tree height were logarithmically transformed to equalize the variance among treatments. If plots of residuals vs. estimates and normal probability plots showed violations of the equal variance and normality assumptions of the ANCOVA, the non-parametric Mann-Whitney test (for the edge-center factor levels) or Kruskal-Wallis test (for the north-south-east-west factor levels) was used. The Kruskal-Wallis test is the nonparametric analogue of a one-way analysis of variance. When there are only two groups (such as the edge-center test), the procedure reduces to the Mann-Whitney test, which is the nonparametric analogue of the two-sample t test (Wilkinson et al. 1992). This analysis was conducted only for species which occurred in 10 or more gaps.

Within-gap spatial patterns: patchiness. Whether individual species tend to grow in random, uniform, or aggregated (clumped) patterns was investigated with Ripley's K(t) analysis. The K(t) function is a cumulative distribution of point-to-point distances between all pairs of points in a plot and includes a boundary-effect correction (Moeur 1993). From a data set of point locations in a plot, the analysis compares the observed value of K(t) at any distance t in the plot to the value expected from a randomly distributed set of point locations. When 19 different simulations are run, in which an equal number of points is randomly assigned x,y coordinates within an equivalent plot and the K(t) is calculated (i.e., 19 different sets of point locations are generated), a 95% confidence envelope is obtained. The result allows a description of the spatial pattern as random, clumped, or regularly dispersed at any distance t up to half the length of the shortest plot side, with 95% certainty; in other words, a description of the spatial pattern at a number of spatial scales is possible. Ripley's K(t) results were transformed to L(t) to provide better visualization of results. This square-root transformation

$$L(t)=\sqrt{\frac{K(t)}{\pi}}-t$$

also linearizes K(t), stabilizes its variance, and has expected value approximately zero for a random point distribution (Moeur 1993). Plots of L(t) versus the distance t were then constructed; a positive value of L(t) indicates clustered patterns, a negative value indicates regular patterns, and a value close to zero indicates random patterns. The 95% confidence envelope was also transformed and plotted.

The computer program used for the Ripley's K(t) analysis requires rectangular plots and allows a maximum of 1,000 point locations to be analyzed at a time (Duncan 1990). All of our study plots were irregularly-shaped; because the program requires the length and width of the rectangular plot as input, I substituted the north-south length and the east-west width of the minimum bounding rectangle. I note that this substitution likely biases the results toward showing a clumped pattern because the simulations are run on plots of larger area (thus the simulated points are more dispersed).

I ran Ripley's K(t) analysis for each tree species in each gap. For cases where there were more than 1,000 individuals in the gap (i.e., giant sequoia in gaps 1, 3, 13, and 18), the gaps were subdivided into smaller rectangles which contained fewer than 1,000 individuals.

Results and Discussion

Gap Characteristics

The gaps used in the study had the characteristics shown in Table 1. The areas of the small gaps ranged from 0.067 to 0.097 hectare, with a mean of 0.086 hectare; areas of the medium gaps ranged from 0.15 to 0.24 hectare, with a mean of 0.20 hectare; and areas of the large gaps ranged from 0.34 hectare to 1.17 hectares,

Table 1. Characteristics of the small, medium, and large gaps used in this study.

Gap Size	Gap Number	Area (ha)	Age (yrs)	Elevation (m)	Aspect (deg)
Small	5	0.095	9	2000	57
	6	0.097	7	2036	248
	7	0.091	13	2063	138
	11	0.075	13	2118	75
	15	0.067	9	2098	144
	17	0.088	12	2042	31
	Mean	0.086	10.5	2060	
Medium	2	0.24	9	1997	118
	4	0.17	9	2000	146
	8	0.23	13	2073	157
	10	0.15	13	2109	359
	12	0.22	15	2036	158
	16	0.20	9	2103	200
	Mean	0.20	11.3	2053	
Large	1	1.17	10	2048	247
	3	0.45	15	2003	129
	9	0.46	13	2128	77
	13	1.14	9	2042	0-200
	14	0.34	13	2115	1
	18	0.43	13	2091	264
	Mean	0.67	12.7	2071	

with a mean of 0.67 hectare. The ages of the gaps ranged from 7 to 15 years since formation by fire; the mean ages for small, medium, and large gaps did not differ substantially. Elevations ranged from 1997 meters to 2128 meters; mean elevations for small, medium, and large gaps did not differ substantially. A range of aspects was well represented for small and large gaps, while medium gaps were less broadly distributed across aspects with southeast-facing slopes predominant.

Species Composition

Nine tree species were present in the gaps, with the large gaps containing the greatest number of species, followed by the medium and small gaps (Table 2). Giant sequoia, sugar pine, and white fir were present in most gaps, and thus can best be used to test the hypothesis that tree species composition changes with gap size. Ponderosa pine and incense cedar were found mainly in the lower-elevation plots, and red fir in the higher-elevation plots and north and northeast aspects. Canyon live oak and black oak each occurred in only 2 gaps.

Table 2. Tree species frequency (presence in number of gaps), followed by relative frequency (percent) in parenthesis, for small, medium, large, and all gaps. Species classifications are from the Jepson Manual (Hickman 1993).

Scientific Name	Common Name	Frequency			
		Small	Medium	Large	Total
Pinus lambertiana	sugar pine	5 (83)	6 (100)	6 (100)	17 (94)
Sequoiadendron giganteum	giant sequoia	4 (67)	6 (100)	6 (100)	16 (89)
Abies concolor	white fir	5 (83)	4 (67)	6 (100)	15 (83)
Calocedrus decurrens	incense cedar	0	4 (67)	3 (50)	7 (39)
Pinus jeffreyi	Jeffrey pine	0	1 (17)	5 (83)	6 (33)
Abies magnifica	red fir	1 (17)	1 (17)	2 (33)	4 (22)
Pinus ponderosa	ponderosa pine	0	1 (17)	2 (33)	3 (17)
Quercus chrysolepis	canyon live oak	0	0	2 (33)	2 (11)
Quercus kelloggii	black oak	0	1 (17)	1 (17)	2 (11)
Total number of species present		4	8	9	9

Twenty-two shrub species were present; the large gaps contained the greatest number of shrub species, followed by the medium and small gaps (Table 3). Whitethorn, greenleaf manzanita, and Sierra gooseberry were present in most gaps, and thus can best be used to test the hypothesis that shrub species composition changes with gap size. Sierra currant, bush chinquapin, creeping snowberry, and littleleaf ceanothus occurred in a majority of gaps and should also be good candidates for testing whether species composition changes with gap size. Three shrub species occurred in only 2 gaps, and 7 species occurred in only 1 gap. For the remainder of the analysis, only species which occurred in more than 2 gaps were included.

Giant sequoia had the highest density of the tree species in all gap sizes, with maximum density occurring in the large gaps (Table 4, Figure 3). Mean density in large gaps was nearly 5 times greater than in medium and small gaps, but mean densities did not differ between medium and small gaps. By contrast, white fir and sugar pine showed only modest trends toward increasing density with increasing gap size (Table 4, Figure 3), and these differences were not statistically significant.

Of the remaining tree species, a trend toward highest densities in medium gaps was shown by red fir and ponderosa pine, but these results were not statistically significant. For incense cedar, tree density in medium gaps was significantly higher than in large and small gaps (Table 4, Figure 4). Because 4 of the 6 medium gaps were located on southeast aspects, it is possible that incense cedar's higher density in medium gaps is a response to aspect rather than gap size. Jeffrey pine was significantly more dense in large gaps than in medium or small gaps (Table 4, Figure 4).

Table 3. Shrub species frequency (presence in number of gaps), followed by relative frequency (percent) in parenthesis, for small, medium, large, and all gaps. Species classifications are from the Jepson Manual (Hickman 1993).

		Frequency			
Scientific Name	Common Name	Small	Medium	Large	Total
Ceanothus cordulatus	whitethorn	5 (83)	6 (100)	6 (100)	17 (94)
Arctostaphylos patula	greenleaf manzanita	4 (67)	6 (100)	6 (100)	16 (89)
Ribes roezlii	Sierra gooseberry	4 (67)	6 (100)	6 (100)	16 (89)
Ribes nevadense	Sierra currant	2 (33)	5 (83)	5 (83)	12 (67)
Ceanothus parvifolius	littleleaf ceanothus	3 (50)	4 (67)	3 (50)	10 (56)
Chrysolepis sempervirens	bush chinquapin	3 (50)	2 (33)	5 (83)	10 (56)
Symphoricarpos rotundifolius var. *parishii*	creeping snowberry	3 (50)	2 (33)	5 (83)	10 (56)
Cornus nuttalli	mountain dogwood	1 (17)	2 (33)	2 (33)	5 (28)
Ribes viscosissimum	sticky currant	1 (17)	1 (17)	3 (50)	5 (28)
Sambucus mexicana	elderberry	0	1 (17)	4 (67)	5 (28)
Prunus emarginata	bitter cherry	0	0	4 (67)	4 (22)
Apocynum androsaemifolium	spreading dogbane	0	1 (17)	2 (33)	3 (17)
Rubus glaucifolius	raspberry	0	1 (17)	1 (17)	2 (11)
Rubus parviflorus	thimbleberry	0	0	2 (33)	2 (11)
Salix sp.	willow	0	1 (17)	1 (17)	2 (11)
Amelanchier alnifolia var. *pumila*	smooth serviceberry	0	1 (17)	0	1 (6)
Ceanothus integerrimus	deer brush	0	0	1 (17)	1 (6)
Chamaebatia foliolosa	bear clover	0	0	1 (17)	1 (6)
Corylus cornuta var. *californica*	hazelnut	0	1 (17)	0	1 (6)
Penstemon newberryi	mountain pride	0	0	1 (17)	1 (6)
Prunus virginiana	western chokecherry	0	0	1 (17)	1 (6)
Rosa sp.	rose	0	1 (17)	0	1 (6)
Total number of species present		9	16	19	22

Table 4. Mean density and ANCOVA results for conifers in small, medium, and large gaps. The F and p-values are shown for the test of no significant difference among factor level means within a species. Significant pairwise differences within a species are indicated by different letter superscripts. Species for which the Kruskal-Wallis test was used are indicated by an asterisk next to the F statistic (see text).

	Mean Density (trees/ha)				
Species	Small	Medium	Large	F	p-value
Giant sequoia	**653^{a}**	**612^{a}**	**2956^{b}**	**4.018**	**0.042**
White fir	62	70	107	1.132	0.350
Sugar pine	50	58	114	1.703	0.218
Incense cedar	**0^{a}**	**62^{b}**	**5^{a}**	**5.036**	**0.022**
Jeffrey pine	**0^{a}**	**2^{a}**	**6^{b}**	**8.550^{*}**	**0.014**
Red fir	29	90	39	0.244^{*}	0.885
Ponderosa pine	0	7	2	2.023^{*}	0.364

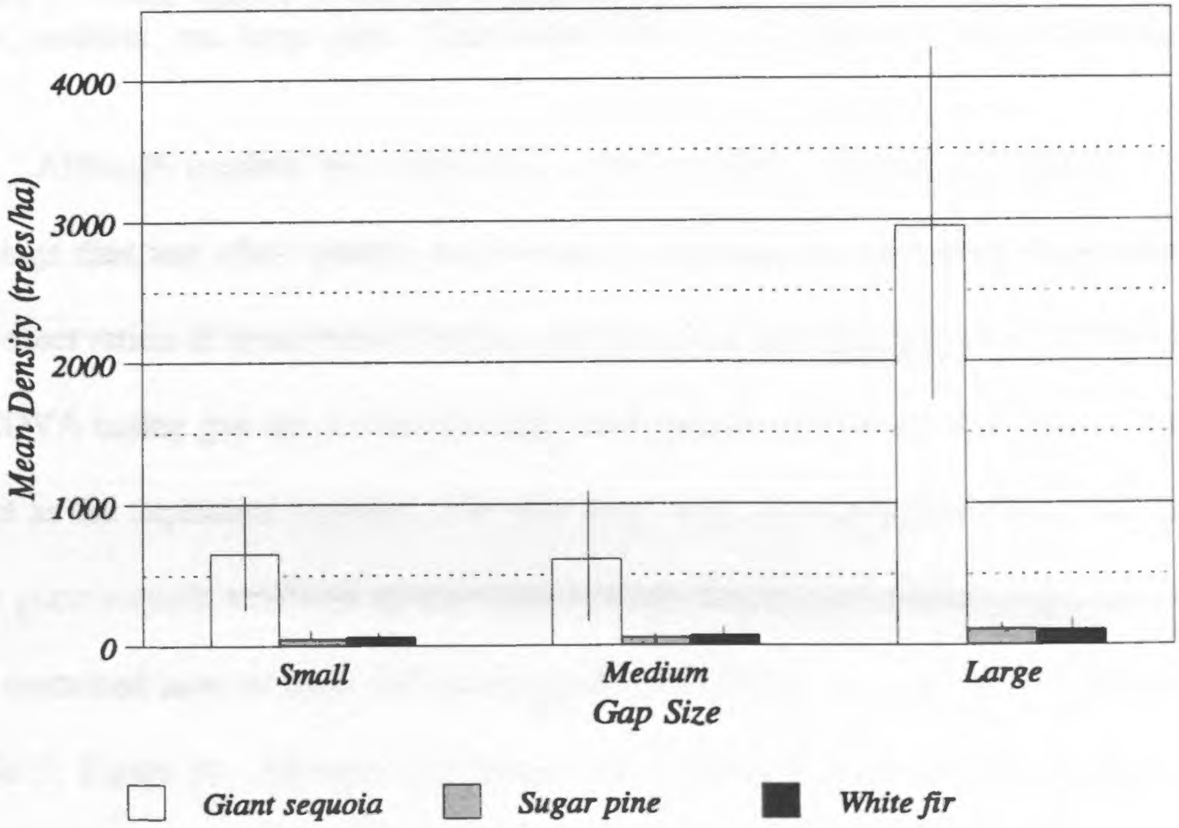

Figure 3. Mean density of giant sequoia, sugar pine, and white fir in small, medium, and large gaps. Error bars show ± one standard error of the mean.

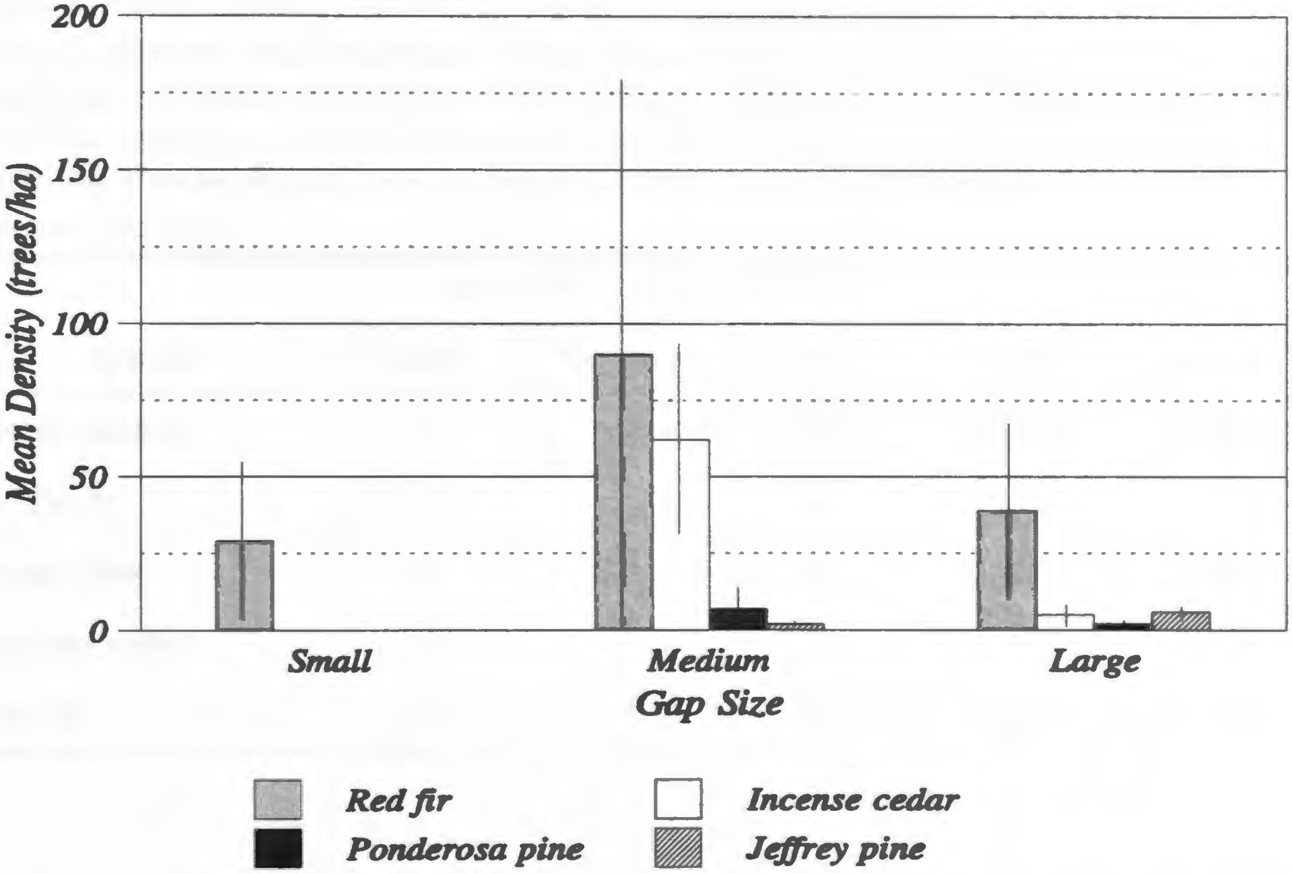

Figure 4. Mean density of incense cedar, Jeffrey pine, ponderosa pine, and red fir in small, medium, and large gaps. Error bars show ± one standard error of the mean.

Although medium and small gaps contained higher densities of sequoia seedlings than any other species, these sequoia seedlings had very slow height growth. This observation of more rapid seedling height growth in large gaps was tested with ANCOVA (using gap age as the covariate) with density of trees greater than 1 meter height as the dependent variable. Per unit area, large gaps contained nearly 20 times more giant sequoia seedlings greater than 1 meter height than medium gaps, and small gaps contained none of these tall seedlings; these differences were highly significant (Table 5, Figure 5). All other tree species had a trend of higher mean densities of seedlings greater than 1 meter height in larger gaps, but only sugar pine showed a statistically significant difference (Table 5, Figure 5).

Table 5. Mean density and ANCOVA results for conifers greater than 1 meter height in small, medium, and large gaps. The F and p-values are shown for the test of no significant difference among factor level means within a species. Significant pairwise differences within a species are indicated by different letter superscripts. Species for which the Kruskal-Wallis test was used are indicated by an asterisk next to the F statistic (see text).

	Mean Density (trees/ha)				
Species	Small	Medium	Large	F	p-value
Giant sequoia	**0^a**	**14^b**	**272^c**	**20.530**	**0.0001**
White fir	2	3	4	0.293	0.751
Sugar pine	**0^a**	**5^{ab}**	**6^b**	**6.673^***	**0.036**
Incense cedar	0	1	1	2.023^*	0.364
Red fir	2	3	5	0.435^*	0.804

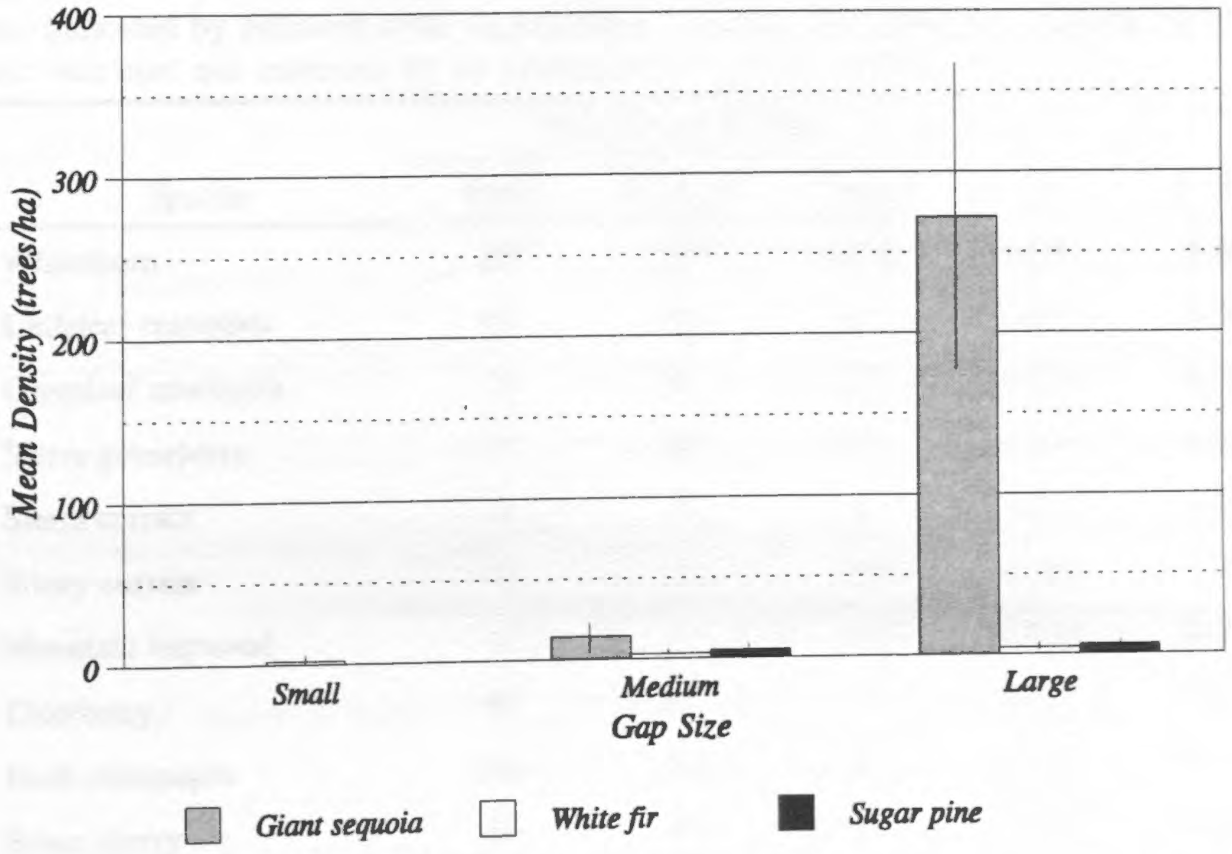

Figure 5. Mean density of seedlings greater than 1 meter height for giant sequoia, white fir, and sugar pine in small, medium, and large gaps. Error bars show ± one standard error of the mean.

The 3 most frequent shrub species showed responses typical of pioneer species, with significantly higher cover in large gaps (Table 6, Figure 6). Whitethorn was the dominant species in large and medium gaps (excluding chinquapin, for which 1 outlier inflated the mean, see Table 11), and had significantly higher cover in large and medium gaps than in small gaps. Sierra gooseberry, greenleaf manzanita, and bitter cherry had significantly higher cover in large gaps than in medium and small gaps. Elderberry and creeping snowberry had significantly higher cover in large gaps than in small gaps (Table 6). Three other species, mountain dogwood, sticky currant, and spreading dogbane, showed nonsignificant trends of higher cover in large gaps.

Table 6. Mean cover and ANCOVA results for shrubs in small, medium, and large gaps. The F and p-values are shown for the test of no significant difference among factor level means within a species. Significant pairwise differences within a species are indicated by different letter superscripts. Species for which the Kruskal-Wallis test was used are indicated by an asterisk next to the F statistic (see text).

