DOE/OR/00033--T704

A COMPARATIVE FIELD STUDY OF GROWTH AND SURVIVAL OF SIERRAN CONIFER SEEDLINGS

by

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Date: 12 December, 1996

Approved:

Norman L. Christensen, Chair

William Dwight

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Botany in the Graduate School
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ABSTRACT

(Plant Ecology)

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ABSTRACT

This study is a comparison of seedling growth and survival of seven species of conifers that make up the mid-elevation Sierra Nevada mixed conifer forest - *Abies concolor*, *Abies magnifica*, *Calocedrus decurrens*, *Pinus jeffreyi*, *Pinus lambertiana*, *Pinus ponderosa*, and *Sequoiadendron giganteum*. The field experiment was designed to test the hypothesis that seedling demography is affected by the study species' relative shade and drought tolerances.

Six discrete treatments were created in the first experiment (Chapter 2) by using three elevations (1600 m, 1900 m, and 2200 m) and two natural light levels (closed canopy 'shade' and open gap 'sun') at each elevation. One or two-year old seedlings were planted in the ground in replicate plots in each treatment and followed for two growing seasons. Four responses were analyzed - survival, height growth, diameter growth, and mass growth (total mass as well as root mass and shoot mass separately).

Data analysis was based on the assumption that, if out-planted in a common optimal environment, survival and vigor of all species would have been similar. Survival was generally lowest in the low elevation treatment (1600 m), especially in the shade plots. Few species are able to survive the dual pressure of a hot (dry) environment and low irradiance. Specific survival effects of elevation and light vary among species. The main effects of elevation and light on growth differ depending on the species and on the growth response measured (height, diameter, mass). Plant height and mass response patterns were quite similar, and different from the diameter growth response. Greater height and mass increases were seen in high light plots at the low and high elevation sites, but not at the medium elevation site. This can be attributed to the higher natural irradiance levels of the low and high elevation sun plots, compared to the irradiance levels of the middle elevation sun plots. Allometric analyses showed no effect of the treatments on root vs. shoot biomass allocation.

In the second experiment (Chapter 3) seedling leaf water potential, growth, and survival are compared in 8 treatment combinations made up of 2 light levels (shade, or closed canopy and sun, or gap) and 4 time lengths of augmented soil moisture availability at one elevation (1900 m) throughout two growing seasons.

Overall, light was the most important factor in survival in the second experiment. Leaf water potential values were lower in the sun than in the shade in all species, leading to decreased growth in most species and decreased survival in a few species.

The range of responses found in these experiments indicate the complexity of seedling responses to elevation, light and drought stress in the Sierra Nevada mixed conifer forest. Climatic change will affect these species differentially, potentially creating a forest of significantly different character in the future. Quantitative, comparative field studies such as this are necessary for understanding possible impacts of global climate change on plant communities and for successful management of forests in the coming decades.

ACKNOWLEDGEMENTS

My heartfelt thanks go to Norm Christensen for introducing me to the Sierra Nevada and gently guiding me through the graduate school experience. I only hope that I can someday mentor my own students as well as Norm has mentored me. I also thank committee members W. Dwight Billings and Bill Schlesinger from the Botany Department and Ram Oren and Dan Richter from the School of the Environment. Virginia Dale and John Beauchamp were very helpful during my internship at Oak Ridge National Laboratory.

Dean Urban, Pat Halpin, and Peter Harrell were very instrumental in my completion of this dissertation and I applaud not only their computer expertise, but especially their patience with me.

This research was performed under appointment to the U.S. Department of Energy, Graduate Fellowships for Global Change Program, administered by Oak Ridge Institute for Science and Education. My thanks to Mary Kinney and Milton Constantin for their kind assistance in all matters related to this generous fellowship.

The bulk of the field research was supported by the National Park Service Global Change Research Program for the Central and Southern Sierra Nevada (now under the auspices of the National Biological Service, a department of the U.S. Geological Survey).

I am grateful for the financial support as well as the intellectual support given by the many scientists involved in this integrated research program. Additional funding was supplied by the Duke Botany Department's Catherine Keever fund for botanical field studies, the Duke University Graduate School for travel to professional meetings, and several pots of mystery money that Norm found to keep me going when necessary. Thank you all!

The better part of four years were spent in the field collecting data for this research and it could not have been accomplished without the help of the research staff based a Sequoia National Park. I thank Annie Esperanza, in particular, for sharing her wealth of knowledge and organizational expertise. Many willing hands assisted me throughout the field and laboratory portion of this work. I am forever indebted to Mary Christensen, Shelly Tanner, Chad Robinson, Steve Sheridan, Christine Elder, John Rapp, Amy Jo Meyer, and many others who helped for an hour, a day, a week (Linda, Sylvia, & Carol - thanks!).