	Mean Cover (m^2/ha)				
Species	Small	Medium	Large	F	p-value
Whitethorn	**48^{a}**	**275^{b}**	**1134^{b}**	**8.361**	**0.004**
Littleleaf ceanothus	96	190	211	0.216	0.807
Greenleaf manzanita	**2^{a}**	**5^{a}**	**60^{b}**	**5.558**	**0.017**
Sierra gooseberry	**7^{a}**	**10^{a}**	**97^{b}**	**6.131**	**0.012**
Sierra currant	0	7	7	1.609	0.235
Sticky currant	1	2	31	3.166^{*}	0.205
Mountain dogwood	0	5	118	0.506^{*}	0.777
Elderberry	**0^{a}**	**5^{ab}**	**7^{b}**	**5.639^{*}**	**0.060**
Bush chinquapin	120	576	46	0.320	0.731
Bitter cherry	**0^{a}**	**0^{a}**	**1^{b}**	**9.525^{*}**	**0.009**
Creeping snowberry	**1^{a}**	**31^{ab}**	**15^{b}**	**2.950**	**0.085**
Spreading dogbane	0	0	19	2.244^{*}	0.326

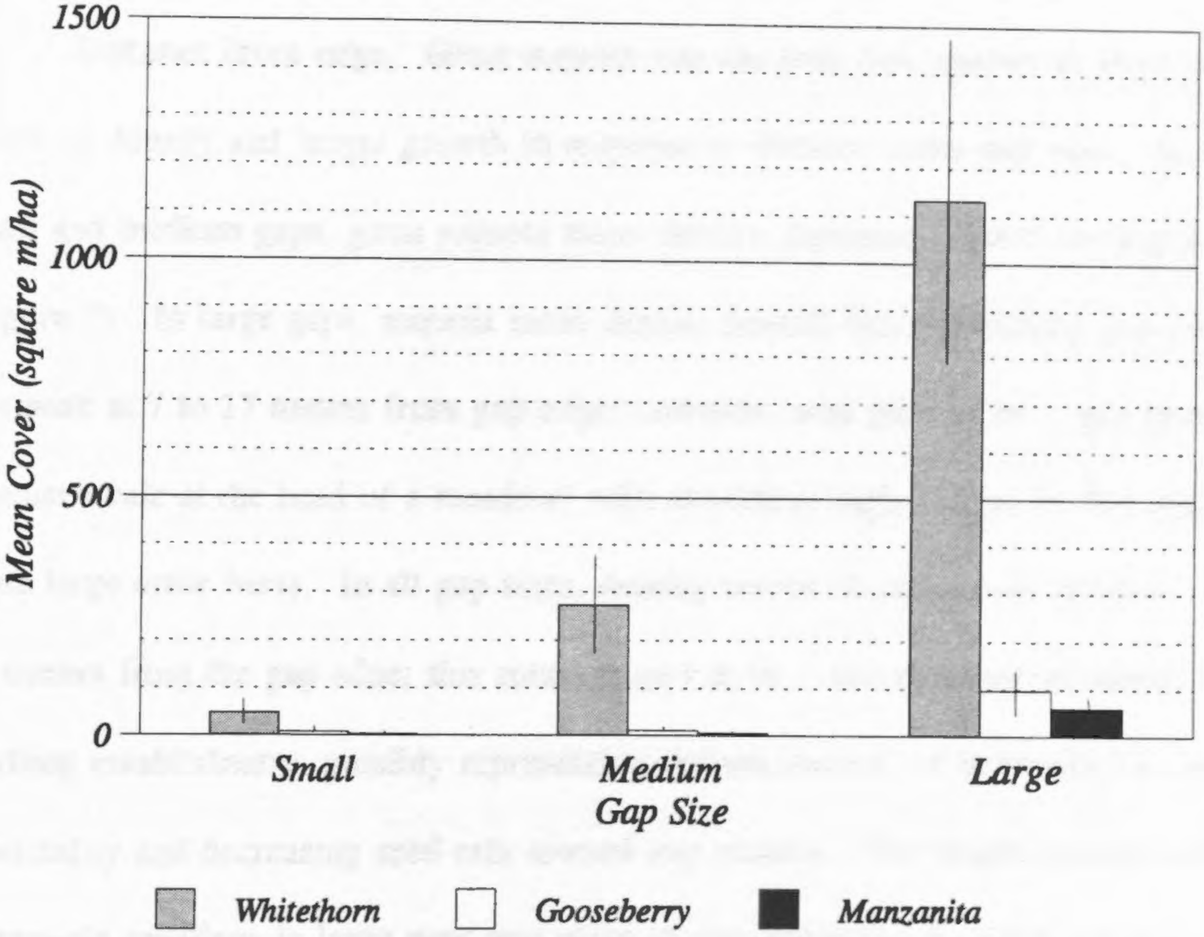

Figure 6. Mean cover of whitethorn, Sierra gooseberry, and greenleaf manzanita in small, medium, and large gaps. Error bars show ± one standard error of the mean.

Littleleaf ceanothus and Sierra currant showed a trend of approximately equal cover in medium and large gaps and less cover in small gaps, but these results were not statistically significant (Table 6). One species, bush chinquapin, showed a trend of the least cover in large gaps and highest in medium gaps, although this medium-gap mean was inflated by 1 gap with very dense cover (Table 6). Bush chinquapin and littleleaf ceanothus were the dominant species in small gaps.

Within-Gap Spatial Patterns

Distance from edge. Giant sequoia was the only tree species to show strong trends in density and height growth in response to distance from gap edge. In both small and medium gaps, giant sequoia mean density increased toward the gap center (Figure 7). In large gaps, sequoia mean density peaked before reaching gap center; this peak at 7 to 17 meters from gap edge, however, was inflated by 1 gap (gap 3, in a moist swale at the head of a meadow) with extremely high density in this region (note large error bars). In all gap sizes, density was at its maximum between 11 and 19 meters from the gap edge; this zone appears to be a favorable environment for seedling *establishment*, possibly representing the intersection of increasing water availability and decreasing seed rain toward gap centers. The height growth response of sequoia seedlings in large gaps was quite strong; mean height increased gradually along with density up to 15 meters from gap edge, then increased dramatically past 21 meters from gap edge while density declined. This zone from 21 meters to 39 meters appears to be a favorable environment for seedling growth, and may be a result of increasing water availability, light, and/or the apparently decreasing intraspecific competition toward gap centers. In contrast, sequoia seedlings in small gaps showed no height response to distance from edge, and seedlings in medium gaps showed only a slight trend of increasing height with distance from edge. Though these regions in small and medium gap centers appear quite favorable for the establishment of high densities of sequoia seedlings, they do not appear favorable for rapid height growth.

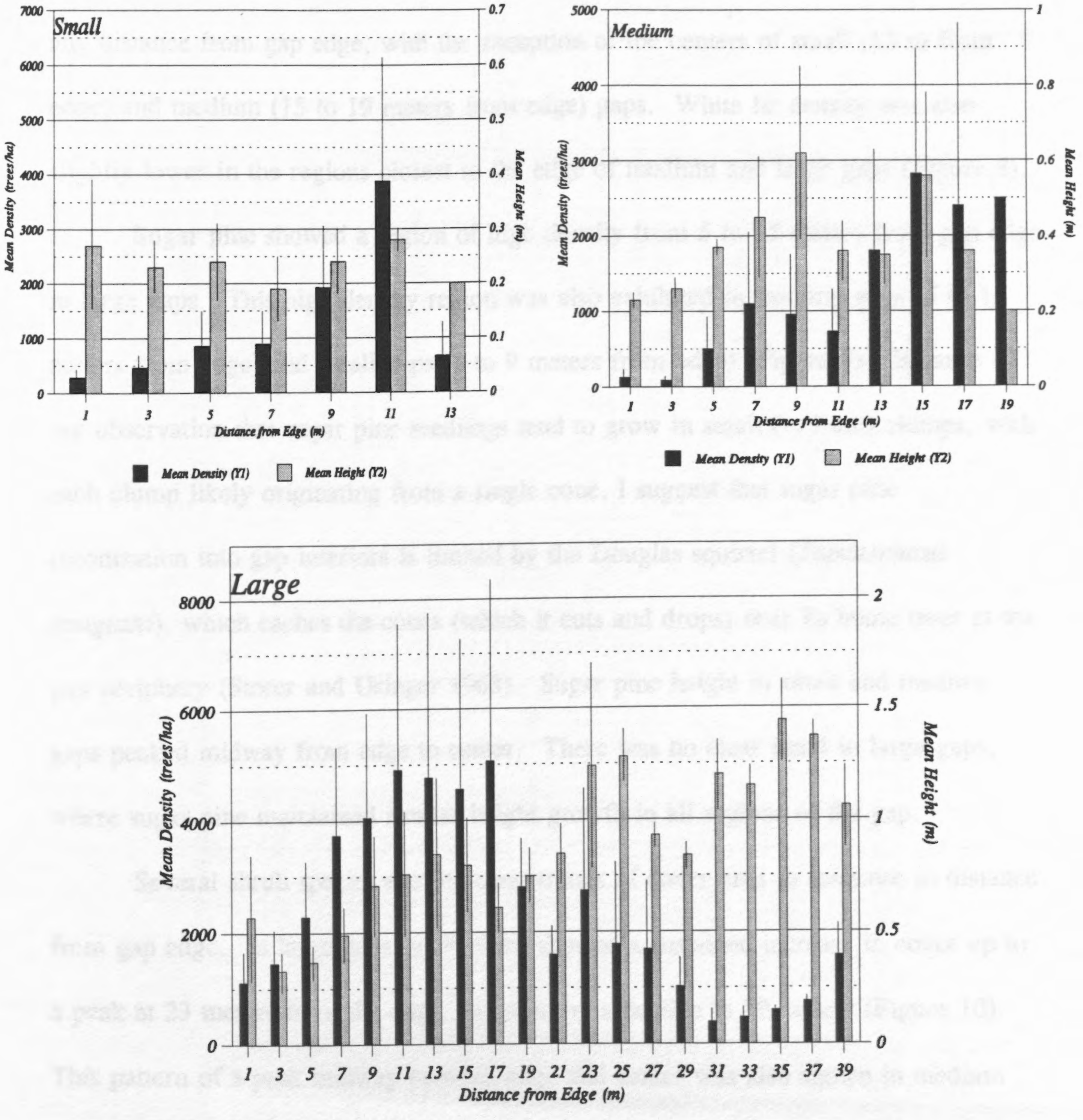

Figure 7. Mean density and mean height of giant sequoia in 2 meter distance categories from gap edge of small (top left), medium (top right), and large (bottom center) gaps. Error bars show ± one standard error of the mean.

White fir was capable of becoming established and maintaining growth at most any distance from gap edge, with the exception of the centers of small (13 m from edge) and medium (15 to 19 meters from edge) gaps. White fir density was also slightly lower in the regions closest to the edge of medium and large gaps (Figure 8).

Sugar pine showed a region of high density from 5 to 15 meters from gap edge in large gaps. This high-density region was also exhibited in medium gaps (5 to 13 meters from edge) and small gaps (3 to 9 meters from edge) (Figure 9). Because of my observation that sugar pine seedlings tend to grow in small (<5 cm) clumps, with each clump likely originating from a single cone, I suggest that sugar pine colonization into gap interiors is limited by the Douglas squirrel (*Tamiasciurus douglasii*), which caches the cones (which it cuts and drops) near its home trees at the gap periphery (Storer and Usinger 1963). Sugar pine height in small and medium gaps peaked midway from edge to center. There was no clear trend in large gaps, where sugar pine maintained similar height growth in all regions of the gap.

Several shrub species showed clear trends of cover area in response to distance from gap edge. In large gaps, whitethorn showed a sustained increase in cover up to a peak at 23 meters from the edge, followed by a decline to 39 meters (Figure 10). This pattern of a peak midway between edge and center was also shown in medium gaps (peak at 9 meters from edge), and less clearly in small gaps (peak at 9 meters from edge). In large gaps, greenleaf manzanita (Figure 11) and Sierra gooseberry (Figure 12) both showed a trend of increasing cover with distance from edge. In medium gaps, both species had their highest cover areas midway to the center, at about 5 to 9 meters from gap edge. No clear trends emerged for these two species

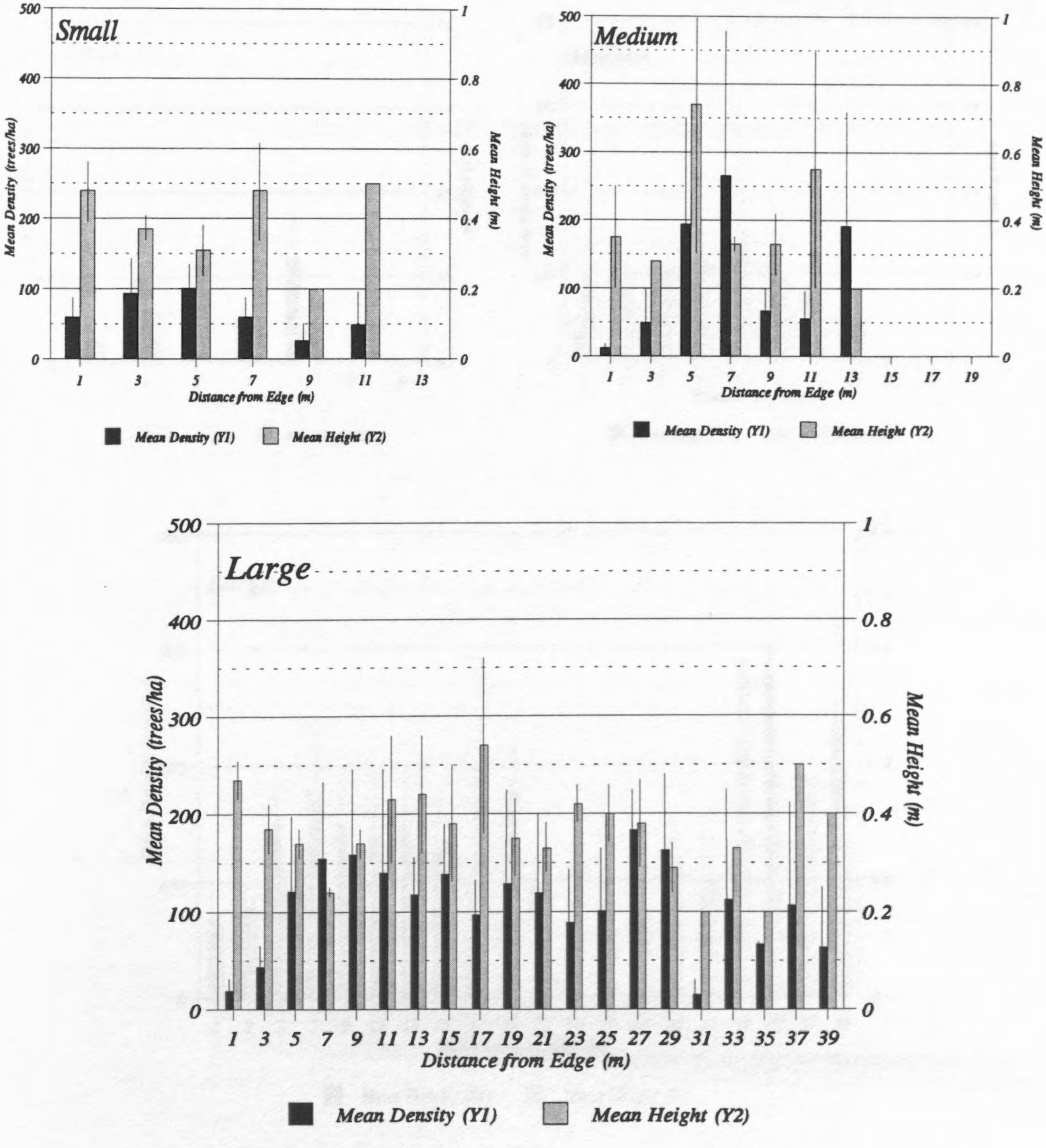

Figure 8. Mean density and mean height of white fir in 2 meter distance categories from gap edge of small (top left), medium (top right), and large (bottom center) gaps. Error bars show ± one standard error of the mean.

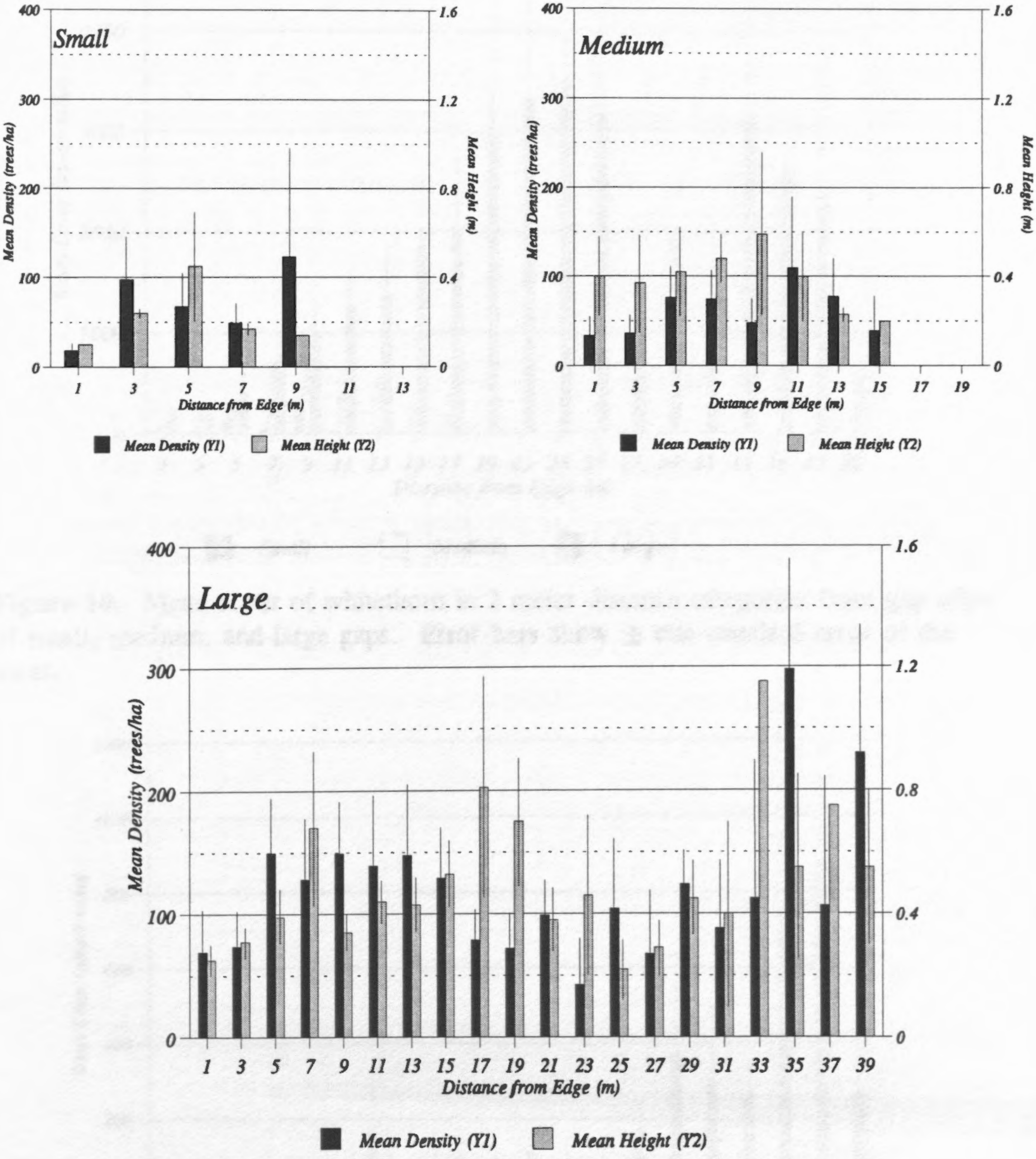

Figure 9. Mean density and mean height of sugar pine in 2 meter distance categories from gap edge of small (top left), medium (top right), and large (bottom center) gaps. Error bars show ± one standard error of the mean.

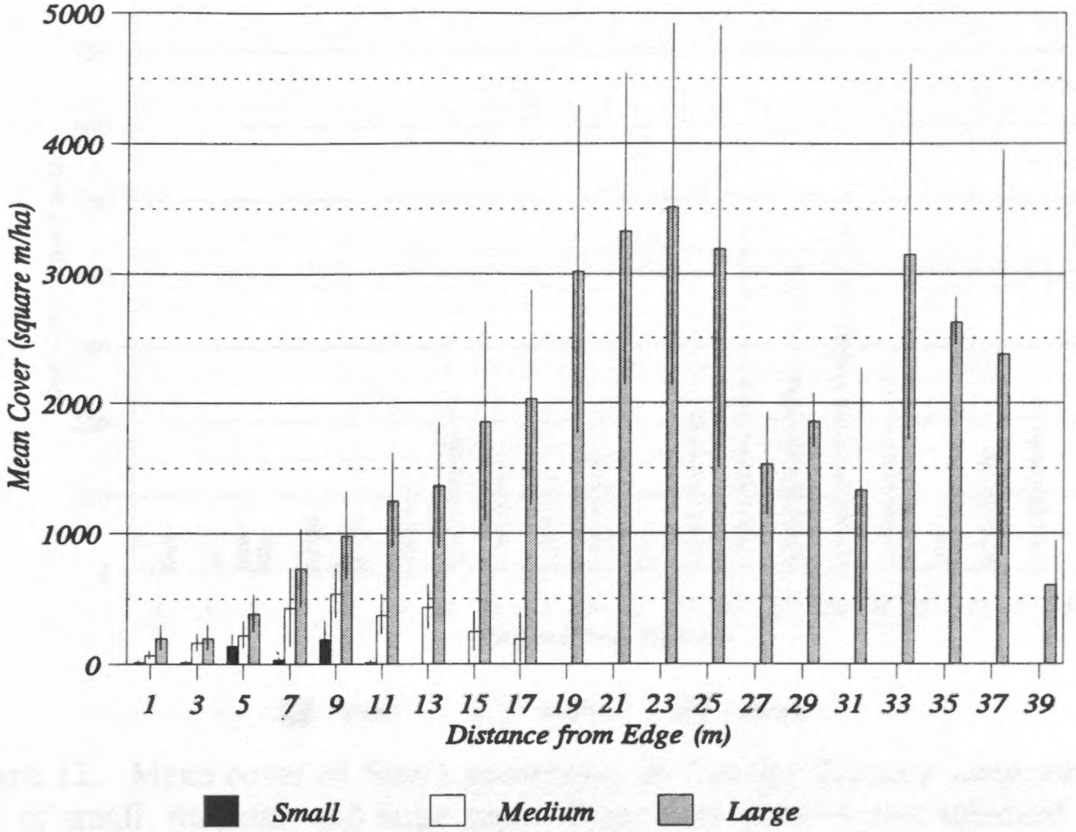

Figure 10. Mean cover of whitethorn in 2 meter distance categories from gap edge of small, medium, and large gaps. Error bars show ± one standard error of the mean.

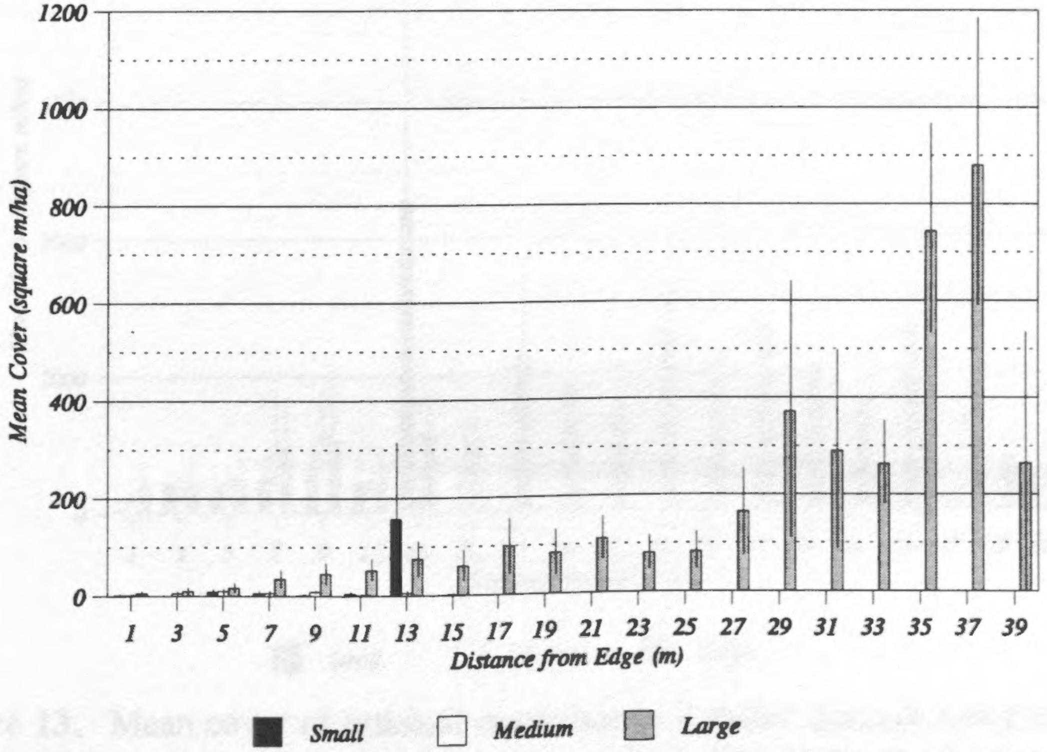

Figure 11. Mean cover of greenleaf manzanita in 2 meter distance categories from gap edge of small, medium, and large gaps. Error bars show ± one standard error of the mean.

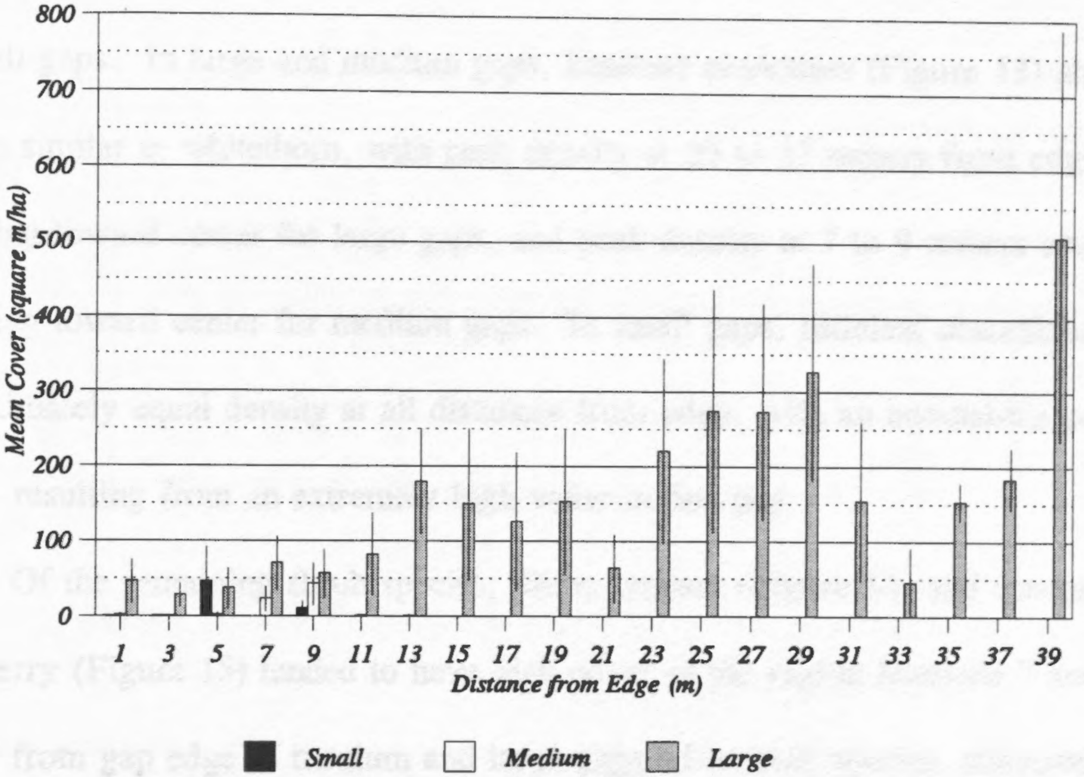

Figure 12. Mean cover of Sierra gooseberry in 2 meter distance categories from gap edge of small, medium, and large gaps. Error bars show ± one standard error of the mean.

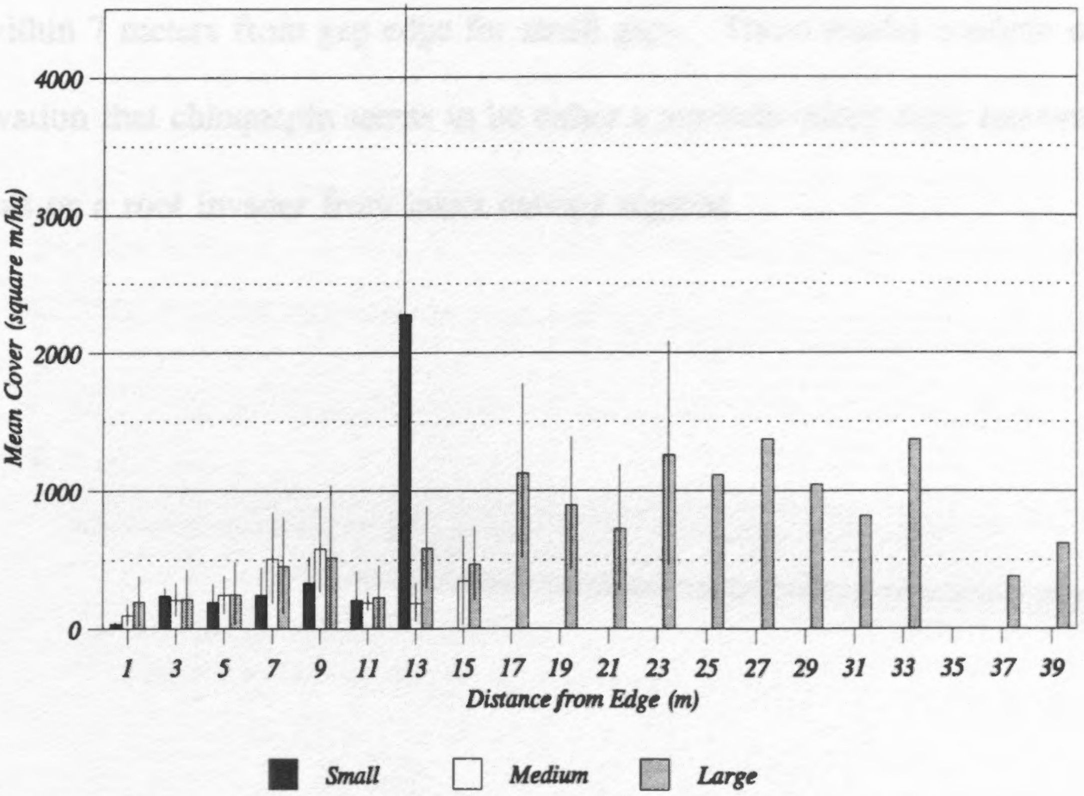

Figure 13. Mean cover of littleleaf ceanothus in 2 meter distance categories from gap edge of small, medium, and large gaps. Error bars show ± one standard error of the mean.

in small gaps. In large and medium gaps, littleleaf ceanothus (Figure 13) showed a pattern similar to whitethorn, with peak density at 23 to 27 meters from edge and declining toward center for large gaps, and peak density at 7 to 9 meters and declining toward center for medium gaps. In small gaps, littleleaf ceanothus showed approximately equal density at all distances from edge, with an anomalous peak at 13 meters resulting from an extremely high value in one gap.

Of the remaining shrub species, Sierra currant (Figure 14) and creeping snowberry (Figure 15) tended to have high cover in the region between 7 and 15 meters from gap edge of medium and large gaps. For both species, substantial cover in small gaps occurred only within 5 meters of the gap edge. Bush chinquapin (Figure 16) grew mostly within 15 meters from gap edge for large and medium gaps, and within 7 meters from gap edge for small gaps. These results confirm my observation that chinquapin seems to be either a survivor along high intensity fire margins or a root invader from intact canopy regions.

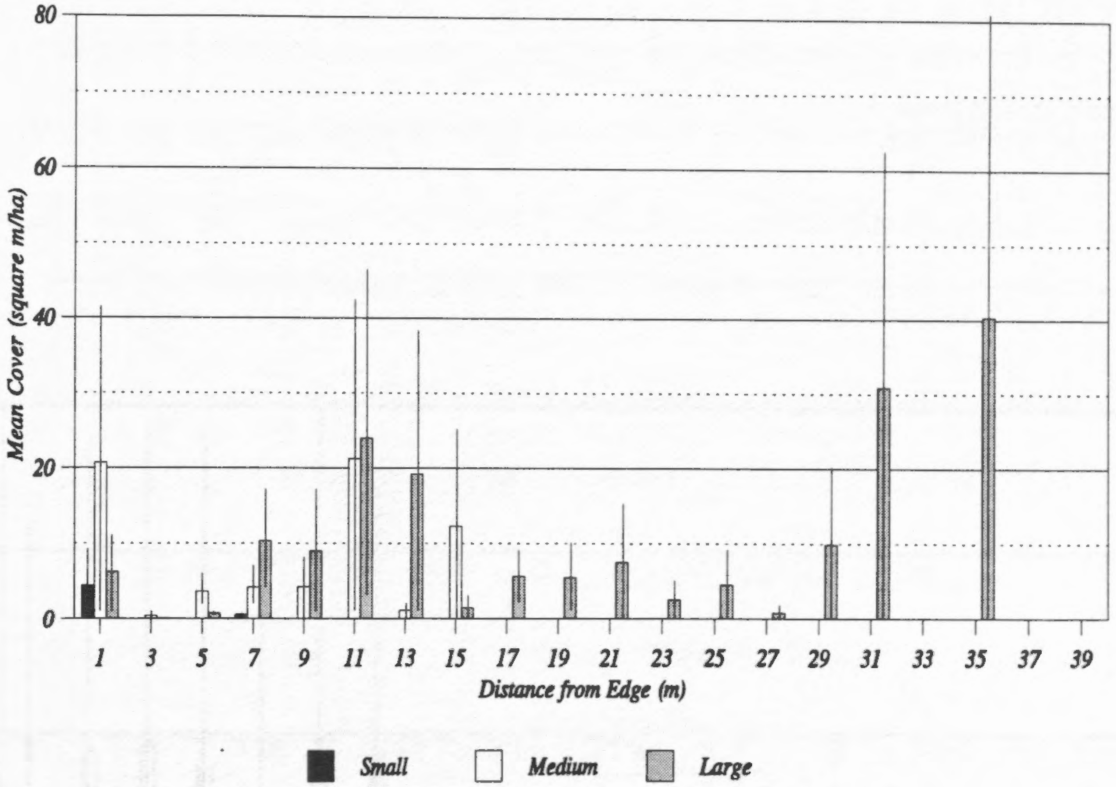

Figure 14. Mean cover of Sierra currant in 2 meter distance categories from gap edge of small, medium, and large gaps. Error bars show ± one standard error of the mean.

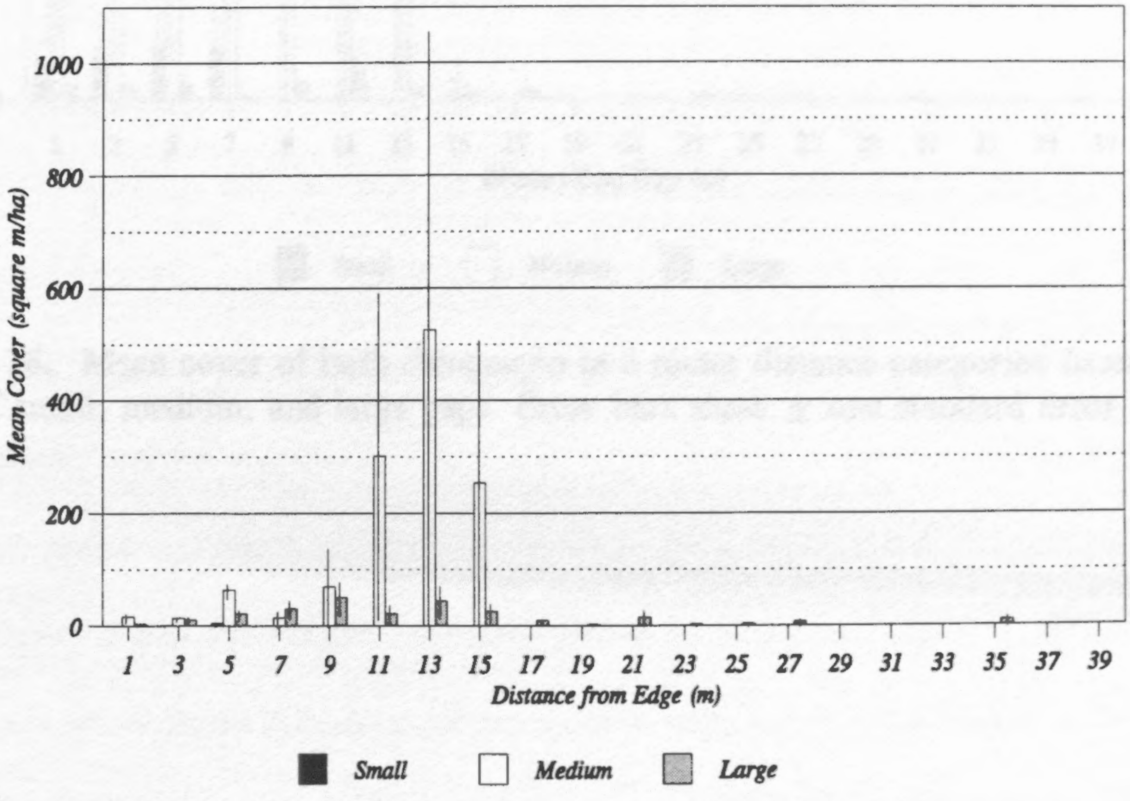

Figure 15. Mean cover of creeping snowberry in 2 meter distance categories from gap edge of small, medium, and large gaps. Error bars show ± one standard error of the mean.

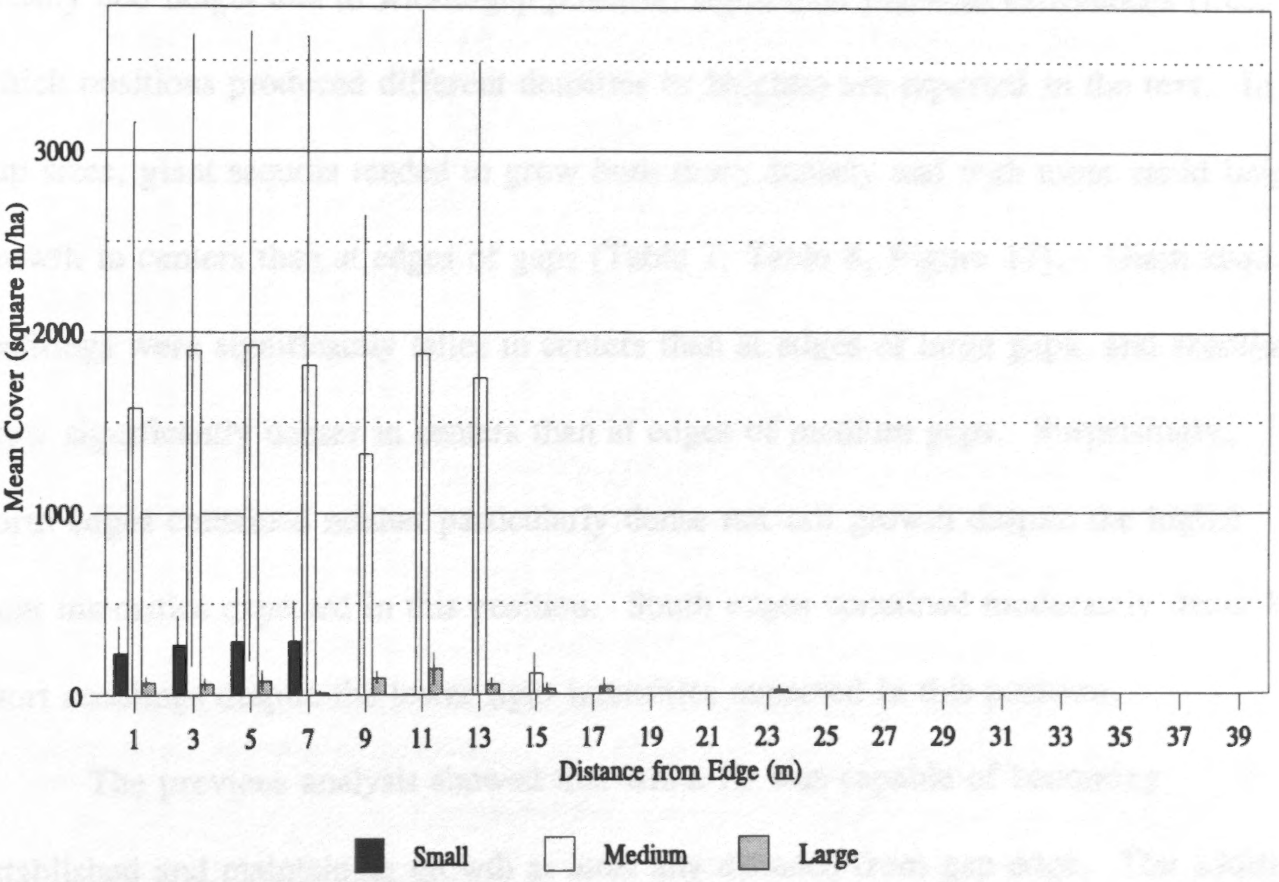

Figure 16. Mean cover of bush chinquapin in 2 meter distance categories from gap edge of small, medium, and large gaps Error bars show ± one standard error of the mean.

Position. Because the analysis of distance from gap edge tended to show that certain species responded strongly to edge or interior position, I attempted to view this response more clearly with the additional criterion of compass position (north, south, east, or west). Tables 7 and 8 report the results of tests for differences in density and height due to within-gap position; significant pairwise differences (i.e., which positions produced different densities or heights) are reported in the text. In all gap sizes, giant sequoia tended to grow both more densely and with more rapid height growth in centers than at edges of gaps (Table 7, Table 8, Figure 17). Giant sequoia seedlings were significantly taller in centers than at edges of large gaps, and seedlings grew significantly denser in centers than at edges of medium gaps. Surprisingly, north edges contained neither particularly dense nor tall growth despite the higher light intensities expected in this position. South edges contained moderately dense but short seedlings despite the lower light intensities expected in this position.

The previous analysis showed that white fir was capable of becoming established and maintaining growth at most any distance from gap edge. The addition of compass position did not provide any further resolution in large gaps; white fir appears able to grow anywhere within large gaps (Table 7, Table 8, Figure 18). An effect of compass position was found in medium gaps, where white fir seedlings grew significantly denser in northern quadrants than in southern and eastern quadrants. A significant interaction effect of edge/center position and compass position on white fir height in medium gaps was due to the lack of seedlings in the south center position. In small gaps, white fir grew significantly denser at gap edges than centers, and significantly taller in eastern quadrants than in northern and western quadrants.

Table 7. Results of two-way ANCOVA for tree density dependent on within-gap position, with gap age as covariate. Significant results are shown in bold.

	Gap	Edge/Center Position		Compass Position		Edge/Center *Compass	
Species	Size	F	p	F	p	F	p
Giant sequoia	S	0.010	0.922	0.459	0.713	0.128	0.942
	M	**4.117**	**0.049**	0.888	0.456	0.539	0.658
	L	0.076	0.785	0.630	0.600	0.040	0.989
White fir	S	**3.095**	**0.088**	0.489	0.693	0.393	0.759
	M	0.046	0.832	**3.892**	**0.022**	0.240	0.867
	L	1.504	0.227	0.467	0.707	0.424	0.737
Sugar pine	S	0.604	0.443	0.096	0.962	0.068	0.977
	M	1.273	0.266	0.203	0.894	0.514	0.675
	L	0.628	0.433	1.127	0.350	0.156	0.925

Table 8. Results of two-way ANCOVA for tree height dependent on within-gap position, with gap age as covariate. Significant results are shown in bold.

	Gap	Edge/Center Position		Compass Position		Edge/Center *Compass	
Species	Size	F	p	F	p	F	p
Giant sequoia	S	1.253	0.344	2.317	0.254	0.751	0.590
	M	0.760	0.396	0.355	0.786	0.718	0.556
	L	**14.683**	**0.000**	1.979	0.134	0.206	0.892
White fir	S	3.071	0.155	**4.090**	**0.104**	2.870	0.167
	M	0.366	0.560	1.497	0.281	**3.822**	**0.051**
	L	0.014	0.906	1.076	0.374	1.377	0.268
Sugar pine	S	1.215	0.332	0.192	0.897	0.363	0.784
	M	0.730	0.407	**5.399**	**0.011**	0.099	0.959
	L	2.642	0.114	1.811	0.165	1.110	0.359

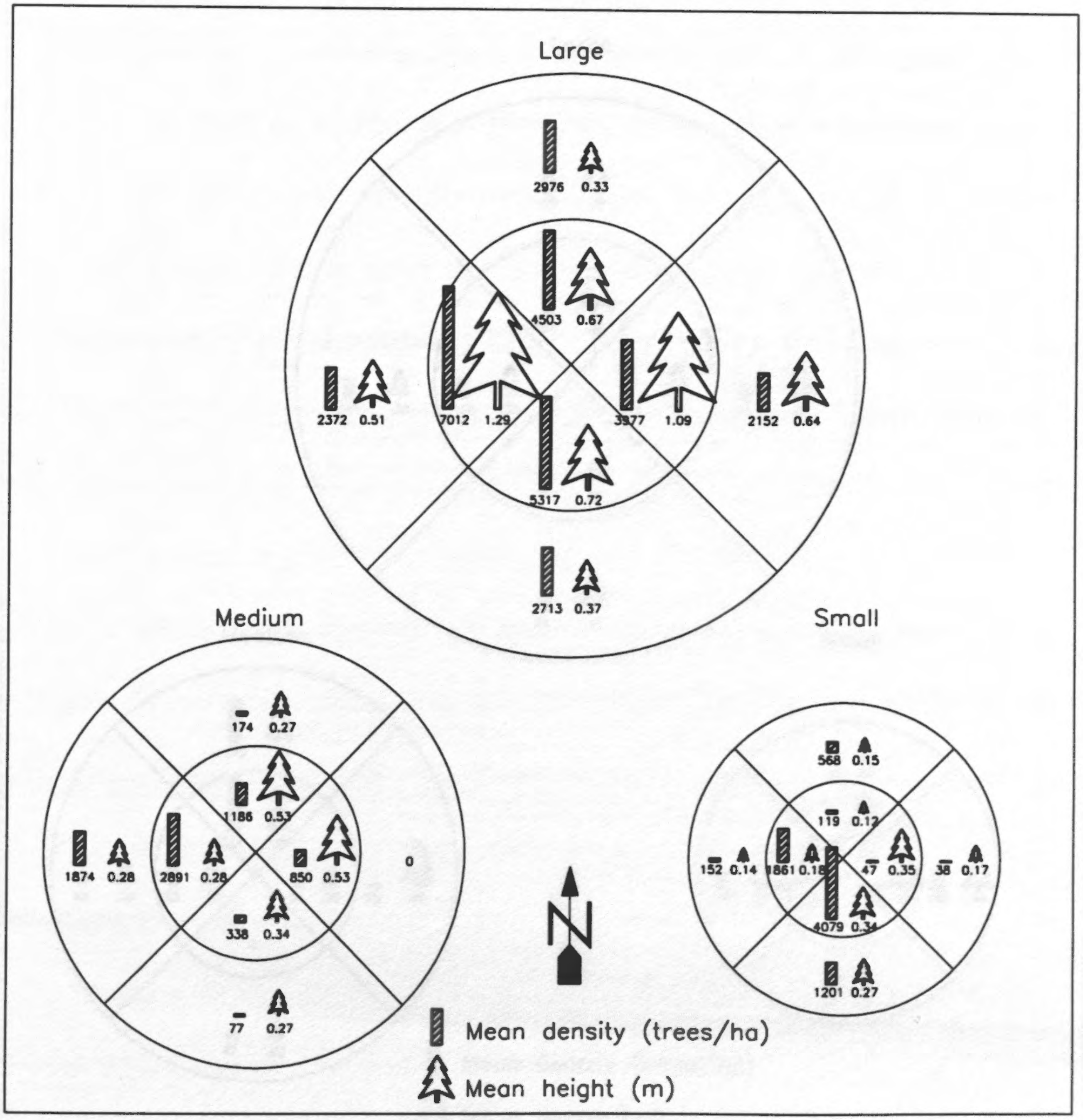

Figure 17. Giant sequoia mean density and height by within-gap position and gap size. Mean density is shown as a bar scaled to density in trees per hectare, and mean height is shown as a tree symbol scaled to height in meters.