I could not have persevered without the support of many friends. My eternal gratitude to Gail Glifort, Pat Peroni, Deb Lawrence, Anne Cross, Anne Hartley, Joy Ward, Lori Moilanen, Jan Gwyer, Karen Steinhauser, Rachel O'Brien, Kevin Griffin, Brian Pedersen and many others.

Finally, I extend many thanks to my family for their unfailing confidence and love. To Mom & Dad for constant loving support and occasional airplane tickets home, Leanne

and her family for a home in California, Barb and her family for always understanding and for including me in occasional family vacations, Nancy and her family for always having faith in me and keeping me mindful of life outside of graduate school, Dede and Bill for always having my room ready and for many long distance phone calls in good times and bad, and Doug & Diane for being invariably supportive and also for sharing their extra truck in my times of "automotive distress".

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CHAPTER 1

INTRODUCTION

The role of seedling dynamics in forests of long-lived tree species is little-understood but clearly important in shaping the composition and structure of mature forests. Climatic change expected to occur in the coming decades will undoubtedly affect plant communities in complex ways. The different responses of members of a community to climate change may lead to shifts in competitive ability and eventually to shifts in community composition (Bazzaz 1990, Eamus and Jarvis 1989). The ability of a species to reproduce successfully and for offspring to survive to maturity under future climatic conditions will determine whether the species is able to maintain its place in the community and possibly flourish, or whether it will disappear. A tree seedling must be able to adapt to environmental change in order to survive to reproductive maturity. Furthermore, seed and seedling biology is crucial in determining the rate at which species distributions change (Leishman et al. 1992).

Grubb (1977) suggested that differences among species in their requirements for regeneration (the 'regeneration niche') are important in maintaining species richness in plant communities. The variations in temperature, moisture, and light requirements for seedling establishment, growth and survival that differentiate species within forest habitats will also be important in determining species' success as climatic conditions change. If a species' requirements are not met, because of rapidly changing environmental conditions, the species could be excluded from the community. However, it is more likely that regeneration conditions will be subtly altered, causing shifts in the relative abundance of members of the community. Therefore, early life history processes have the potential to be very useful in predicting future forest composition.

SIERRA NEVADA MIXED CONIFER FORESTS

The middle elevations (1500-2400 m) of the western slope of the central and southern Sierra Nevada of California are vegetated by a mixed conifer forest dominated by such species as ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), sugar pine (*P. lambertiana*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), and California red fir (*A. magnifica* var. *shastensis*). The giant sequoia (*Sequoiadendron giganteum*) is especially prominent in groves scattered throughout this region, its only remaining native habitat. Although each of these species may be found across the entire elevational range of the mixed conifer zone, their relative abundances change in a predictable manner from low to high elevation (Stephenson 1988, Vankat 1982).

Seedlings and saplings of all of the mixed conifer tree species are present as advanced regeneration in the forest understory (e.g., Fowells & Schubert 1956, Schubert 1957a&b, Hallin 1957, Maul 1958, Fowells and Stark 1965, Stark 1968a&b,

Gordon 1970, Harvey et al. 1980, Barbour et al. 1990). However, few comparative studies of early life history and demography have been performed on these species. The sensitivity of processes, such as seedling establishment, growth and survival, to year-to-year climatic variation is not well understood but nonetheless thought to be largely responsible for the dynamic character of seedling and sapling populations. Given that the eventual composition of the forest overstory is dependent on patterns of early establishment, changes in the dynamics of these populations may have truly far-reaching consequences.

One of the most interesting, yet daunting aspects of Sierran forest communities is the longevity of the dominant species. Pines and firs routinely survive hundreds of years and giant sequoias survive thousands of years. Thus, any individual tree will experience considerable climatic variation within its lifetime. Indeed, many extant trees have likely survived climatic extremes considerably greater than those predicted within the next century as a consequence of increasing greenhouse gas concentrations. However, subtle genetic shifts in carbon sequestering, nutrient cycling, and water use may accumulate with time. Changes in seedling dynamics caused by such shifts may be important in shaping the future mature forest.