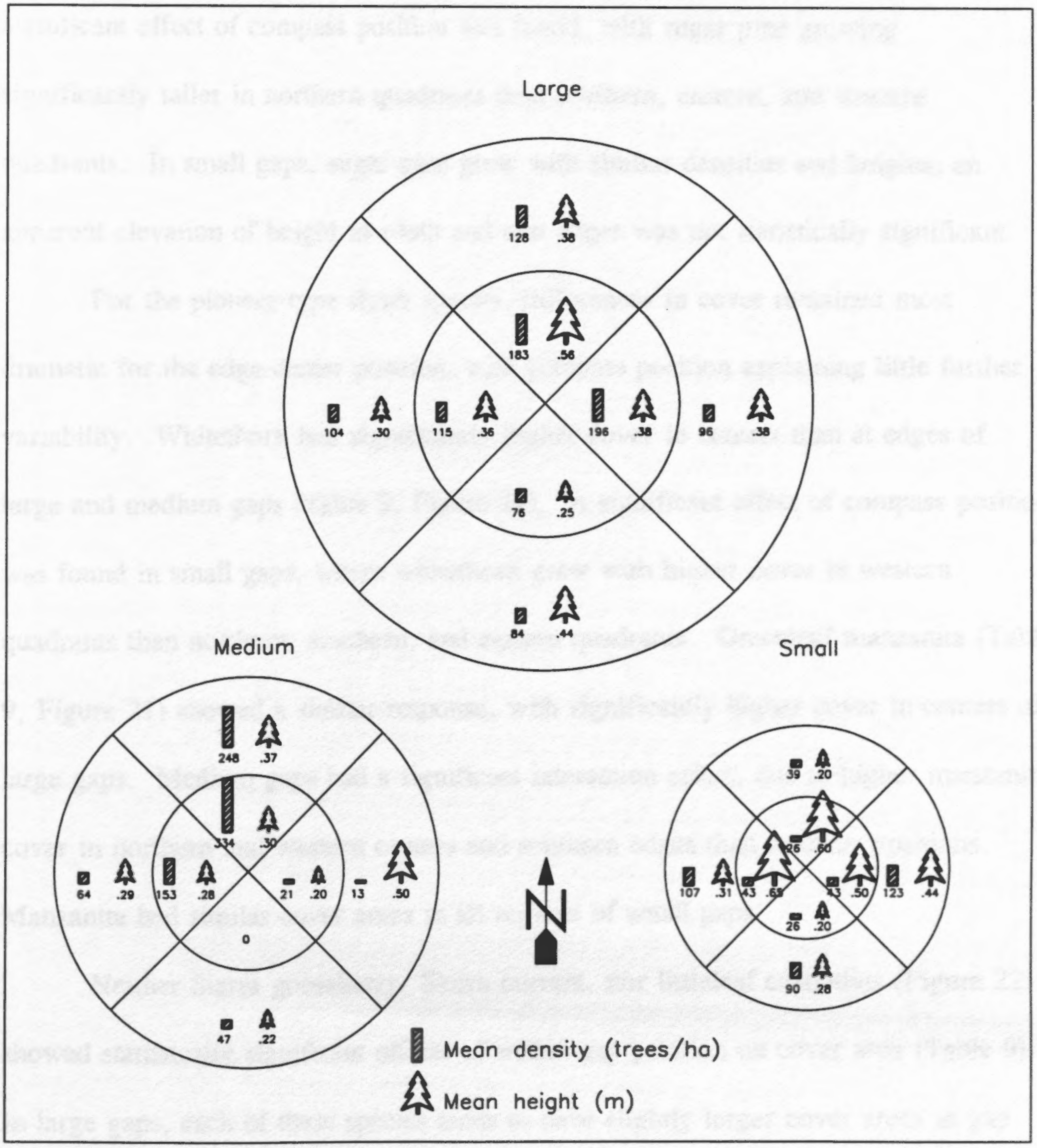

Figure 18. White fir mean density and height by within-gap position and gap size. Mean density is shown as a bar scaled to density in trees per hectare, and mean height is shown as a tree symbol scaled to height in meters.

Like white fir, sugar pine grew with similar densities and heights in all positions within large gaps (Table 7, Table 8, Figure 19); an apparent elevation of height in the north center position was not statistically significant. In medium gaps, a significant effect of compass position was found, with sugar pine growing significantly taller in northern quadrants than southern, eastern, and western quadrants. In small gaps, sugar pine grew with similar densities and heights; an apparent elevation of height in south and east edges was not statistically significant.

For the pioneer-type shrub species, differences in cover remained most dramatic for the edge-center position, with compass position explaining little further variability. Whitethorn had significantly higher cover in centers than at edges of large and medium gaps (Table 9, Figure 20). A significant effect of compass position was found in small gaps, where whitethorn grew with higher cover in western quadrants than northern, southern, and eastern quadrants. Greenleaf manzanita (Table 9, Figure 21) showed a similar response, with significantly higher cover in centers of large gaps. Medium gaps had a significant interaction effect, due to higher manzanita cover in northern and western centers and southern edges than in other positions. Manzanita had similar cover areas in all regions of small gaps.

Neither Sierra gooseberry, Sierra currant, nor littleleaf ceanothus (Figure 22) showed statistically significant effects of within-gap position on cover area (Table 9). In large gaps, each of these species tends to have slightly larger cover areas in gap centers. The response of littleleaf ceanothus is notable when compared to that of whitethorn, which dominates both centers and edge of large gaps. In small and medium gaps, littleleaf ceanothus is more dominant at gap edges than whitethorn and

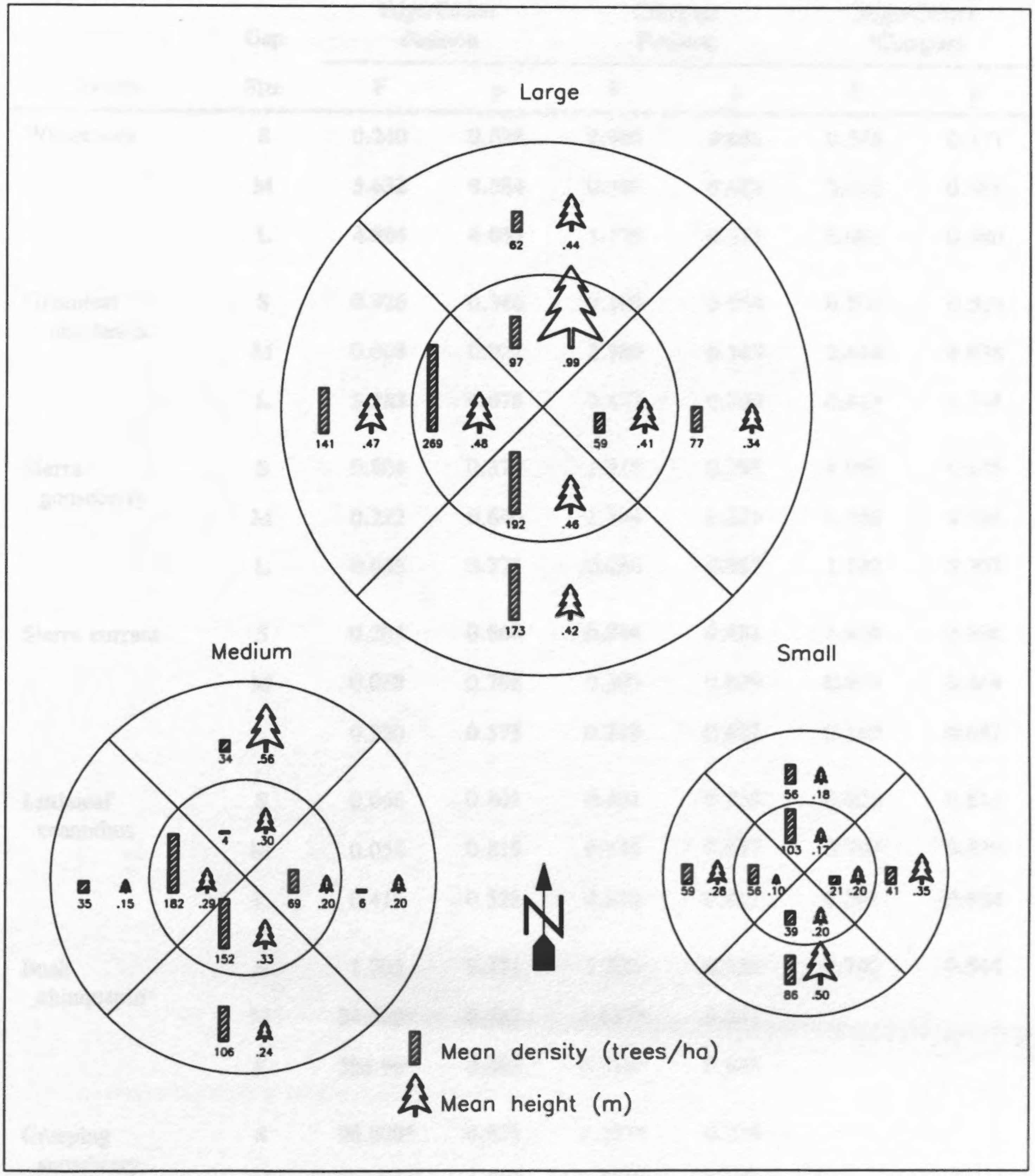

Figure 19. Sugar pine mean density by within-gap position and gap size. Mean density is shown as a bar scaled to density in trees per hectare, and mean height is shown as a tree symbol scaled to height in meters.

Table 9. Results of two-way ANCOVA for shrub cover area dependent on within-gap position. Cases for which the Kruskal-Wallis test or Mann-Whitney test was used are indicated by an asterisk next to the F statistic. Significant results are shown in bold.

	Gap	Edge/Center Position		Compass Position		Edge/Center *Compass	
Species	Size	F	p	F	p	F	p
Whitethorn	S	0.240	0.628	**2.901**	**0.051**	0.376	0.771
	M	**3.632**	**0.064**	0.497	0.686	0.212	0.888
	L	**4.905**	**0.033**	1.176	0.331	0.061	0.980
Greenleaf manzanita	S	0.926	0.346	0.109	0.954	0.800	0.506
	M	0.008	0.927	**2.189**	**0.105**	**2.444**	**0.078**
	L	**3.283**	**0.078**	0.477	0.700	0.413	0.744
Sierra gooseberry	S	0.804	0.379	1.318	0.293	1.980	0.145
	M	0.222	0.640	1.194	0.325	0.358	0.784
	L	0.085	0.773	0.086	0.967	1.128	0.353
Sierra currant	S	0.201	0.668	0.914	0.481	1.628	0.268
	M	0.068	0.796	0.509	0.679	0.877	0.464
	L	0.320	0.575	0.213	0.887	0.549	0.652
Littleleaf ceanothus	S	0.066	0.801	0.401	0.755	0.622	0.612
	M	0.054	0.819	0.545	0.657	0.794	0.510
	L	0.417	0.528	0.310	0.817	0.301	0.824
Bush chinquapin	S	1.305	0.271	1.223	0.336	0.740	0.544
	M	34.500*	0.787	1.657*	0.647		
	L	**286.00***	**0.005**	0.818*	0.845		
Creeping snowberry	S	**90.000***	**0.071**	4.257*	0.235		
	M	32.000*	1.000	2.620*	0.454		
	L	**12.202**	**0.001**	1.279	0.299	1.684	0.191

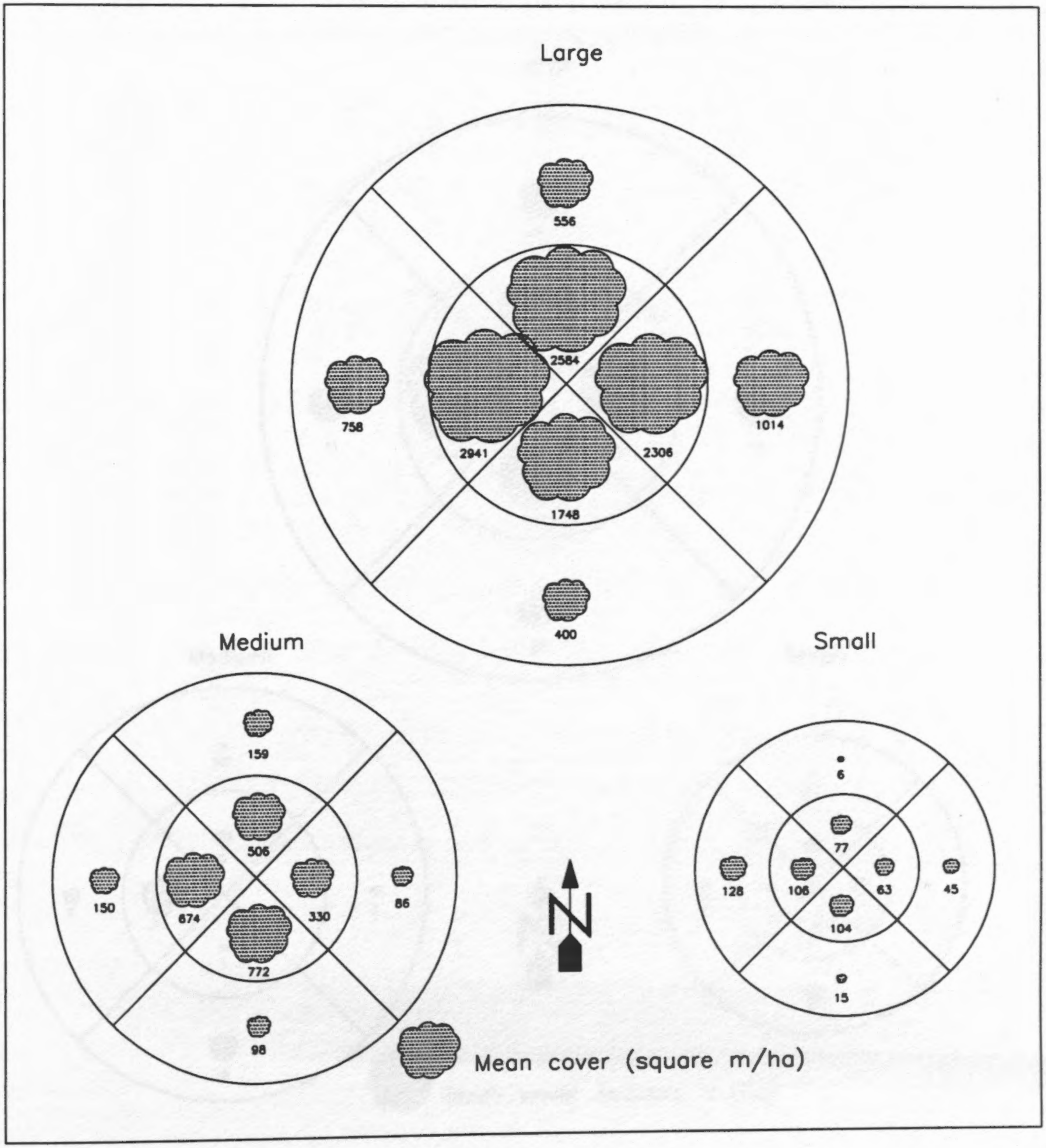

Figure 20. Whitethorn mean cover by within-gap position and gap size. Mean cover is shown as a shrub symbol scaled to cover area in square meters per hectare of available area.

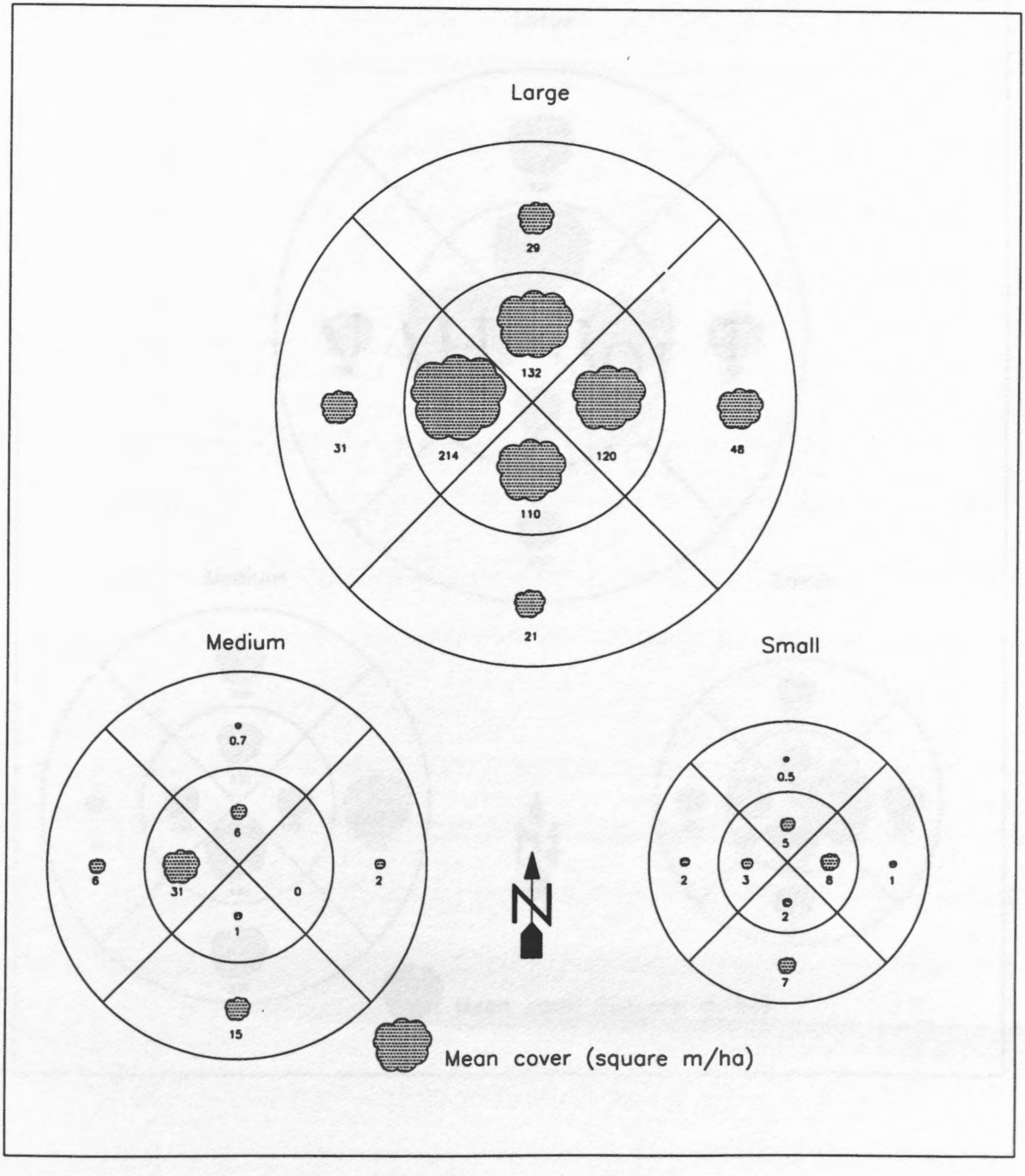

Figure 21. Greenleaf manzanita mean cover by within-gap position and gap size. Mean cover is shown as a shrub symbol scaled to cover area in square meters per hectare of available area.

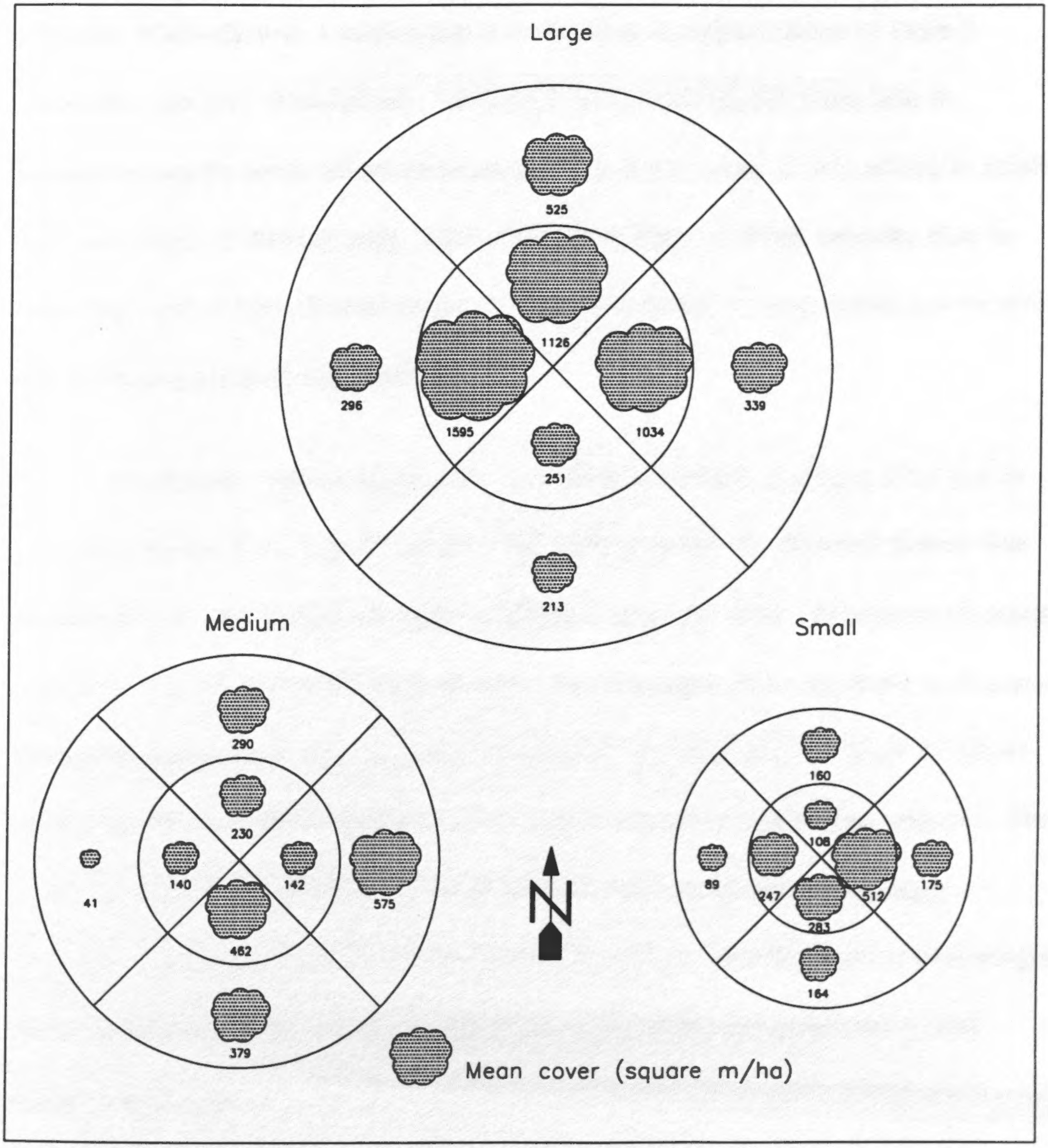

Figure 22. Littleleaf ceanothus mean cover by within-gap position and gap size. Mean cover is shown as a shrub symbol scaled to cover area in square meters per hectare of available area.

dominates all areas, particularly centers, of small gaps. Because of this ability of littleleaf ceanothus to maintain growth in these positions where available moisture is probably relatively low, I suspect that it is the more drought-tolerant of these 2 *Ceanothus* species. Alternatively, whitethorn seeds may require more heat to adequately scarify seeds before germination. The lower cover of whitethorn in small gaps and edges of medium gaps, where fires were likely of lower intensity than in large gaps and centers of medium gaps, might be a result of lower initial colonization due to inadequate seed scarification.