ROLE OF EARLY LIFE HISTORY

The role of early-life history dynamics in determining future forest composition and in detecting environmental change is completely unknown in the Sierra Nevada, as in most of the world. The relative stability of species composition from young mixed-conifer stands to old (Dunning and Reineke, 1933) and the potential longevity of the dominant species of the mixed conifer forest make this role especially interesting. Oliver and Dolph (1992) explain that the Sierra Nevada mixed-conifer forest is unique in its tendency for the component species of most young stands to have a similar likelihood of predominance at maturity. They believe that this unique feature is probably the result of the longevity of each species, which allows them to survive the average frequency of forest perturbations and the mix of ecological amplitudes or tolerances in the range of this forest type. By these arguments, the potential for using seedling and sapling dynamics to predict future forest composition is very high in the Sierra Nevada mixed-conifer forest.

It is also possible that seedling dynamics are not ultimately important in determining mature forest composition and that it is successional events following the rare, catastrophic fire or storm events that determine which individuals are recruited from the understory into the canopy (Cattelino et al. 1979). If this is the case, the species that are able to take advantage of such an event must be present in the system either as advance regeneration or as seed, and it will be important to understand the potential effect of climatic change on the growth and survival of these seedlings.

Despite the potential importance of seed and seedling dynamics in detecting environmental change and in determining mature forest composition, relatively few studies of forest trees have focused on these early life history processes. A number of studies have looked at the effect of elevated atmospheric CO_2 concentrations on seedling growth in controlled growth chambers (Conroy et al. 1986, 1988, 1990, Tolley & Strain 1984 a&b, 1985; Sionit et al. 1985, Bazzaz et al. 1985) and others have described patterns of seedling establishment, growth and survival in a variety of forest types (Augspurger 1984, Barbour et al. 1990, Christy and Mack 1984, Clark and Clark 1985, Collins and Good 1987, Connell et al. 1984, Cypher and Boucher 1982, Fried et al. 1988, Good and Good 1972, Harcombe et al. 1982, Hett 1971, Hughes and Fahey 1988, Leak and Graber 1976, McDonald 1976, Monk 1961, 1981, Peet and Christensen 1987, Skeen 1976, Streng et al. 1989, Tappeiner and Helms 1971, Taylor and Aarssen 1989, Turner 1990, Ustin et al. 1984). The studies describing patterns of seedling dynamics have largely focused on small scale variation in performance and on comparisons between pairs of species. Only the growth chamber studies have considered the consequences of climatic change on seedling physiology and population dynamics (and subsequent changes in forest composition), and none have linked the effect of field studies of environmental variables on seedling physiology with observations of seed and seedling dynamics in natural populations.

GLOBAL CHANGE

Climatic change is by no means a new phenomenon in the Sierran mixed conifer forests, although the current rate of change may be unprecedented (Davis 1989). Pollen and macrofossils from sediment cores have shown that from the end of the Pleistocene to about 7,000 yr before present (BP), mid-elevation Sierran forests, today dominated by *Pinus*, *Abies*, and *Quercus*, were more heavily dominated by *Pinus* and *Artemisia* (Davis et al. 1985). This flora corresponds to a warmer and drier climate than today's (Anderson 1990a). A shift to cooler and moister conditions is inferred from a sudden drop in *Artemisia* and a rise in *Pinus* about 7,000 years BP, and the gradual increase in *Abies* and *Quercus* pollen approximately 3,000 years BP indicates further development of cool and moist conditions. Anderson (1990b) has shown that the giant sequoia was relatively rare in this area up to about 4,500 yr BP, but its abundance subsequently increased dramatically to its current populations, which are the greatest of the last 70,000 to 80,000 years. This change corresponded with a general cooling trend that probably resulted in increased moisture availability (Anderson et al. 1985). Dendrochronological studies have documented considerable climate variation in this region on scales of decades and centuries over the past two millennia (e.g., the Medieval Warm Epoch (1000-700 BP) and the Little Ice Age (600-350 BP), Swetnam, et al. 1990).

The primary short-term effects of increased atmospheric carbon dioxide (CO_2) concentration on plants are generally accepted to be an increase in photosynthetic rate and a decrease in stomatal conductance, with a corresponding increase in water use efficiency (Pearcy and Bjorkman 1983, Bazzaz 1990; but see also Eamus and Jarvis 1989). The magnitude of response, however, varies greatly among species and is complicated by other secondary responses and their interactions. For example, species sensitive to the increases in vapor pressure deficit (VPD) expected with global warming will decrease their stomatal conductance which may lead to decreased photosynthetic rates. Alternatively, the greater partial pressure of CO_2 could eliminate such a decrease. Species unable to compensate for increases in VPD (i.e., unable to conserve water by closing stomates sufficiently) will experience drought stress earlier in the growing season. While specific predictions concerning the effect of increased CO_2 concentration on community-level dynamics cannot presently be made, it is clear that differences in response to elevated atmospheric CO_2 concentration among members of a plant community will result in changes in community composition through time.