Patchiness. Giant sequoia grew in a clumped pattern in all gap sizes and at all spatial scales, from 1 to 45 meters. The scale at which the clumped pattern was maximum (i.e., the largest L(t) value) differed among gap sizes. Maximum clumping was from 7 to 12 meters in clump diameter for small gaps, 9 to 19 meters in diameter for medium gaps, and 10 to 24 meters in diameter for large gaps. Figure 23 shows the results of the Ripley's K(t) analysis for giant sequoia in a large gap, gap 14. The observed L(t) shows inflection points at about 6, 18, and 25 meters in clump diameter, suggesting a pattern of hierarchical clumping. This hierarchical clumping is illustrated in Figure 24, where clumps of just a few stems are positioned within larger-scale clumps.

White fir showed more variation in spatial pattern. In small gaps and 1 medium gap, white fir grew in a clumped pattern at small scales (maximum clumping from 3 to 8 meters in clump diameter) and in a random pattern at larger scales; in the remaining 2 medium gaps for which there were enough points to analyze, white fir

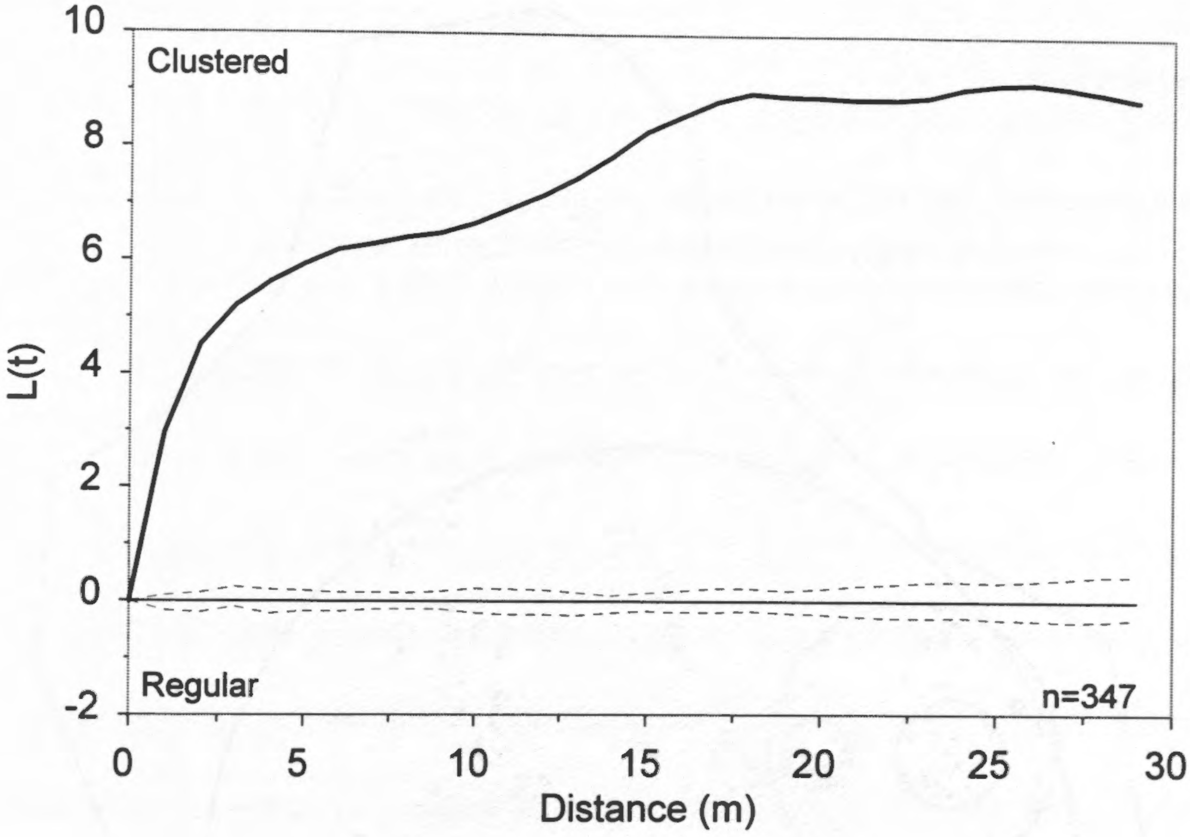

Figure 23. Results of Ripley's K(t) analysis for gap 14 (large). The heavy line is the observed value of L(t), a transformation of K(t) (see Methods). The single line shows the expected value of L(t)=0 for randomly distributed points, and the dashed lines show the upper and lower boundaries of the 95% confidence envelope.

grew in clumped patterns with maximum clumping from 14 to 16 meters in diameter. In large gaps, white fir tended to grow in clumped patterns, with maximum clumping from 12 to 32 meters in diameter.

Sugar pine grew mainly in clumped patterns in all gap sizes, at scales from 1 to 56 meters in diameter. During field work, I observed that small-scale clumping (<5 cm) often occurred, and is probably due to germination from a single cone.

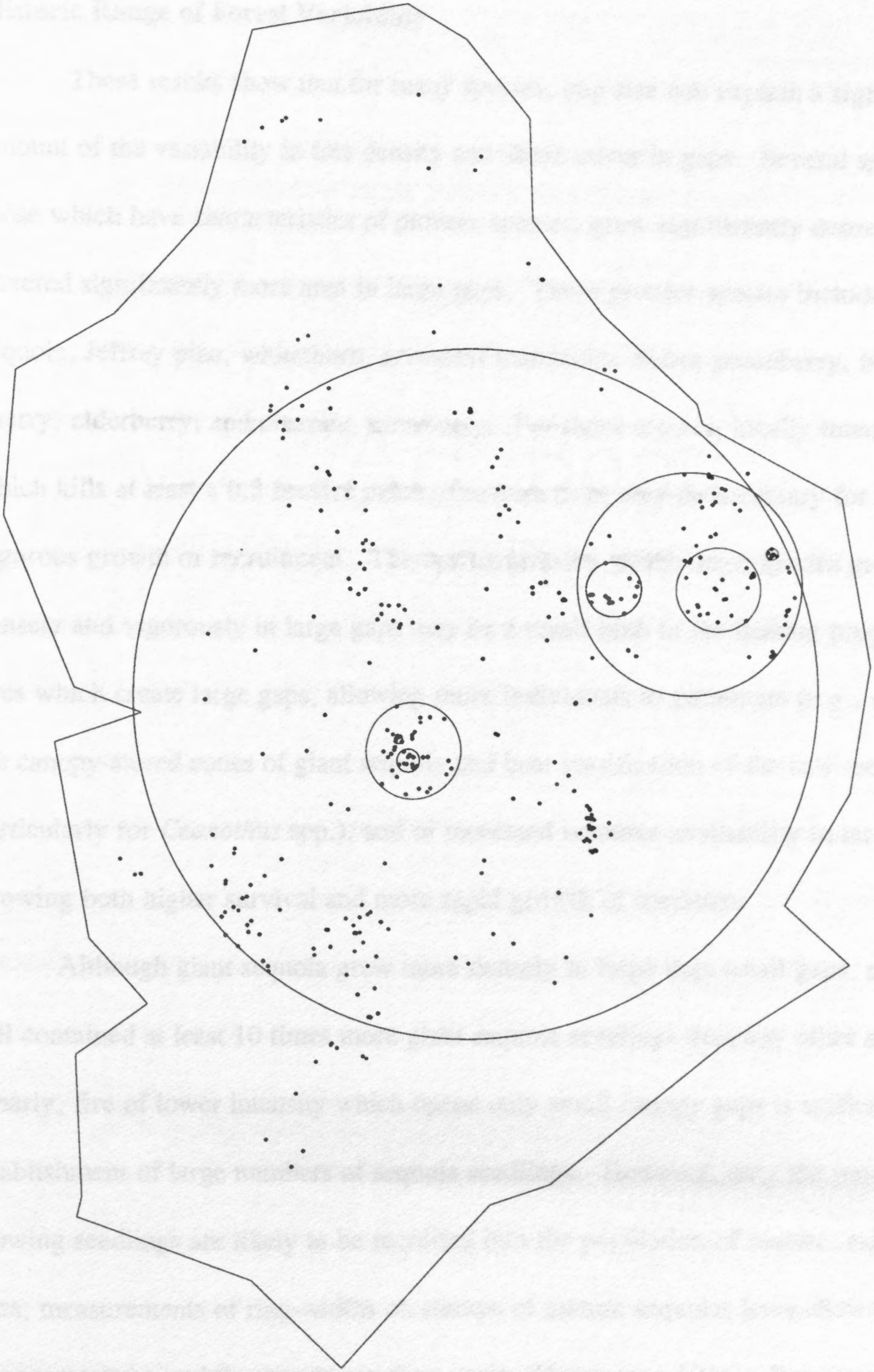

Figure 24. Stem map of giant sequoia seedlings in a large gap (gap 14), with several clumped groups of trees circled. The irregular polygon is the gap boundary.

Historic Range of Forest Variability

These results show that for many species, gap size can explain a significant amount of the variability in tree density and shrub cover in gaps. Several species, those which have characteristics of pioneer species, grew significantly denser or covered significantly more area in large gaps. These pioneer species include giant sequoia, Jeffrey pine, whitethorn, greenleaf manzanita, Sierra gooseberry, bitter cherry, elderberry, and creeping snowberry. For these species, locally intense fire which kills at least a 0.3 hectare patch of mature trees may be necessary for their vigorous growth or recruitment. The mechanisms by which these species grow more densely and vigorously in large gaps may be a result both of the heating properties of fires which create large gaps, allowing more individuals to germinate (e.g., drying of the canopy-stored cones of giant sequoia and heat scarification of the soil seed bank, particularly for *Ceanothus* spp.), and of increased resource availability in large gaps, allowing both higher survival and more rapid growth of seedlings.

Although giant sequoia grew more densely in large than small gaps, small gaps still contained at least 10 times more giant sequoia seedlings than any other species. Clearly, fire of lower intensity which opens only small canopy gaps is sufficient for the establishment of large numbers of sequoia seedlings. However, only the most rapidly-growing seedlings are likely to be recruited into the population of mature, reproductive trees; measurements of ring-widths on stumps of mature sequoias have shown that these trees were rapidly-growing in their youth (Huntington 1914). Resource availability within small gaps is probably not sufficient to support the rapid height growth necessary for sequoia recruitment. The 6 small gaps surveyed in this study contained no seedlings of at least 1 meter height (after 7 to 13 years of growth). These seedlings are likely in a suppressed condition and may soon die from one of the following causes: (1) "starvation" in shade (negative carbon balance), (2) increased vulnerability to pathogens and insects due to low vigor, or (3) high susceptibility to mortality during the next fire due to lack of height. Large gaps, with nearly 20 times greater density of seedlings of at least 1 meter height than medium gaps, are likely the predominant source of young recruits into the mature giant sequoia population.

The clearest within-gap spatial pattern to emerge from the data is increasing tree seedling height and shrub cover toward gap centers. Contrary to my initial hypotheses, density, height, and shrub cover did not vary consistently with compass position. For example, northern edges contained neither higher plant densities nor taller seedlings than other positions. My interpretation is that moisture availability, rather than light, is the limiting resource in these gaps. Increased moisture availability in gap centers due to the absence of water uptake by mature boundary trees is the likely mechanism for the rapid plant growth in gap centers. This hypothesis is supported by results of several studies in western coniferous forests. In experimentally-created gaps in Douglas-fir forests of Oregon and Washington, Gray (1995) found that soil moisture content was higher and seedling growth greater at gap centers than edges. Additionally, surface temperatures at north positions in large gaps (D:H ratio of 1) were high and may have limited growth. Gray (1995) suggests from this and other evidence that below-ground controls on seedling establishment may be more important than light levels within gaps. A study in a giant sequoia-mixed conifer forest found that the center of a 0.2 ha gap contained from 7.5 to 15 cm more moisture in the top

1.5 m of soil than was found in surrounding forested areas (Kilgore 1973). Working in a Sierra Nevada mixed-conifer forest, Ziemer (1964) measured soil moisture along a transect from mature forest across canopy gaps approximately 0.24 ha in size and from 1 to 12 years in age. In recently-cut gaps (age 1 year), soil moisture at depths from 15 cm to 100 cm became progressively greater toward the center of the gap, an effect that persisted throughout the growing season, from June to November. This gradient of increasing moisture toward gap centers was ameliorated by gap age. The 5-year-old gaps had an abrupt change in moisture about 9 meters from the tree canopy, probably caused by roots of the surrounding forest extending into the gap. This change in moisture at 9 meters from the tree canopy persisted in 10-year-old gaps, but the gradient was much less striking due to the growth and transpiration of tree and shrub seedlings within the gap. By 12 years after gap formation, the soil moisture pattern had essentially returned to the mature forest condition (Ziemer 1964).

There are several alternate, or additional, factors which may contribute to this pattern of rapid growth in gaps centers. One alternate explanation is that a pulse of mineralized nitrogen was made available in gap centers from higher fire intensities in these positions. A second alternate explanation is that rapid height growth takes place where *Ceanothus* spp. are abundant, due to soil fertilization by these nitrogen-fixing shrubs. Because whitethorn is most abundant in gap centers, spatial autocorrelation of rapidly-growing trees with dense whitethorn cover in gap centers may result. This latter explanation has much anecdotal though no quantitative support.

For the giant sequoia-mixed conifer forest, the highly variable fire frequencies of the past millennia likely caused shifts in the predominant gap size over time, producing gap-size distributions similar to those suggested in Figure 1. These results have shown that species composition and within-gap spatial patterns of regeneration in gaps vary with gap size. How compositional and structural changes at the scale of the gap can affect the species composition and structure at the scale of the community can be better understood with a hierarchical model (Figure 25). This model depicts the forest community, at the highest level, as a mosaic of patches with each patch having its origin in a gap. The gap, at the central level, is composed of plant aggregations. Because of feedbacks and interactions in this system, a change in the attributes of one level can have effects at other levels.

In hierarchically organized systems, interactions among structural components at one level generate the behaviors of a component at the next higher level, and higher level processes, in turn, constrain (control) lower-level behavior (Urban et al. 1987). For instance, competition between plants within a gap (its results dependent on the life span, growth rate, stress tolerance of each species) determines the species composition, density, and thus rates of fuel production at the gap level. Interactions between gaps (seed dispersal, nutrient flow down slope, fuel continuity at gap boundaries) depend on their size, shape, age, and spatial distribution, and influence the mosaic structure, fire spread, and fire intensities characteristic of the community. Fire, acting at the community level and itself constrained by climate at the highest level, constrains gap size, gap shape, and resource gradients at the gap level. These characteristics at the gap level constrain the light, soil moisture, and nutrients available to each plant. Thus, a continuously interacting system results where structure influences process on the right side of the diagram, and process constrains structure on the left side. By this

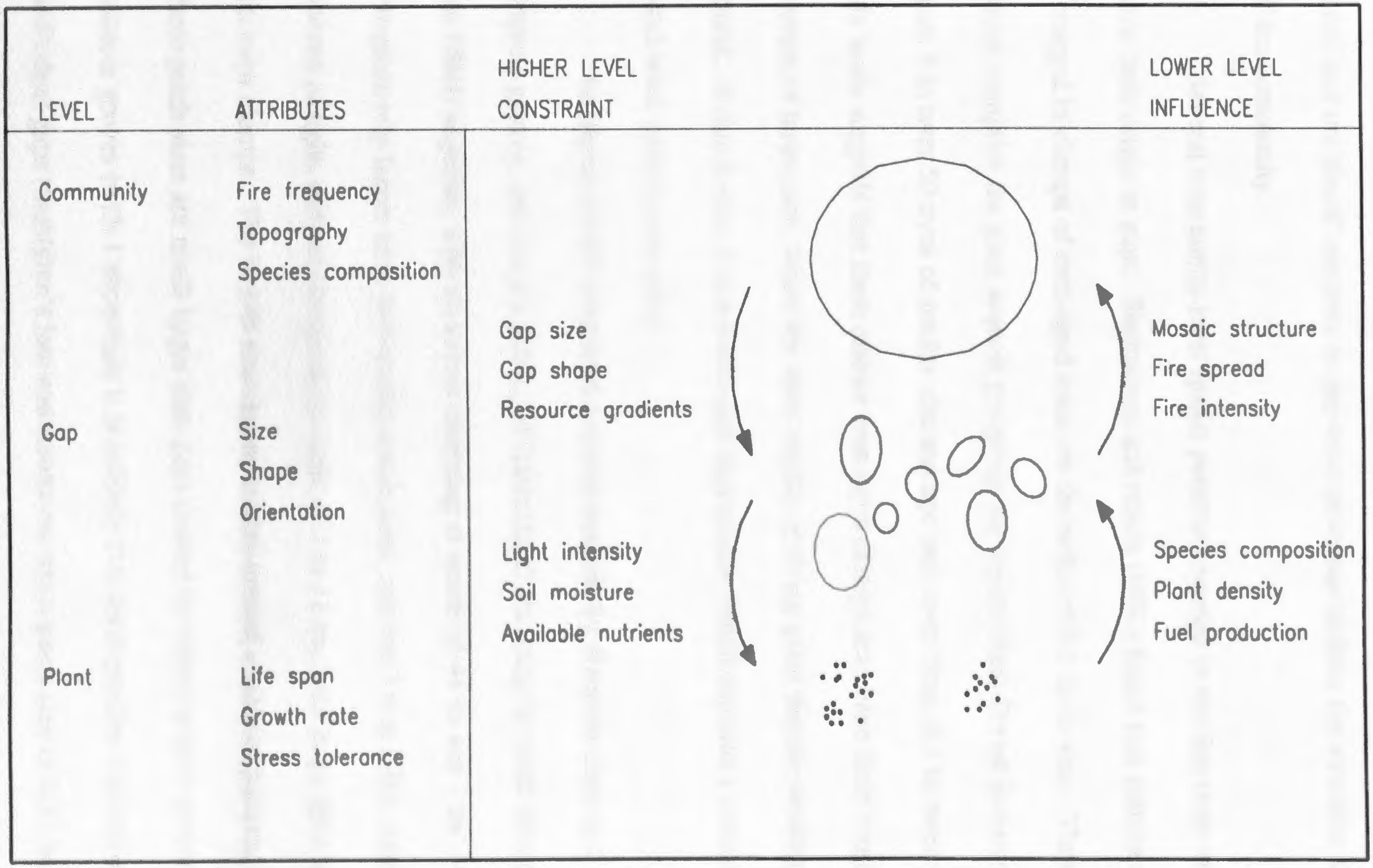

Figure 25. A hierarchical model showing the plant, gap, and community levels and their attributes, constraints, and influences.

model, a variable fire regime, responding to a climatic cue, acts mainly at the gap level, and the plants' response to gap-level processes defines the structure and behavior of the community.

Several community-level spatial patterns reported in the literature are shown to have their origin in gaps. Stephenson and others (1991) found that mature sequoias are arranged in clumps of even-aged trees, on the order of 0.1 ha in size. These clumps, which comprise the giant sequoia groupings for which Giant Forest is renowned, range from 5 to over 50 trees of similar size and age and cover from 0.1 to more than 0.5 ha. My work suggests that these mature even-aged clumps may have their origin in the centers of large gaps, where the most rapidly-growing giant sequoia seedlings are found. If this is true, it is a within-gap aggregation which explains a community-level patchwork pattern seen today.

Stohlgren (1993) conducted a spatial analysis by diameter class in 2 giant sequoia groves, and found a pattern of hierarchical clumping in small diameter (<14 cm DBH) sequoias, with maximum clumping at scales of 44 ha and 7 ha. Progressively larger trees had smaller patch sizes, and the 3.0 m DBH class exhibited a pattern of tight, distinct clumps at the scale of 7 to 12 ha, with large open spaces between clumps. The largest size classes tended toward a random pattern. Because these patch sizes are much larger than gaps created by contemporary prescribed fire in sequoia groves (with 1 exception) it is unlikely that these patches correspond to individual gaps (Stohlgren's low-end resolution was a patch size of 0.25 ha). The trees in these patches most likely originated from many spatially-clustered gaps, perhaps the result of a single fire erupting in many local hot-spots (creating a cluster of large gaps), or of several fires each creating large gaps in an area where the topography favors high-intensity fire. I interpret the progression toward tight, distinct clumps as trees become larger as the suppression and mortality of those trees which did not originate in the most favorable sites, i.e. trees located in medium gaps or edges of large gaps. Bonnicksen and Stone (1981) investigated smaller-scale spatial patterns of mature mixed conifer stems, on 3 plots 0.64 ha in size, and found that even-aged aggregations ranged in size from 0.031 ha to 0.16 ha. In my study, these aggregation sizes correspond to the small and medium gaps, or to clumps of trees within large gaps.

To describe the structural variability which the historically variable fire regime might have produced, I use the species response to gaps to explain how the structure of the community may have varied according to the model shown in Figure 25. When the climate shifts from hot and dry to cool and wet, the fire frequency shifts from very frequent to less frequent fires (see Figure 1), hypothetically producing a shift from the predominance of small gaps to the predominance of larger gaps. During this shift, I'd expect those species which showed little change in density or growth with increasing gap size (white fir, red fir, sugar pine, and ponderosa pine) to maintain fairly steady recruitment over time, on the landscape scale. In addition, these more shade-tolerant species (with the exception of ponderosa pine) were probably the most spatially homogeneous; though they would be aggregated in even-aged clumps due to their origin in gaps, they would establish and be recruited in gaps of all sizes as well as in the mature forest matrix. By contrast, those species which did show increasing density and growth with gap size (giant sequoia, Jeffrey pine, and the pioneer-type shrub species) would show little recruitment in small gaps during periods of frequent fires, and show pulses of recruitment in large gaps when the fire regime shifted to less frequent fires. Thus, they would be the most temporally variable as well as the most spatially variable, with recruitment confined mainly to larger gaps with little or no recruitment occurring in the forest matrix. That giant sequoia populations have been shown to be near equilibrium (exhibiting the inverse-J shape of a stationary age structure) over several millenia suggests that this variability, which would be most pronounced at the scale of decades, may be small relative to the overall millenia-scale trend (Stephenson 1994).

Finally, this approach of inferring historic variability in forest composition and structure based on contemporary response to prescribed fire relies on the assumption that fires burning in present-day fuel accumulations, following a century of fire exclusion, produce similar results as in the past. Extreme fuel accumulations would be expected to produce more, larger gaps which experienced greater fire severity than occurred historically. However, evidence suggests that fire behavior in giant sequoia-mixed conifer forest today is no more severe than in the past. Using post-fire release in sequoia radial growth rings as a proxy for fire severity, Mutch (1994) studied the severity of several prescribed fires and found them comparable to historic fire severities (Caprio et al. 1994). Stephenson and others (1991) cite historical accounts describing patchy high intensity fires prior to fire exclusion. Most gaps in Giant Forest are less than 2 ha (A. Demetry, unpublished data, 1995), but a few fires in other groves have opened larger gaps, including a 4 ha gap in the Redwood Mountain Grove of Kings Canyon National Park (Stephenson et al. 1991). But even these very large gaps are not unprecendented historically. An A.D. 1297 fire in the Mountain Home

Grove was estimated from a tree-ring study to be of high severity over a large area, from 16 ha to several square kilometers in size (Caprio et al. 1994). The most probable deviation of modern fire effects from historical effects is a higher proportion of the landscape in gaps today. A final caveat is that the gaps investigated in this study are the result of single fires, not of a fire regime. In many of these gaps, fuel loads are very high due to the fall of the many snags which were created by the fire. A second fire may enlarge the gaps as well as thin the regeneration growing within the gaps. Whether the results of second and further fires following a century of fire exclusion will be similar to those produced in the past is a critical question.

Contemporary large-scale patterns of gaps on the landscape will be investigated in the next phase of this study, in which all gaps in the Giant Forest Grove will be delineated from large-scale aerial photos and overlaid with prescribed fire boundaries and topography in a GIS model. In addition, the light environment in these gaps will be studied using hemispherical photography to further illuminate how gap size constrains the light available to plants, and what role light plays in producing within-gaps spatial patterns.

Ecological Restoration of Giant Forest

The broad goal for the ecological restoration of Giant Forest is to mimic a fire burning through the area in the absence of human development and fire suppression. Because of tree removals for buildings and parking lots, which created canopy gaps, the canopy-opening characteristic of fire has already been achieved. Missing from these gap sites, however, are the following: the loose, ashy, mineral seedbed produced by fire; the heating of seeds requiring scarification to germinate (*Ceanothus* spp.); the seed rain produced by the rising heat and subsequent drying of giant sequoia cones; the soil nutrient pulse produced by rapid mineralization of organic matter; and the soil seed bank left by recent plant occupants of the site. Wherever possible, the sole use of prescribed fire for obtaining these missing characteristics is recommended. This may be possible in long-abandoned sites, such as Firwood Campground (abandoned in the 1960's), where large fuels, litter, and duff have sufficiently accumulated to allow the spread of fire, where effects of soil compaction have possibly been ameliorated by freeze-thaw cycles, and where a soil seed bank may be present to provide propagules following the fire. Direct manipulation becomes necessary only when fuels are not present in sufficient quantity to allow the spread of fire, when fire of sufficient intensity to produce a seed rain is not possible, when soils have been compacted or eroded, or when the soil seedbank is diminished or absent due to the long absence of plant occupants on the site. On these sites requiring direct manipulation, it is desirable to advance the stage of native plant regeneration to prevent undesirable post-human disturbance effects, such as erosion and colonization by exotic plant species. "Fire plus 10," or the mimicking of species composition, density, and spatial patterns within gaps 10 years following fire, is the proposed objective. The 10-year goal was chosen because the mean age of the model gaps was just over 10 years. Once the desired vegetation is established, which may entail a period of post-planting care, natural processes (fire, self-thinning/mortality) should be allowed to proceed. Although most of the seedlings planted to mimic the "Fire plus 10" vegetation will not survive to be recruited into the canopy, I suggest that natural processes should do the thinning rather than managers planting fewer seedlings to account for future mortality (i.e., creating a "Fire plus 20" vegetation).

Because these results show that the size of fire-caused gaps is a significant source of variation of species densities and spatial patterns of woody plants within gaps, gap size can be used as the principal criterion for identifying a natural analogue for each restoration site. The basic unit for restoration will be a gap, since the closest analogue to these sites within Giant Forest is the discrete unit of a fire-caused gap. Gaps in developed Giant Forest should be delineated, and their areas calculated and classified as small, medium, or large using the same methods described in the Methods section. For each of these potential gap sites requiring restoration (referred to also as a "restoration gap" in the following discussion), I propose the following process for defining a desired species composition, density, and spatial pattern of woody vegetation. The restoration process described below could be used for any forest for which gap-phase regeneration is an important component of forest dynamics, and for which the scale of artificial disturbance approximates the scale of natural disturbance.

(1) The principal criterion for defining a desired vegetation should be the size of the gap: small, medium, or large.

(2) The 18 model gaps should be used to define the *range of variability* that is allowable within a gap size category. Within the limits of this range, the knowledge and discretion of the restorationist should be used to define the desired vegetation of a particular restoration gap (Figure 26). For example, if it is assumed that the

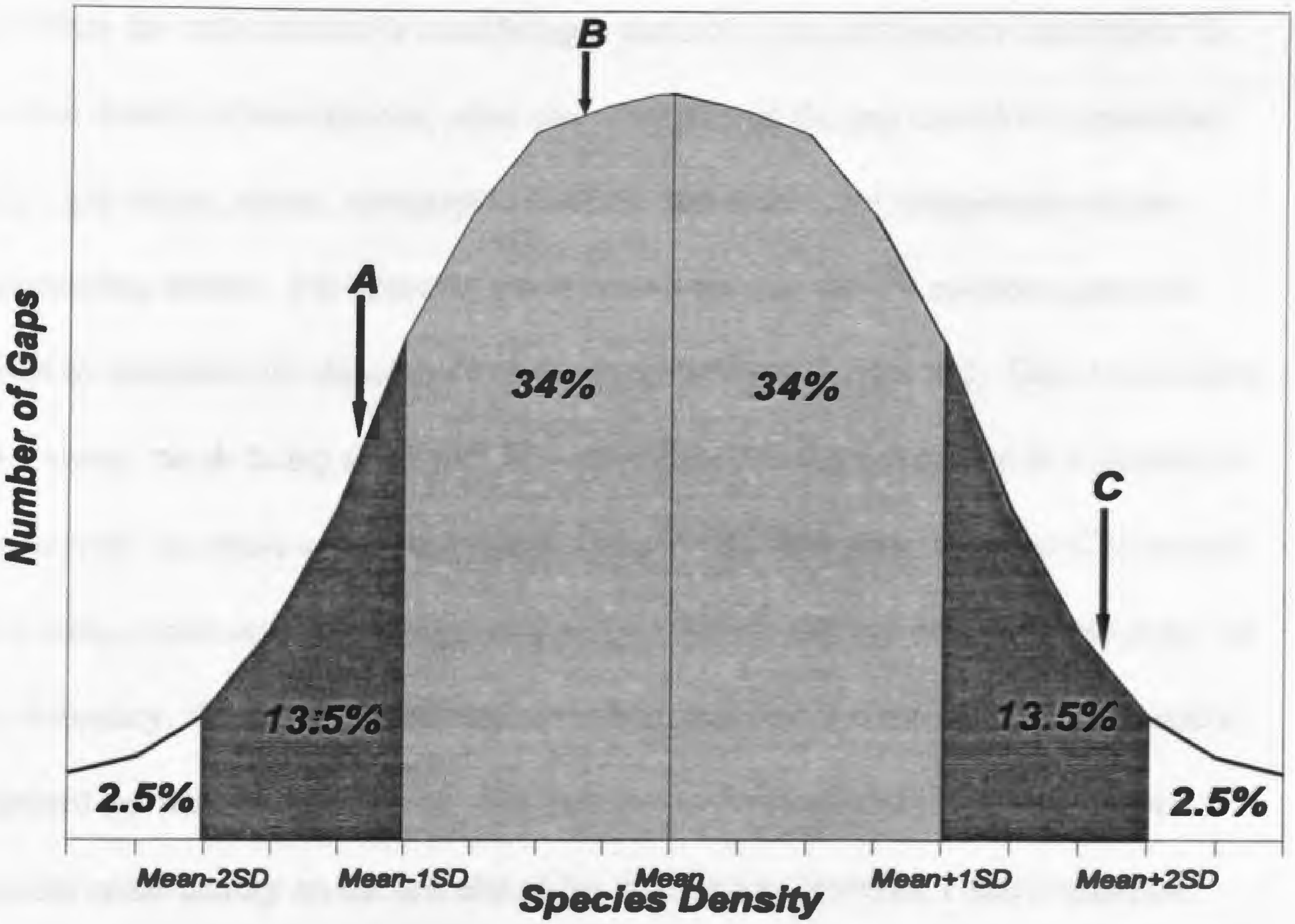

Figure 26. A normal curve showing how this study defines the range of variability for species density. Such a curve would be used for one species in one gap size, for which the mean and standard deviation (SD) are defined (see Appendix). 68% of the restoration gaps should have densities within 1 SD from the mean, and 95% of the restoration gaps should have densities within 2 SD from the mean. Points A, B, and C show single density values for a particular restoration gap (see text).

population of sugar pine densities within large gaps follows an approximately normal distribution (which is indicated by data not shown here), then approximately 34% of the restoration gaps should contain a sugar pine density between the mean (114 trees/ha) and 1 standard deviation above the mean (114 trees/ha + 76 trees/ha = 190 trees/ha; see Appendix A for means and standard deviations), and approximately 34% of the restoration gaps should contain a sugar pine density between the mean and 1 standard deviation below the mean (between 38 and 114 trees/ha).

(3) When the restorationist is considering a particular gap and needs to determine its desired density of each species, other characteristics of the gap should be considered (e.g., gap shape, aspect, topographic position, soil depth, and composition of the surrounding forest). For example, the restorationist may have 3 medium gaps and needs to determine the density of incense cedar desired for each gap. Gap A is located on a shady, north-facing slope with no surrounding incense cedar; Gap B is located on a relatively flat swale with a few incense cedar on the boundary; and Gap C is located on a steep, southwest-facing slope with rocky, shallow soil and many incense cedar on the boundary. Incense cedar density in medium gaps has a mean of 62 trees/ha and a standard deviation of 78 trees/ha. For Gap A, the restorationist might choose an incense cedar density on the low end of the distribution, between 1 and 2 standard deviations below the mean (e.g. 0 trees/ha, see point A, Figure 26). For Gap B, the restorationist might choose an incense cedar density near the mean (e.g., 60 trees/ha, see point B, Figure 26). For Gap C, the restorationist might choose an incense cedar density on the high end of the distribution, between 1 and 2 standard deviations above the mean (e.g., 190 trees/ha, see point C, Figure 26). When all incense cedar densities in all medium gaps have been chosen, a histogram of these densities should be approximately normal with a mean near 62 trees/ha, with approximately 68% of the densities between 0 and 140 trees/ha (62±78), and with approximately 95% of the densities between 0 and 218 trees/ha (62±(2*78)).

(4) A rigid "gap pairing" procedure where the exact vegetation of a model gap is replicated within a restoration gap is **NOT** recommended. The vegetation that ultimately regenerates in a gap is influenced by many factors, not all of which can be

modeled; chance events likely play a major role. In other words, there should not be only 6 vegetation models which are exactly reproduced in 100 small restoration gaps; rather, there should be 100 different desired vegetation states, each within the range seen in the 6 small model gaps.

(5) The relative frequency of a species in restoration gaps should reflect that species' frequency in model gaps of the same size (see Tables 2 and 3), within the bounds of the surrounding vegetation (e.g. red fir would only be planted in the higher elevation sites which have red fir in the surrounding vegetation). For example, 83% of the small gaps should contain sugar pine, whereas 100% of the medium and large gaps should contain sugar pine.

(6) After deciding the density of each species in a gap, guidelines for the desired spatial pattern should be formed. Densities at specific within-gap positions (e.g. north edge, south center) can be based on the model gap(s) or on a range about the mean for each species and each gap size (Appendix A, Tables 14-19). Clumped, random, or regular patterns of trees should follow the results of the Ripley's K(t) spatial analysis. The most useful resource for determining the desired spatial pattern for a restoration gap will be the model gap plots, available on AutoCAD or hard copy in the GIS laboratory of Sequoia National Park. Rather than attempt to summarize the size and density of these hierarchically-clumped thickets, I suggest that the restorationist examine a model gap plot with similar desired vegetation and approximate the size and density of thickets seen within the model gap.

Because the light environment is thought to be a major factor influencing the vegetation in canopy gaps, and because the same size gaps can have different light environments depending on the structure of the surrounding forest canopy, the quantification of light regimes in the model gaps might add significantly to our ability to explain and predict vegetation composition and structure. For this reason, I have begun to quantify light regimes in the 18 model gaps using hemispherical photography. With this method, a full 180 degree photograph is taken using a hemispherical, or fish-eye, lens. The photograph is then scanned into a digital format. The geometry of the canopy (open sky vs. leaf area) is then combined with a solar-tracking simulation to produce an estimate of the annual photosynthetically-active radiation (PAR) available at the photo point.

A second area for further study concerns the pattern of gaps on a landscape scale. In this approach to the restoration of Giant Forest, I have assumed that the analogy of a fire burning through the area and opening canopy gaps is valid. However, I do not know if the spatial pattern and frequency distribution of gap sizes is similar to what natural (or prescribed) fire would produce. For example, the Giant Forest developed area could contain more small gaps and fewer large gaps than is found on a naturally-burned landscape, or the gaps could be more spatially clustered than on a burned landscape. I propose that the large-scale aerial photographs purchased for this study be used to develop a GIS database of canopy gaps on the Giant Forest plateau. By overlaying the gaps with historic fire boundaries, I will be better able to address these unknowns about the validity of the fire analogy for the Giant Forest restoration.

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APPENDIX A

GAP SUMMARY TABLES

Table 10. Tree density for each gap showing mean and standard deviation (SD) by species and gap size. Tree names are abbreviated by the first two letters each of the genus and the specific epithet.

SMALL			DENSITY (trees/ha)			
Gap Num.	Area (ha)	Age	ABCO	ABMA	PILA	SEGI
5	0.095	9	42.1	0.0	73.7	10.5
6	0.097	7	61.9	0.0	30.9	958.8
7	0.091	13	142.9	0.0	22.0	0.0
11	0.075	13	93.3	160.0	0.0	2453.3
15	0.067	9	29.9	0.0	164.2	492.5
17	0.088	12	0.0	11.4	11.4	0.0
mean	0.085	8.5	61.7	26.7	48.5	652.5
SD			50.6	64.6	61.2	961.9

MEDIUM										
Gap Num.	Area (ha)	Age	ABCO	ABMA	CADE	PIJE	PILA	PIPO	QUKE	SEGI
2	0.24	9	33.3	0.0	195.8	0.0	95.8	0.0	8.3	20.8
4	0.17	9	0.0	0.0	100.0	0.0	47.1	0.0	0.0	76.5
8	0.23	13	8.7	0.0	0.0	0.0	4.3	0.0	0.0	347.8
10	0.15	13	346.7	540.0	0.0	0.0	73.3	0.0	0.0	66.7
12	0.22	15	0.0	0.0	72.7	9.1	109.1	40.9	0.0	9.1
16	0.20	9	30.0	0.0	5.0	0.0	20.0	0.0	0.0	3150.0
mean	0.20	11.3	69.8	90.0	62.3	1.5	58.3	6.8	1.4	611.8
SD			136.4	220.4	78.0	3.7	41.8	16.7	3.4	1249.7

LARGE											
Gap Num.	Area (ha)	Age	ABCO	ABMA	CADE	PIJE	PILA	PIPO	QUCH	QUKE	SEGI
1	1.17	10	139.3	0.0	24.8	17.1	171.8	8.5	0.9	0.0	2025.6
3	0.45	15	31.1	0.0	2.2	0.0	184.4	0.0	0.0	0.0	8171.1
9	0.46	13	84.8	58.7	0.0	4.3	10.9	0.0	0.0	0.0	310.9
13	1.14	9	14.9	0.0	0.9	3.5	42.1	0.0	3.5	0.9	1016.7
14	0.34	13	23.5	173.5	0.0	8.8	179.4	0.0	0.0	0.0	1020.6
18	0.43	13	351.2	0.0	0.0	4.7	97.7	2.3	0.0	0.0	5188.4
mean	0.67	12.17	107.5	38.7	4.7	6.4	114.4	1.8	0.7	0.2	2955.6
SD			128.4	70.1	9.9	5.9	75.7	3.4	1.4	0.4	3083.8

Table 11. Shrub cover for each gap, showing mean and standard deviation (SD) by species and gap size. Shrub names are abbreviated by the first two letters each of the genus and the specific epithet.

COVER (m²/ha)

SMALL

Gap Num.	Gap Size	Gap Age	ARPA	CECO	CEPA	CHSE	CONU	RINE	RIRO	RIVI	SYRO
5	0.095	9	0.3	15.1	183.1	229.1	0.0	0.1	0.0	0.0	0.0
6	0.097	7	0.5	68.3	326.0	18.3	1.3	0.0	5.4	0.0	2.8
7	0.091	13	0.0	36.0	67.5	471.3	0.0	2.5	0.3	5.4	0.6
11	0.075	13	11.1	166.4	0.0	0.0	0.0	0.0	33.7	0.0	0.1
15	0.067	9	0.3	1.8	0.0	0.0	0.0	0.0	0.2	0.0	0.0
17	[illegible]	12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
mean	0.09	10.50	2.0	47.9	96.1	119.8	0.2	0.4	6.6	0.9	0.6
SD			4.4	63.4	133.4	194.4	0.5	1.0	13.5	2.2	1.1

MEDIUM

Gap Num.	Gap Size	Gap Age	AMAL	APAN	ARPA	CECO	CEPA	CHSE	COCO	CONU	RINE	RIRO	RIVI	ROSP	RUGL	SAME	SASP	SYRO
2	0.24	9	6.7	2.2	0.8	189.5	519.3	58.3	0.0	0.3	37.2	25.3	0.0	749.1	7.8	0.0	0.0	167.3
4	0.17	9	0.0	0.0	0.2	30.6	584.7	0.0	0.0	29.4	1.2	0.6	0.0	0.0	0.0	0.0	0.0	0.0
8	0.23	13	0.0	0.0	8.8	487.0	22.3	3394.9	35.0	0.0	0.2	1.7	0.0	0.0	0.0	0.0	0.0	17.9
10	0.15	13	0.0	0.0	1.1	108.8	0.0	0.0	0.0	0.0	0.4	0.5	0.0	0.0	0.0	0.0	0.0	0.0
12	0.22	15	0.0	0.0	20.4	687.1	0.0	0.0	0.0	0.0	1.4	30.6	0.0	0.0	0.0	31.1	10.9	0.0
16	0.20	9	0.0	0.0	0.7	148.1	13.2	0.0	0.0	0.0	0.0	1.8	11.0	0.0	0.0	0.0	0.0	0.0
mean	0.20	11.33	1.1	0.4	5.3	275.2	189.9	575.5	5.8	4.9	6.7	10.1	1.8	124.9	1.3	5.2	1.8	30.9
SD			2.7	0.9	8.0	255.2	281.3	1381.4	14.2	12.0	14.9	14.0	4.5	305.9	3.2	12.7	4.4	67.2

LARGE

Gap Num.	Gap Size	Gap Age	APAN	ARPA	CECO	CEIN	CEPA	CHFO	CHSE	CONU	PENE	PREM	PRVI	RINE	RIRO	RIVI	RUGL	RUPA	SAME	SASP	SYRO
1	1.17	10	2.1	98.9	1005.9	0.0	0.0	0.0	48.5	0.0	0.1	0.7	3.9	6.0	306.2	43.9	0.0	0.0	28.3	0.0	48.8
3	0.45	15	0.0	1.2	77.8	0.0	242.4	0.0	0.0	705.7	0.0	0.0	0.0	31.6	20.0	0.0	24.5	4.5	1.8	0.0	0.6
9	0.46	13	111.2	107.0	2212.5	0.0	0.0	0.0	71.1	0.0	0.0	1.1	0.0	0.0	6.9	0.0	0.0	0.0	0.0	0.0	9.9
13	1.14	9	0.0	131.6	1117.4	6.7	1024.5	11.9	34.4	0.1	0.0	0.0	0.0	4.2	43.7	0.0	0.0	0.2	3.5	0.0	20.6
14	0.34	13	0.0	3.8	1978.2	0.0	0.1	0.0	19.5	0.0	0.0	0.0	0.0	1.4	28.4	76.9	0.0	0.0	0.0	0.0	13.0
18	0.43	13	0.0	19.1	409.3	0.1	0.0	0.0	103.7	0.0	0.0	3.2	0.0	0.7	174.8	65.1	0.0	0.0	7.0	2.4	0.0
mean	0.67	12.17	18.9	60.3	1133.5	1.1	211.2	2.0	46.2	117.6	0.0	0.8	0.6	7.3	96.7	31.0	4.1	0.8	6.8	0.4	15.5
SD			45.2	58.5	840.6	2.7	410.1	4.8	37.2	288.1	0.0	1.2	1.5	12.1	119.5	35.5	10.0	1.80	10.9	1.0	18.1

Table 12. Estimated shrub density for each gap, showing mean and standard deviation (SD) by species and gap size. Shrub names are abbreviated by the first two letters each of the genus and the specific epithet.

SMALL — DENSITY (shrubs/ha)

Gap Num.	Gap Size	Gap Age	ARPA	CECO	CEPA	CHSE	CONU	RINE	RIRO	RIVI	SYRO
5	0.095	9	42	116	442	347	0	11	0	0	0
6	0.097	7	10	52	495	31	31	0	31	0	31
7	0.091	13	0	253	99	714	0	33	11	44	11
11	0.075	13	227	280	0	0	0	0	13	0	13
15	0.067	9	15	45	0	0	0	0	15	0	0
[illegible]	0.088	12	0	0	0	0	0	0	0	0	0
mean	0.09	10.50	49.0	124.1	172.6	182.1	5.2	7.2	11.7	7.3	9.2
SD			88.4	116.5	232.9	294.2	12.6	13.3	11.5	17.9	12.2

MEDIUM

Gap Num.	Gap Size	Gap Age	AMAL	APAN	ARPA	CECO	CEPA	CHSE	COCO	CONU	RINE	RIRO	RIVI	ROSP	RUGL	SAME	SASP	SYRO
2	0.24	9	4	25	17	167	475	88	0	4	375	25	0	3729	21	0	0	504
4	0.17	9	0	0	12	35	382	0	0	24	18	12	0	0	0	0	0	0
8	0.23	13	0	0	117	387	22	5091	4	0	9	4	0	0	0	0	0	61
10	0.15	13	0	0	53	120	0	0	0	0	13	7	0	0	0	0	0	0
12	0.22	15	0	0	86	268	0	0	0	0	14	41	0	0	0	14	5	0
16	0.20	9	0	0	70	995	25	0	0	0	0	20	40	0	0	0	0	0
mean	0.20	11.33	0.7	4.2	59.3	328.7	150.7	863.1	0.7	4.6	71.4	18.1	6.7	621.5	3.5	2.3	0.8	94.2
SD			1.7	10.2	40.8	348.4	217.6	2071.7	1.8	9.4	148.9	13.6	16.3	1522.4	8.5	5.6	1.9	202.3

LARGE

Gap Num.	Gap Size	Gap Age	APAN	ARPA	CECO	CEIN	CEPA	CHFO	CHSE	CONU	PENE	PREM	PRVI	RINE	RIRO	RIVI	RUGL	RUPA	SAME	SASP	SYRO
1	1.17	10	39	397	499	0	0	0	73	0	1	1	15	18	272	38	0	0	15	0	147
3	0.45	15	0	13	47	0	69	0	0	2058	0	0	4	113	40	0	33	29	4	0	2
9	0.46	13	391	789	1074	0	0	0	107	0	0	7	0	0	11	0	0	0	0	0	30
13	1.14	9	0	230	559	6	443	25	52	1	0	0	0	6	54	0	0	2	2	0	62
14	0.34	13	0	106	1118	0	3	0	29	0	0	3	0	24	59	188	0	0	0	0	41
18	0.43	13	0	321	300	2	0	0	156	0	0	47	0	12	179	42	0	0	2	12	0
mean	0.67	12.17	71.8	276.1	599.4	1.4	85.8	4.1	69.4	343.1	0.1	9.5	3.2	28.8	102.5	44.6	5.6	5.1	3.8	1.9	47.2
SD			157.3	283.6	424.4	2.5	177.1	10.0	55.8	840.0	0.3	18.3	5.8	42.3	101.0	73.0	13.6	11.7	5.5	4.7	54.3

Table 13. Tree density and mean height by within-gap position in small gaps, showing mean and standard deviation (SD) by species. Tree names are abbreviated by the first two letters each of the genus and the specific epithet.

		DENSITY (trees/ha)				MEAN HEIGHT (m)			
Position	Gap Num	ABCO	ABMA	PILA	SEGI	ABCO	ABMA	PILA	SEGI
North Edge	5	196	–	196	0	0.20	–	0.27	–
	6	0	–	0	0	–	–	–	–
	7	0	–	85	–	–	–	0.10	–
	11	0	192	–	0	–	0.30	–	–
	15	0	–	0	2273	–	–	–	0.15
	17	–	0	0	–	–	–	–	–
Mean		39	96	56	568	0.20	0.30	0.19	0.15
SD		88	136	83	1136	–	–	0.12	–
South Edge	5	0	–	0	0	–	–	–	–
	6	0	–	0	424	–	–	–	0.18
	7	376	–	75	–	0.36	–	0.90	–
	11	73	73	–	4380	0.20	0.40	–	0.36
	15	0	–	357	0	–	–	0.10	–
	17	–	0	0	–	–	–	–	–
Mean		90	36	86	1201	0.28	0.40	0.50	0.27
SD		163	52	155	2129	0.11	–	0.57	0.13
East Edge	5	0	–	53	0	–	–	0.40	–
	6	305	–	152	152	0.48	–	0.30	0.17
	7	119	–	0	–	0.50	–	–	–
	11	0	85	–	0	–	0.40	–	–
	15	190	–	0	0	0.35	–	–	–
	17	–	0	0	–	–	–	–	–
Mean		123	42	41	38	0.44	0.40	0.35	0.17
SD		130	60	66	76	0.08	–	0.07	–
West Edge	5	56	–	112	0	0.20	–	0.35	–
	6	0	–	0	333	–	–	–	0.15
	7	192	–	0	–	0.33	–	–	–
	11	286	0	–	0	0.40	–	–	–
	15	0	–	183	275	–	–	0.20	0.13
	17	–	0	0	–	–	–	–	–
Mean		107	0	59	152	0.31	–	0.28	0.14
SD		127	0	85	177	0.10	–	0.11	0.01
North Center	5	0	–	0	130	–	–	–	0.10
	6	0	–	0	0	–	–	–	–
	7	0	–	0	–	–	–	–	–
	11	130	519	–	0	0.60	0.45	–	–
	15	0	–	517	345	–	–	0.17	0.15
	17	–	0	0	–	–	–	–	–
Mean		26	260	103	119	0.60	0.45	0.17	0.13
SD		58	367	231	163	–	–	–	0.03

Table 13. continued.

		DENSITY (trees/ha)				MEAN HEIGHT (m)			
Position	Gap Num	ABCO	ABMA	PILA	SEGI	ABCO	ABMA	PILA	SEGI
South Center	5	0	--	0	0	--	--	--	--
	6	0	--	0	0	--	--	--	--
	7	0	--	0	--	--	--	--	--
	11	132	263	--	16316	0.20	0.20	--	0.34
	15	0	-	196	0	--	--	0.20	--
	17	--	122	0	--	--	0.20	--	--
Mean		26	193	39	4079	0.20	0.20	0.20	0.34
SD		59	100	88	8158	--	0.00	--	--
East Center	5	0	--	0	0	--	--	--	--
	6	0	--	0	189	--	--	--	0.35
	7	0	--	0	--	--	--	--	--
	11	217	217	--	0	0.50	0.20	--	--
	15	0	--	0	0	--	--	--	--
	17	--	0	106	--	--	--	0.20	--
Mean		43	109	21	47	0.50	0.20	0.20	0.35
SD		97	154	48	94	--	--	--	--
West Center	5	0	--	109	0	--	--	0.10	--
	6	0	--	0	6937	--	--	--	0.24
	7	215	--	0	--	0.65	--	--	--
	11	0	0	--	0	--	--	--	--
	15	0	--	169	508	--	--	0.10	0.13
	17	--	0	0	--	--	--	--	--
Mean		43	0	56	1861	0.65	--	0.10	0.19
SD		96	0	79	3392	--	--	0.00	0.08

Table 14. Tree density and mean height by within-gap position in medium gaps, showing mean and standard deviation (SD) by species. Tree names are abbreviated by the first two letters each of the genus and the specific epithet.

		DENSITY (trees/ha)								MEAN HEIGHT (m)							
Position	Gap Num	ABCO	ABMA	CADE	PIJE	PILA	PIPO	QUKE	SEGI	ABCO	ABMA	CADE	PIJE	PILA	PIPO	QUKE	SEGI
North	2	35.3	–	247.4	–	141.3	–	0.0	0.0	0.50	–	0.59	–	0.98	–	–	–
Edge	4	–	–	286.5	–	28.7	–	–	286.5	–	–	0.36	–	0.20	–	–	0.37
	8	0.0	–	–	–	0.0	–	–	234.2	–	–	–	–	–	–	–	0.22
	10	931.0	620.7	–	–	34.5	–	–	0.0	0.32	0.33	–	–	0.50	–	–	–
	12	–	–	0.0	0.0	0.0	0.0	–	0.0	–	–	–	–	–	–	–	–
	16	24.8	–	24.8	–	0.0	–	–	521.1	0.30	–	0.20	–	–	–	–	0.21
Mean		247.8	620.7	139.7	0.0	34.1	0.0	0.0	173.6	0.37	0.33	0.38	–	0.56	–	–	0.27
SD		455.7	–	148.2	–	54.8	–	–	213.3	0.09	–	0.20	–	0.39	–	–	0.09
South	2	156.9	–	78.4	–	235.3	–	39.2	0.0	0.23	–	0.25	–	0.38	–	0.30	–
Edge	4	–	–	0.0	–	0.0	–	–	0.0	–	–	–	–	–	–	–	–
	8	0.0	–	–	–	0.0	–	–	207.2	–	–	–	–	–	–	–	0.44
	10	32.8	98.4	–	–	0.0	–	–	0.0	0.20	0.20	–	–	–	–	–	–
	12	–	–	300.8	37.6	375.9	188.0	–	0.0	–	–	0.14	0.30	0.24	0.22	–	–
	16	0.0	–	0.0	–	25.4	–	–	254.5	–	–	–	–	0.10	–	–	0.10
Mean		47.4	98.4	94.8	37.6	106.1	188.0	39.2	76.9	0.22	0.20	0.20	0.30	0.24	0.22	0.30	0.27
SD		74.6	–	142.25	–	161.1	–	–	120.1	0.02	–	0.08	–	0.14	–	–	0.24
East	2	0.0	–	19.0	–	38.1	–	0.0	0.0	–	–	0.20	–	0.20	–	–	–
Edge	4	–	–	0.0	–	0.0	–	–	0.0	–	–	–	–	–	–	–	–
	8	0.0	–	–	–	0.0	–	–	0.0	–	–	–	–	–	–	–	–
	10	51.8	207.3	–	–	0.0	–	–	0.0	0.50	0.38	–	–	–	–	–	–
	12	–	–	0.0	0.0	0.0	0.0	–	0.0	–	–	–	–	–	–	–	–
	16	0.0	–	0.0	–	0.0	–	–	0.0	–	–	–	–	–	–	–	–
Mean		13.0	207.3	4.8	0.0	6.3	0.0	0.0	0.0	0.50	0.38	0.20	–	0.20	–	–	–
SD		25.9	–	9.5	–	15.6	–	–	0.0	–	–	–	–	–	–	–	–
West	2	32.9	–	378.3	–	65.8	–	0.0	82.2	0.40	–	0.33	–	0.13	–	–	0.20
Edge	4	–	–	101.5	–	0.0	–	–	50.8	–	–	0.10	–	–	–	–	0.20
	8	0.0	–	–	–	0.0	–	–	0.0	–	–	–	–	–	–	–	–
	10	113.0	508.5	–	–	0.0	–	–	0.0	0.25	0.27	–	–	–	–	–	–
	12	–	–	0.0	0.0	106.8	0.0	–	0.0	–	–	–	–	0.23	–	–	–
	16	111.1	–	0.0	–	37.0	–	–	11111.	0.23	–	–	–	0.10	–	–	0.45
Mean		64.3	508.5	120.0	0.0	34.9	0.0	0.0	1874.0	0.29	0.27	0.22	–	0.15	–	–	0.28
SD		56.8	–	178.8	–	44.2	–	–	4525.4	0.09	–	0.16	–	0.07	–	–	0.14

Table 14. continued.

		DENSITY (trees/ha)								MEAN HEIGHT (m)							
Position	Gap Num	ABCO	ABMA	CADE	PIJE	PILA	PIPO	QUKE	SEGI	ABCO	ABMA	CADE	PIJE	PILA	PIPO	QUKE	SEGI
North Center	2	312.5	--	0.0	--	0.0	--	0.0	0.0	0.50	--	--	--	--	--	--	--
	4	--	--	212.8	--	0.0	--	--	106.4	--	--	0.33	--	--	--	--	0.35
	8	25.0	--	--	--	25.0	--	--	1225.0	0.20	--	--	--	0.30	--	--	0.56
	10	949.7	1117.3	--	--	0.0	--	--	55.9	0.32	0.34	--	--	--	--	--	0.20
	12	--	--	0.0	0.0	0.0	29.2	--	29.2	--	--	--	--	--	0.20	--	1.20
	16	50.0	--	0.0	--	0.0	--	--	5700.0	0.20	--	--	--	--	--	--	0.33
Mean		334.3	1117.3	53.2	0.0	4.2	29.2	0.0	1186.1	0.31	0.34	0.33	--	0.30	0.20	--	0.53
SD		430.4	--	106.4	--	10.2	--	--	2261.2	0.14	--	--	--	--	--	--	0.40
South Center	2	0.0	--	76.9	--	76.9	--	0.0	0.0	--	--	0.30	--	0.20	--	--	--
	4	--	--	0.0	--	0.0	--	--	0.0	--	--	--	--	--	--	--	--
	8	0.0	--	--	--	0.0	--	--	149.3	--	--	--	--	--	--	--	0.38
	10	0.0	867.1	--	--	346.8	--	--	115.6	--	0.37	--	--	0.37	--	--	0.20
	12	--	--	487.8	0.0	487.8	122.0	--	0.0	--	--	0.53	--	0.43	0.40	--	--
	16	0.0	--	0.0	--	0.0	--	--	1764.7	--	--	--	--	--	--	--	0.44
Mean		0.0	867.1	141.2	0.0	151.9	122.0	0.0	338.3	--	0.37	0.42	--	0.33	0.40	--	0.34
SD		0.0	--	233.9	--	212.5	--	--	701.9	--	--	0.16	--	0.12	--	--	0.13
East Center	2	0.0	--	0.0	--	36.2	--	36.2	0.0	--	--	--	--	0.10	--	1.20	--
	4	--	--	0.0	--	0.0	--	--	0.0	--	--	--	--	--	--	--	--
	8	0.0	--	--	--	0.0	--	--	114.9	--	--	--	--	--	--	--	0.20
	10	84.0	504.2	--	--	168.1	--	--	336.1	0.20	0.43	--	--	0.30	--	--	0.18
	12	--	--	0.0	48.8	97.6	0.0	--	48.8	--	--	--	0.30	0.20	--	--	1.50
	16	0.0	--	0.0	--	114.9	--	--	4597.7	--	--	--	--	0.20	--	--	0.25
Mean		21.0	504.2	0.0	48.8	69.5	0.0	36.2	849.6	0.20	0.43	--	0.30	0.20	--	1.20	0.53
SD		42.0	--	0.0	--	68.3	--	--	1840.5	--	--	--	--	0.08	--	--	0.65
West Center	2	0.0	--	509.8	--	117.6	--	0.0	0.0	--	--	0.37	--	0.47	--	--	--
	4	--	--	122.0	--	853.7	--	--	0.0	--	--	0.40	--	0.20	--	--	--
	8	0.0	--	--	--	0.0	--	--	816.3	--	--	--	--	--	--	--	0.13
	10	408.2	1224.5	--	--	0.0	--	--	612.2	0.35	0.38	--	--	--	--	--	0.13
	12	--	--	0.0	0.0	123.5	123.5	--	0.0	--	--	--	--	0.20	0.40	--	--
	16	204.1	--	0.0	--	0.0	--	--	15918.	0.20	--	--	--	--	--	--	0.58
Mean		153.1	1224.5	157.9	0.0	182.5	123.5	0.0	2891.2	0.28	0.38	0.39	--	0.29	0.40	--	0.28
SD		195.4	--	241.5	--	334.1	--	--	6391.9	0.11	--	0.02	--	0.16	--	--	0.26

Table 15. Tree density and mean height by within-gap position in large gaps, showing mean and standard deviation (SD) by species. Tree names are abbreviated by the first two letters each of the genus and the specific epithet.

		DENSITY (trees/ha)									MEAN HEIGHT (m)								
Position	Gap Num	ABCO	ABMA	CADE	PIJE	PILA	PIPO	QUCH	QUKE	SEGI	ABCO	ABMA	CADE	PIJE	PILA	PIPO	QUCH	QUKE	SEGI
North	1	199.7	–	4.1	61.1	101.9	8.2	0.0	–	3280.4	0.35	–	1.30	0.47	0.68	0.45	–	–	0.45
Edge	3	62.1	–	0.0	–	103.5	–	–	–	9223.6	0.25	–	–	–	0.41	–	–	–	0.31
	9	62.1	72.5	–	0.0	0.0	–	–	–	10.4	0.68	0.47	–	–	–	–	–	–	0.40
	13	6.5	–	0.0	13.0	19.4	–	0.0	0.0	32.4	0.30	–	–	0.25	0.40	–	–	–	0.42
	14	43.0	272.6	–	0.0	86.1	–	–	–	358.7	0.33	0.43	–	–	0.38	–	–	–	0.17
	18	394.4	–	–	0.0	63.6	0.0	–	–	4949.1	0.38	–	–	–	0.32	–	–	–	0.23
Mean		128.0	172.5	1.4	14.8	62.4	4.1	0.0	0.0	2975.8	0.38	0.45	1.30	0.36	0.44	0.45	–	–	0.33
SD		146.1	141.5	2.4	26.5	43.7	5.8	0.0	–	3669.6	0.15	0.03	–	0.16	0.14	–	–	–	0.11
South	1	149.7	–	46.1	5.8	115.1	8.6	2.9	–	2251.0	1.00	–	0.62	0.60	0.43	0.43	1.20	–	0.59
Edge	3	21.2	–	0.0	–	218.9	–	–	–	5134.2	0.30	–	–	–	0.35	–	–	–	0.39
	9	0.0	0.0	–	0.0	12.1	–	–	–	12.1	–	–	–	–	0.20	–	–	–	0.30
	13	5.4	–	0.0	0.0	21.5	–	0.0	0.0	424.0	0.20	–	–	–	1.18	–	–	–	0.32
	14	0.0	278.6	–	0.0	403.9	–	–	–	334.3	–	0.41	–	–	0.24	–	–	–	0.24
	18	326.5	–	–	0.0	265.3	0.0	–	–	8122.4	0.24	–	–	–	0.12	–	–	–	0.37
Mean		83.8	139.3	15.4	1.2	172.8	4.3	1.4	0.0	2713.0	0.44	0.41	0.62	0.60	0.42	0.43	1.20	–	0.37
SD		132.2	197.0	26.6	2.6	152.4	–	2.0	–	3272.0	0.38	–	–	–	0.39	–	–	–	0.12
East	1	180.6	–	20.1	13.4	167.2	6.7	0.0	–	2066.9	0.34	–	0.40	0.55	0.42	0.50	–	–	0.58
Edge	3	14.7	–	0.0	–	132.4	–	–	–	5205.9	0.30	–	–	–	0.54	–	–	–	0.28
	9	52.4	20.9	–	20.9	20.9	–	–	–	1130.9	0.62	0.75	–	0.30	0.25	–	–	–	1.63
	13	6.9	–	0.0	0.0	24.1	–	0.0	0.0	1034.4	0.30	–	–	–	0.46	–	–	–	0.60
	14	0.0	61.2	–	0.0	40.8	–	–	–	1530.6	–	0.23	–	–	0.15	–	–	–	0.23
	18	322.2	–	–	0.0	74.3	0.0	–	–	1945.5	0.35	–	–	–	0.23	–	–	–	0.54
Mean		96.1	41.1	6.7	6.9	76.6	3.3	0.0	0.0	2152.4	0.38	0.49	0.40	0.43	0.34	0.50	–	–	0.64
SD		129.6	28.5	11.6	9.8	60.8	4.7	0.0	–	1552.7	0.14	0.37	–	0.18	0.15	–	–	–	0.51
West	1	26.3	–	26.3	0.0	400.8	0.0	0.0	–	1898.8	0.35	–	0.75	–	0.53	–	–	–	0.69
Edge	3	0.0	–	0.0	–	180.4	–	–	–	3487.0	–	–	–	–	0.37	–	–	–	0.49
	9	208.9	55.7	–	0.0	13.9	–	–	–	0.0	0.29	0.45	–	–	0.90	–	–	–	–
	13	4.4	–	0.0	0.0	78.7	–	13.1	4.4	2351.4	0.30	–	–	–	0.46	–	1.10	0.90	0.79
	14	0.0	61.2	–	0.0	102.0	–	–	–	224.5	–	0.20	–	–	0.32	–	–	–	0.28
	18	382.3	–	–	11.9	71.7	11.9	–	–	6272.4	0.25	–	–	0.30	0.23	0.20	–	–	0.29
Mean		103.6	58.5	8.8	2.4	141.2	6.0	6.6	4.4	2372.3	0.30	0.33	0.75	0.30	0.47	0.20	1.10	0.90	0.51
SD		158.8	3.9	15.2	5.3	138.1	8.4	9.3	–	2320.3	0.04	0.18	–	–	0.24	–	–	–	0.23

Table 15. continued.

		DENSITY (trees/ha)									MEAN HEIGHT (m)								
Position	Gap Num	ABCO	ABMA	CADE	PIJE	PILA	PIPO	QUCH	QUKE	SEGI	ABCO	ABMA	CADE	PIJE	PILA	PIPO	QUCH	QUKE	SEGI
North	1	122.7	--	7.2	0.0	209.4	14.4	0.0	--	714.8	0.37	--	1.00	--	0.62	0.75	--	--	1.12
Center	3	29.8	--	29.8	--	208.3	--	--	--	12529.8	0.50	--	0.60	--	0.66	--	--	--	0.41
	9	319.6	365.3	--	0.0	45.7	--	--	--	137.0	1.09	1.15	--	--	2.20	--	--	--	0.53
	13	0.0	--	0.0	0.0	0.0	--	0.0	0.0	0.0	--	--	--	--	--	--	--	--	--
	14	30.0	180.2	--	0.0	120.1	--	--	--	1621.6	0.30	0.47	--	--	0.50	--	--	--	0.42
	18	597.0	--	--	0.0	0.0	0.0	--	--	12014.9	0.54	--	--	--		--	--	--	0.88
Mean		183.2	272.7	12.3	0.0	97.3	7.2	0.0	0.0	4503.0	0.56	0.81	0.80	--	1.00	0.75	--	--	0.67
SD		234.1	130.9	15.5	0.0	97.0	10.2	0.0	--	6047.31	0.31	0.48	0.28	--	0.81	--	--	--	0.32
South	1	70.4	--	23.5	0.0	305.2	23.5	0.0	--	821.6	0.10	--	0.50	--	0.66	0.40	--	--	0.95
Center	3	49.8	--	0.0	--	447.8	--	--	--	23134.3	0.20	--	--	--	0.62	--	--	--	0.42
	9	67.8	0.0	--	0.0	0.0	--	--	--	0.0	0.25	--	--	--	--	--	--	--	--
	13	108.7	--	15.5	15.5	62.1	--	0.0	0.0	590.1	0.21	--	1.20	0.30	0.38	--	--	--	1.06
	14	106.4	212.8	--	79.8	266.0	--	--	--	2393.6	0.23	0.23	--	0.27	0.32	--	--	--	0.49
	18	54.5	--	--	0.0	72.7	0.0	--	--	4963.6	0.50	--	--	--	0.30	--	--	--	0.68
Mean		76.3	106.4	13.0	19.1	192.3	11.7	0.0	0.0	5317.2	0.25	0.23	0.85	0.29	0.46	0.40	--	--	0.72
SD		25.5	150.4	11.9	34.6	174.2	16.6	0.0	--	8910.1	0.13	--	0.50	0.02	0.17	--	--	--	0.28
East	1	268.7	--	29.9	0.0	0.0	0.0	0.0	--	447.8	0.37	--	1.50	--	--	--	--	--	1.36
Center	3	25.4	--	0.0	--	127.2	--	--	--	13816.8	0.20	--	--	--	0.54	--	--	--	0.34
	9	133.3	133.3	--	0.0	0.0	--	--	--	1288.9	0.67	0.80	--	--	--	--	--	--	1.89
	13	53.4	--	0.0	17.8	89.0	--	0.0	0.0	1690.4	0.20	--	--	0.50	0.14	--	--	--	0.82
	14	0.0	0.0	--	0.0	79.7	--	--	--	2549.8	--	--	--	--	0.30	--	--	--	0.49
	18	697.7	--	--	0.0	58.1	0.0	--	--	4069.8	0.44	--	--	--	0.65	--	--	--	1.64
Mean		196.4	66.7	10.0	3.6	59.0	0.0	0.0	0.0	3977.2	0.38	0.80	1.50	0.50	0.41	--	--	--	1.09
SD		264.1	94.3	17.2	8.0	50.9	0.0	0.0	--	4975.5	0.20	--	--	--	0.23	--	--	--	0.63
West	1	38.4	--	38.4	19.2	153.6	19.2	0.0	--	691.0	0.30	--	1.15	0.70	0.81	0.90	--	--	0.95
Center	3	344.8	--	0.0	--	1034.5	--	--	--	35172.4	0.30	--	--	--	0.57	--	--	--	0.55
	9	23.9	71.6	--	0.0	0.0	--	--	--	23.9	0.50	1.37	--	--	--	--	--	--	3.50
	13	13.9	--	0.0	0.0	48.7	--	7.0	0.0	661.6	0.30	--	--	--	0.33	--	1.50	--	1.52
	14	0.0	0.0	--	0.0	215.1	--	--	--	430.1	--	--	--	--	0.55	--	--	--	0.65
	18	269.5	--	--	27.0	161.7	0.0	--	--	5094.3	0.40	--	--	0.20	0.15	--	--	--	0.57
Mean		115.1	35.8	12.8	9.2	268.9	9.6	3.5	0.0	7012.2	0.36	1.37	1.15	0.45	0.48	0.90	1.50	--	1.29
SD		151.2	50.6	22.2	12.9	383.3	13.6	4.9	--	13922.1	0.09	--	--	0.35	0.25	--	--	--	1.14

Table 16. Shrub cover by within-gap position in small gaps, showing mean and standard deviation (SD) by species. Shrub names are abbreviated by the first two letters each of the genus and the specific epithet.

		COVER AREA (m^2/ha)								
Position	Gap Num	ARPA	CECO	CEPA	CHSE	CONU	RINE	RIRO	RIVI	SYRO
North	5	0.5	12.3	125.2	2.0	–	0.0	–	–	–
Edge	6	0.0	0.0	161.9	0.0	0.0	–	1.0	–	0.0
	7	–	16.1	194.0	0.0	–	0.0	0.0	0.0	0.0
	11	1.5	0.0	–	–	–	–	0.0	–	0.0
	15	0.0	0.0	–	–	–	–	0.0	–	–
	17	–	–	–	–	–	–	–	–	–
Mean		0.5	5.7	160.4	0.7	0.0	0.0	0.2	0.0	0.0
SD		0.7	7.9	34.4	1.2	–	0.0	0.5	–	0.0
South	5	0.0	5.2	18.2	364.2	–	0.0	–	–	–
Edge	6	0.0	0.0	473.1	0.0	0.0	–	5.3	–	0.0
	7	–	0.0	0.0	155.3	–	0.0	0.0	0.6	0.0
	11	27.0	65.4	–	–	–	–	184.6	–	0.6
	15	0.0	2.8	–	–	–	–	0.7	–	–
	17	–	–	–	–	–	–	–	–	–
Mean		6.8	14.7	163.8	173.2	0.0	0.0	47.7	0.6	0.2
SD		13.5	28.4	258.1	182.8	–	0.0	91.3	–	0.3
East	5	0.0	1.3	172.4	0.0	–	0.0	–	–	–
Edge	6	0.0	0.0	351.3	89.7	2.4	–	0.0	–	13.5
	7	–	0.0	0.0	0.0	–	0.0	1.8	0.0	2.8
	11	4.0	222.4	–	–	–	–	0.0	–	0.0
	15	0.0	0.0	–	–	–	–	0.0	–	–
	17	–	–	–	–	–	–	–	–	–
Mean		1.0	44.7	174.5	29.9	2.4	0.0	0.5	0.0	5.4
SD		2.0	99.3	175.6	51.8	–	0.0	0.9	–	7.1
West	5	0.0	37.9	74.6	778.3	–	0.0	–	–	–
Edge	6	2.6	239.6	69.8	0.0	0.0	–	0.0	–	0.0
	7	–	74.0	122.4	1315.7	–	10.6	0.0	23.0	0.0
	11	4.5	281.2	–	–	–	–	0.0	–	0.0
	15	0.0	8.0	–	–	–	–	0.0	–	–
	17	–	–	–	–	–	–	–	–	–
Mean		1.8	128.1	88.9	698.0	0.0	5.3	0.0	23.0	0.0
SD		2.2	123.9	29.1	661.5	–	7.5	0.0	–	0.0
North	5	0.0	0.0	277.5	4.0	–	0.0	–	–	–
Center	6	0.0	353.4	0.0	0.0	0.0	–	0.0	–	0.0
	7	–	0.0	47.0	0.0	–	0.0	0.0	0.0	0.0
	11	15.5	30.6	–	–	–	–	0.0	–	0.0
	15	2.8	0.0	–	–	–	–	0.0	–	–
	17	–	–	–	–	–	–	–	–	–
Mean		4.6	76.8	108.2	1.3	0.0	0.0	0.0	0.0	0.0
SD		7.4	155.2	148.5	2.3	–	0.0	0.0	–	0.0

Table 16. continued.

		COVER AREA (m^2/ha)								
Position	Gap Num	ARPA	CECO	CEPA	CHSE	CONU	RINE	RIRO	RIVI	SYRO
South	5	0.0	0.0	312.4	0.0	--	0.0	--	--	--
Center	6	0.0	0.0	535.5	0.0	0.0	--	0.0	--	0.0
	7	--	91.8	0.0	0.0	--	0.0	0.0	0.0	0.0
	11	6.2	426.8	--	--	--	--	0.0	--	0.0
	15	0.0	0.0	--	--	--	--	0.0	--	--
	17	--	--	--	--	--	--	--	--	--
Mean		1.5	103.7	282.6	0.0	0.0	0.0	0.0	0.0	0.0
SD		3.1	184.9	269.0	0.0	--	0.0	0.0	--	0.0
East	5	0.0	0.0	779.9	353.3	--	1.1	--	--	--
Center	6	0.0	0.0	754.3	0.0	0.0	--	41.5	--	0.0
	7	--	77.0	0.8	0.0	--	0.8	0.0	0.0	0.0
	11	30.7	235.7	--	--	--	--	0.0	--	0.0
	15	0.0	0.0	--	--	--	--	0.0	--	--
	17	--	--	--	--	--	--	--	--	--
Mean		7.7	62.5	511.7	117.8	0.0	1.0	10.4	0.0	0.0
SD		15.3	102.4	442.6	204.0	--	0.2	20.8	--	0.0
West	5	2.6	50.4	166.5	0.0	--	0.0	--	--	--
Center	6	0.0	48.8	441.5	0.0	7.1	--	0.0	--	0.0
	7	--	20.3	131.7	1483.8	--	0.0	0.0	0.0	0.0
	11	8.9	410.9	--	--	--	--	0.0	--	0.0
	15	0.0	0.0	--	--	--	--	0.0	--	--
	17	--	--	--	--	--	--	--	--	--
Mean		2.9	106.1	246.6	494.6	7.1	0.0	0.0	0.0	0.0
SD		4.2	171.7	169.7	856.7	--	0.0	0.0	--	0.0

Table 17. Shrub cover by within-gap position in medium gaps, showing mean and standard deviation (SD) by species. Shrub names are abbreviated by the first two letters each of the genus and the specific epithet.

		COVER AREA (m²/ha)															
Position	Gap Num	AMAL	APAN	ARPA	CECO	CEPA	CHSE	COCO	CONU	RINE	RIRO	RIVI	ROSP	RUGL	SAME	SASP	SYRO
North Edge	2	0.0	0.0	0.0	0.0	64.9	0.0	–	0.0	20.0	0.0	–	808.8	0.0	–	–	1.7
	4	–	–	0.0	105.3	1086.6	–	–	2.5	5.9	0.0	–	–	–	–	–	–
	8	–	–	4.2	529.7	0.0	3774.6	0.0	–	0.0	0.0	–	–	–	–	–	0.0
	10	–	–	0.0	0.0	–	–	–	–	0.0	0.0	–	–	–	–	–	–
	12	–	–	0.0	277.9	–	–	–	–	0.0	0.0	–	–	–	0.0	0.0	–
	16	–	–	0.0	42.5	6.8	–	–	–	–	7.0	0.0	–	–	–	–	–
Mean		0.0	0.0	0.7	159.2	289.6	1887.3	0.0	1.2	5.2	1.2	0.0	808.8	0.0	0.0	0.0	0.8
SD		–	–	1.7	209.1	532.2	2669.0	–	1.8	8.7	2.9	–	–	–	–	–	1.2
South Edge	2	0.0	0.0	5.9	37.3	1510.8	0.0	–	0.0	25.6	0.3	–	448.3	0.0	–	–	83.8
	4	–	–	0.0	0.0	3.4	–	–	0.0	0.0	2.4	–	–	–	–	–	–
	8	–	–	11.1	336.3	0.0	3435.7	151.5	–	0.0	7.1	–	–	–	–	–	71.3
	10	–	–	0.0	0.0	–	–	–	–	0.0	0.0	–	–	–	–	–	–
	12	–	–	69.7	197.3	–	–	–	–	0.0	8.3	–	–	–	5.3	0.0	–
	16	–	–	1.0	19.1	0.0	–	–	–	–	0.0	8.0	–	–	–	–	–
Mean		0.0	0.0	14.6	98.3	378.5	1717.9	151.5	0.0	5.1	3.0	8.0	448.3	0.0	5.3	0.0	77.5
SD		–	–	27.3	138.4	754.8	2429.4	–	0.0	11.5	3.7	–	–	–	–	–	–
East Edge	2	30.5	1.8	0.6	248.8	1008.0	271.6	–	1.2	75.5	111.4	–	223.9	16.0	–	–	53.4
	4	–	–	0.0	0.0	1271.1	–	–	0.0	0.0	0.0	–	–	–	–	–	–
	8	–	–	0.0	90.3	0.0	6435.5	0.0	–	0.0	0.0	–	–	–	–	–	0.0
	10	–	–	0.0	0.0	–	–	–	–	0.0	0.0	–	–	–	–	–	–
	12	–	–	12.7	128.9	–	–	–	–	0.0	0.0	–	–	–	0.0	0.0	–
	16	–	–	0.5	46.2	19.7	–	–	–	–	0.0	0.0	–	–	–	–	–
Mean		30.5	1.8	2.3	85.7	574.7	3353.5	0.0	0.6	15.1	18.6	0.0	223.9	16.0	0.0	0.0	26.7
SD		–	–	5.1	94.6	661.1	4358.6	–	0.8	33.8	45.5	–	–	–	–	–	37.8
West Edge	2	0.0	0.0	0.0	57.2	24.0	0.0	–	0.0	5.3	0.0	–	721.2	0.0	–	–	12.8
	4	–	–	0.0	7.2	141.2	–	–	0.0	0.0	0.0	–	–	–	–	–	–
	8	–	–	12.8	18.4	0.0	585.8	0.0	–	1.3	0.0	–	–	–	–	–	0.0
	10	–	–	0.9	31.1	–	–	–	–	1.8	4.0	–	–	–	–	–	–
	12	–	–	18.1	471.2	–	–	–	–	0.0	0.0	–	–	–	158.5	0.0	–
	16	–	–	1.2	315.3	0.0	–	–	–	–	0.3	48.9	–	–	–	–	–
Mean		0.0	0.0	5.5	150.1	41.3	292.9	0.0	0.0	1.7	0.7	48.9	721.2	0.0	158.5	0.0	6.4
SD		–	–	7.9	195.4	67.5	414.2	–	0.0	2.2	1.6	–	–	–	–	–	9.0

Table 17. (continued).

		COVER AREA (m^2/ha)															
Position	Gap Num	AMAL	APAN	ARPA	CECO	CEPA	CHSE	COCO	CONU	RINE	RIRO	RIVI	ROSP	RUGL	SAME	SASP	SYRO
North	2	0.0	0.0	0.0	0.0	0.0	0.0	–	0.0	0.0	0.0	–	4961.9	0.0	–	–	19.7
Center	4	–	–	2.1	66.8	710.2	–	–	0.0	0.0	0.0	–	–	–	–	–	–
	8	–	–	21.8	1430.2	125.9	2642.4	0.0	–	0.0	0.0	–	–	–	–	–	0.0
	10	–	–	4.9	650.2	–	–	–	–	1.7	0.0	–	–	–	–	–	–
	12	–	–	6.4	500.2	–	–	–	–	0.0	0.0	–	–	–	0.0	0.0	–
	16	–	–	0.8	388.2	86.0	–	–	–	–	0.0	16.1	–	–	–	–	–
Mean		0.0	0.0	6.0	505.9	230.5	1321.2	0.0	0.0	0.3	0.0	16.1	4961.9	0.0	0.0	0.0	9.8
SD		–	–	8.1	517.3	324.1	1868.4	–	0.0	0.8	0.0	–	–	–	–	–	13.9
South	2	0.0	0.0	1.2	268.2	1092.8	0.6	–	0.0	237.4	15.2	–	582.0	1.2	–	–	826.9
Center	4	–	–	0.0	8.6	753.0	–	–	335.7	0.0	0.0	–	–	–	–	–	–
	8	–	–	1.2	278.3	2.8	3550.9	0.0	–	0.0	0.0	–	–	–	–	–	0.0
	10	–	–	3.2	29.0	–	–	–	–	0.0	0.0	–	–	–	–	–	–
	12	–	–	0.0	3934.5	–	–	–	–	16.3	215.5	–	–	–	136.5	145.6	–
	16	–	–	2.1	116.1	0.0	–	–	–	–	4.6	15.4	–	–	–	–	–
Mean		0.0	0.0	1.3	772.5	462.2	1775.7	0.0	167.8	50.7	39.2	15.4	582.0	1.2	136.5	145.6	413.5
SD		–	–	1.2	1553.3	549.8	2510.4	–	237.4	104.6	86.6	–	–	–	–	–	584.7
East	2	0.0	0.0	0.0	836.1	568.3	0.0	–	0.0	12.0	0.0	–	1293.0	36.4	–	–	0.0
Center	4	–	–	0.0	0.0	0.0	–	–	0.0	0.0	0.0	–	–	–	–	–	–
	8	–	–	0.0	22.6	0.0	5573.6	0.0	–	0.0	0.0	–	–	–	–	–	37.9
	10	–	–	0.0	0.0	–	–	–	–	0.0	0.0	–	–	–	–	–	–
	12	–	–	0.0	802.7	–	–	–	–	2.3	53.7	–	–	–	0.0	0.0	–
	16	–	–	0.0	318.7	0.0	–	–	–	–	0.0	0.0	–	–	–	–	–
Mean		0.0	0.0	0.0	330.0	142.1	2786.8	0.0	0.0	2.9	8.9	0.0	1293.0	36.4	0.0	0.0	19.0
SD		–	–	0.0	398.0	284.1	3941.1	–	0.0	5.2	21.9	–	–	–	–	–	26.8
West	2	0.0	17.2	0.0	55.5	0.0	0.0	–	0.0	0.0	0.0	–	1721.7	0.0	–	–	928.1
Center	4	–	–	0.0	0.0	558.4	–	–	0.0	0.0	0.0	–	–	–	–	–	–
	8	–	–	6.3	464.7	0.0	510.2	0.0	–	1.6	0.0	–	–	–	–	–	0.0
	10	–	–	1.6	740.4	–	–	–	–	0.0	0.0	–	–	–	–	–	–
	12	–	–	176.5	2364.0	–	–	–	–	0.0	232.7	–	–	–	0.0	0.0	–
	16	–	–	0.0	418.6	0.0	–	–	–	–	0.0	0.0	–	–	–	–	–
Mean		0.0	17.2	30.8	673.8	139.6	255.1	0.0	0.0	0.3	38.8	0.0	1721.7	0.0	0.0	0.0	464.1
SD		–	–	71.5	872.5	279.2	360.8	–	0.0	0.7	95.0	–	–	–	–	–	656.3

Table 18. Shrub cover by within-gap position in large gaps, showing mean and standard deviation (SD) by species. Shrub names are abbreviated by the first two letters each of the genus and the specific epithet.

		COVER AREA (m²/ha)																		
Position	Gap Num	APAN	ARPA	CECO	CEIN	CEPA	CHFO	CHSE	CONU	PENE	PREM	PRVI	RINE	RIRO	RIVI	RUGL	RUPA	SAME	SASP	SYRO
North	1	0.0	87.0	762.5	--	--	--	235.2	--	0.4	0.0	0.6	1.6	223.4	35.0	--	--	4.6	--	136.9
Edge	3	--	2.7	132.1	--	113.3	--	--	880.0	--	--	--	10.0	9.0	--	0.0	12.1	7.3	--	2.9
	9	416.3	69.8	557.3	--	--	--	0.0	--	--	0.0	--	--	0.0	--	--	--	--	--	21.5
	13	--	1.8	554.7	0.0	1461.9	0.0	0.0	0.8	--	--	--	0.0	1.7	--	--	0.0	0.0	--	11.3
	14	--	1.7	832.7	--	0.0	--	60.8	--	--	0.0	--	0.1	2.7	0.0	--	--	--	--	60.0
	18	--	12.0	496.9	0.4	--	--	131.3	--	--	1.6	--	2.8	64.5	19.7	--	--	0.0	3.3	--
Mean		208.2	29.2	556.0	0.2	525.0	0.0	85.5	440.4	0.4	0.4	0.6	2.9	50.2	18.2	0.0	6.1	3.0	3.3	46.5
SD		294.4	38.7	245.9	0.3	813.3	--	99.7	621.7	--	0.8	--	4.1	88.3	17.5	--	8.6	3.6	--	55.0
South	1	0.0	34.3	422.6	--	--	--	0.0	--	0.0	2.4	4.5	1.3	357.8	96.7	--	--	41.1	--	28.8
Edge	3	--	0.0	0.0	--	29.1	--	--	1058.7	--	--	--	45.0	17.9	--	67.5	0.0	0.0	--	0.0
	9	14.1	40.7	1456.3	--	--	--	314.4	--	--	0.0	--	--	0.0	--	--	--	--	--	0.0
	13	--	53.6	441.9	6.5	608.9	2.2	0.0	0.0	--	--	--	0.5	10.7	--	--	0.0	0.0	--	17.4
	14	--	0.4	43.2	--	0.0	--	33.3	--	--	0.0	--	1.1	55.8	142.0	--	--	--	--	3.4
	18	--	0.0	39.1	0.0	--	--	15.7	--	--	4.3	--	0.0	117.5	0.0	--	--	0.0	0.0	--
Mean		7.1	21.5	400.5	3.2	212.6	2.2	72.7	529.3	0.0	1.7	4.5	9.6	93.3	79.6	67.5	0.0	10.3	0.0	9.9
SD		10.0	24.2	554.2	4.6	343.4	--	135.8	748.6	--	2.1	--	19.8	136.5	72.5	--	0.0	20.6	--	12.8
East	1	16.6	114.8	906.9	--	--	--	0.0	--	0.0	0.0	16.9	7.9	441.3	0.0	--	--	37.1	--	83.4
Edge	3	--	0.0	0.0	--	51.0	--	--	322.1	--	--	--	12.9	0.0	--	1.2	0.0	0.0	--	0.0
	9	0.0	45.9	2883.0	--	--	--	72.0	--	--	1.3	--	--	0.0	--	--	--	--	--	0.0
	13	--	55.5	1281.2	0.0	966.9	0.3	0.2	0.0	--	--	--	4.6	22.0	--	--	0.7	13.5	--	52.4
	14	--	0.3	467.0	--	0.6	--	0.0	--	--	0.2	--	1.1	0.0	4.5	--	--	--	--	0.0
	18	--	68.8	543.6	0.0	--	--	307.3	--	--	4.0	--	1.3	188.0	233.5	--	--	0.0	9.4	--
Mean		8.3	47.5	1013.6	0.0	339.5	0.3	75.9	161.0	0.0	1.4	16.9	5.6	108.5	79.3	1.2	0.4	12.7	9.4	27.2
SD		11.7	43.6	1012.4	0.0	543.9	--	133.0	227.8	--	1.8	--	5.0	178.8	133.6	--	0.5	17.5	--	38.8
West	1	0.0	60.2	775.7	--	--	--	0.0	--	0.0	0.0	0.0	2.5	53.1	32.7	--	--	0.0	--	0.0
Edge	3	--	3.8	0.0	--	0.0	--	--	390.1	--	--	--	1.2	32.4	--	30.4	0.0	0.0	--	0.0
	9	0.0	73.6	804.8	--	--	--	0.0	--	--	0.0	--	--	1.3	--	--	--	--	--	20.4
	13	--	36.9	968.7	4.5	887.8	0.7	178.1	0.0	--	--	--	3.2	92.1	--	--	0.0	0.1	--	11.1
	14	--	9.1	1762.3	--	0.0	--	0.0	--	--	0.0	--	0.2	18.9	320.9	--	--	--	--	0.0
	18	--	1.1	236.9	0.0	--	--	0.4	--	--	4.3	--	0.0	8.8	0.0	--	--	0.0	0.0	--
Mean		0.0	30.8	758.1	2.3	295.9	0.7	35.7	195.1	0.0	1.1	0.0	1.4	34.4	117.9	30.4	0.0	0.0	0.0	6.3
SD		0.0	31.0	616.7	3.2	512.6	--	79.6	275.8	--	2.2	--	1.4	33.7	176.6	--	0.0	0.1	--	9.2

Table 18. continued.

		COVER AREA (m^2/ha)																		
Position	Gap Num	APAN	ARPA	CECO	CEIN	CEPA	CHFO	CHSE	CONU	PENE	PREM	PRVI	RINE	RIRO	RIVI	RUGL	RUPA	SAME	SASP	SYRO
North	1	0.0	152.4	2668.0	–	–	–	0.0	–	0.0	0.0	2.4	28.5	245.4	9.9	–	–	87.9	–	7.7
Center	3	–	2.8	598.2	–	1011.8	–	–	482.6	–	–	–	92.1	0.0	–	0.0	0.0	0.0	–	0.0
	9	22.8	391.9	4210.0	–	–	–	0.0	–	–	0.0	–	–	60.3	–	–	–	–	–	0.0
	13	–	191.3	2039.8	0.0	2366.8	1.5	0.0	0.0	–	–	–	0.0	0.0	–	–	0.0	0.0	–	0.0
	14	–	5.9	5234.3	–	0.0	–	0.0	–	–	0.0	–	0.9	135.6	0.0	–	–	–	–	0.0
	18	–	47.5	752.5	0.0	–	–	468.9	–	–	0.0	–	0.0	123.1	0.0	–	–	0.0	0.0	–
Mean		11.4	132.0	2583.8	0.0	1126.2	1.5	93.8	241.3	0.0	0.0	2.4	24.3	94.1	3.3	0.0	0.0	22.0	0.0	1.5
SD		16.1	149.2	1858.4	0.0	1187.5	–	209.7	341.3	–	0.0	–	39.8	94.1	5.7	–	0.0	44.0	–	3.4
South	1	0.0	55.3	1213.5	–	–	–	0.0	–	0.0	0.0	0.0	0.0	819.5	0.0	–	–	0.0	–	0.0
Center	3	–	0.0	0.0	–	0.0	–	–	692.0	–	–	–	121.1	198.2	–	0.0	0.0	0.0	–	0.0
	9	339.7	47.4	3472.9	–	–	–	0.0	–	–	0.0	–	–	0.0	–	–	–	–	–	4.8
	13	–	541.2	2184.7	67.1	754.2	0.0	0.0	0.0	–	–	–	0.0	80.2	–	–	0.0	0.0	–	8.5
	14	–	8.5	3208.0	–	0.0	–	0.0	–	–	0.0	–	0.0	0.0	16.3	–	–	–	–	0.4
	18	–	5.0	411.4	0.0	–	–	0.0	–	–	2.9	–	0.0	24.9	0.0	–	–	0.0	0.0	–
Mean		169.8	109.6	1748.4	33.5	251.4	0.0	0.0	346.0	0.0	0.7	0.0	24.2	187.1	5.4	0.0	0.0	0.0	0.0	2.7
SD		240.2	212.7	1444.0	47.4	435.4	–	0.0	489.3	–	1.4	–	54.2	318.7	9.4	–	0.0	0.0	–	3.8
East	1	0.0	18.8	989.8	–	–	–	0.0	–	0.0	0.0	0.0	0.0	903.6	0.0	–	–	0.0	–	0.0
Center	3	–	0.0	55.0	–	1139.6	–	–	206.6	–	–	–	10.6	0.0	–	0.0	22.0	2.4	–	0.0
	9	0.0	507.2	4056.3	–	–	–	0.0	–	–	0.0	–	–	78.5	–	–	–	–	–	0.0
	13	–	177.8	3113.1	0.0	1961.3	0.0	0.0	0.0	–	–	–	0.0	162.8	–	–	0.0	0.0	–	0.0
	14	–	0.0	5204.5	–	0.0	–	0.0	–	–	0.0	–	0.3	0.0	1.9	–	–	–	–	0.0
	18	–	19.2	417.7	0.0	–	–	0.0	–	–	0.0	–	0.0	1112.6	201.8	–	–	86.8	0.0	–
Mean		0.0	120.5	2306.1	0.0	1033.6	0.0	0.0	103.3	0.0	0.0	0.0	2.2	376.3	67.9	0.0	11.0	22.3	0.0	0.0
SD		0.0	201.2	2120.4	0.0	984.9	–	0.0	146.1	–	0.0	–	4.7	497.5	116.0	–	15.5	43.0	–	0.0
West	1	0.0	615.5	2589.8	–	–	–	0.0	–	0.0	0.0	0.0	11.9	112.9	53.7	–	–	0.0	–	0.0
Center	3	–	0.0	0.0	–	4021.7	–	–	406.2	–	–	–	0.0	0.0	–	0.0	0.0	0.0	–	0.0
	9	0.0	191.9	5469.6	–	–	–	0.0	–	–	8.6	–	–	0.0	–	–	–	–	–	20.4
	13	–	460.0	1337.2	7.7	764.1	84.9	0.0	0.0	–	–	–	18.3	40.3	–	–	0.0	0.0	–	0.0
	14	–	16.9	7620.4	–	0.0	–	0.0	–	–	0.0	–	29.6	0.0	0.0	–	–	–	–	0.0
	18	–	1.3	629.6	0.0	–	–	47.6	–	–	5.3	–	0.0	174.9	0.0	–	–	0.0	0.0	–
Mean		0.0	214.3	2941.1	3.9	1595.3	84.9	9.5	203.1	0.0	3.5	0.0	12.0	54.7	17.9	0.0	0.0	0.0	0.0	4.1
SD		0.0	265.4	2989.2	5.5	2135.8	–	21.3	287.2	–	4.2	–	12.6	73.5	31.0	–	0.0	0.0	–	9.1

APPENDIX B

BIOGRAPHICAL INFORMATION

Name of Author: Athena Demetry

Place of Birth: Carmel, California

Date of Birth: June 30, 1969

Educational Degrees Awarded

Worcester Polytechnic Institute, B.S., 1991

Professional Positions Held

Biological Science Technician, National Park Service, Sequoia and Kings Canyon National Parks, Research Division, 1993

Biological Technician, National Park Service, Sequoia and Kings Canyon National Parks, Vegetation Management, 1991-1992

Professional and Honor Societies

Society for Ecological Restoration
Xi Sigma Pi (Forestry Honor Society)
Phi Sigma (Biology Honor Society)
Phi Lambda Upsilon (Chemistry Honor Society)
Tau Beta Pi (Engineering Honor Society)

Scholarly Publications

Demetry, A., W.W. Covington, and D.M. Duriscoe. 1995. Regeneration patterns within canopy gaps in a giant sequoia-mixed conifer forest: implications for forest restoration. Abstract *in* Bulletin of the Ecological Society of America 76(2): 62-63.

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