Although it is impossible to know with any certainty the magnitude of future climatic change in any particular location, differences in environmental factors associated with elevation and site moisture gradients within the current range of the mixed conifer forest provide a range of contrasting environments that can serve as an analog for components of environmental change. I have used this existing range of elevation and natural light availability in combination with artificial extension of growing season to evaluate, in a natural setting, potential species responses to varying climatic conditions.

ENVIRONMENTAL GRADIENTS AND THE DROUGHT-SHADE TOLERANCE TRADE-OFF

The west slope of the Sierra Nevada of California comprises one of the most extreme elevation gradients in temperate North America. A vertical rise of over 4300 meters occurs in less than 100 km horizontal distance from the floor of the San Joaquin Valley to the peak of Mount Whitney. The associated temperature gradient has a lapse rate (the change in mean daily temperature with increasing elevation) of $-5.6\ ^{\circ}\mathrm{C} \bullet \mathrm{km}^{-1}$ (Stephenson 1988). In addition, precipitation and soil moisture increase with increasing elevation.

This pattern of increasing soil moisture, described by Shreve (1915), results in increased total ecosystem plant biomass with elevation (Whittaker and Niering 1975). This increase in plant biomass is seen in the typical Sierran elevational transition from chaparral to montane mixed conifer forest (Rundel et al. 1977, Vankat 1982). Tilman (1988) theorized that the increase in standing biomass associated with soil gradients leads to decreasing understory light availability, thus setting up a physiological trade-off between light and moisture, or shade tolerance and drought tolerance.

The theoretical trade-off between drought tolerance and shade tolerance makes it very difficult for any species in this environment to be simultaneously highly shade tolerant and highly drought tolerant or simultaneously highly intolerant to shade and drought. Figure 1 shows the expected placement of the study species in a combined drought tolerance-shade tolerance diagram (tolerances based on Burns and Honkala 1990, Minore 1979, and Baker 1949). As theory would predict, there is a more or less linear trade-off between shade tolerance and drought tolerance. This trade-off is believed to constrain each species' lower elevational range to its drought tolerance limit, whereas the upper elevational limit is controlled by a combination of shade tolerance and temperature (Smith and Huston 1989).

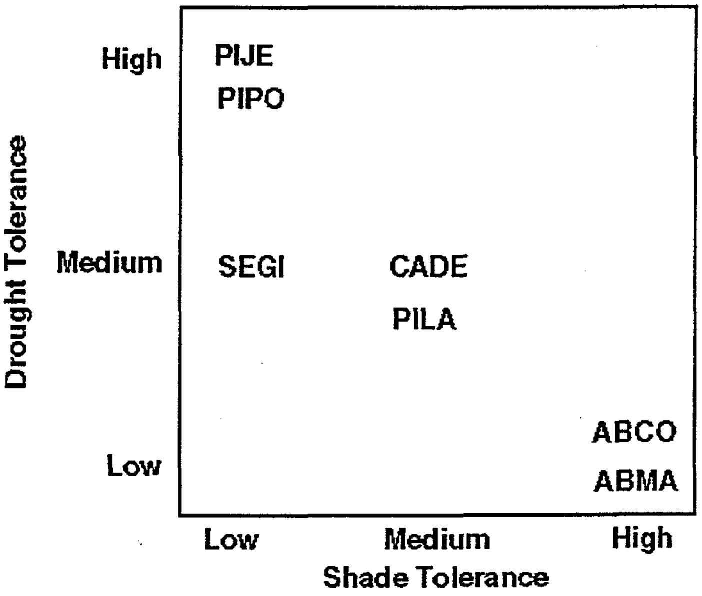

Figure 1. Expected shade and drought tolerance rankings of the study species, based on Burns and Honkala (1990), Minore (1979), and Baker (1949). Species codes are described in Table 1.

OBJECTIVES AND EXPECTATIONS

The objective of the first experiment is to quantify the effects of elevation and light availability on survival and growth of Sierran conifer seedlings in a field setting. Despite the much-discussed theory of adaptive trade-offs in community ecology, field studies of simultaneous resource limitation are rare (Bazzaz and Morse 1991). Elevation was used as a discrete experimental treatment in this study, with plots established at three elevations within the mixed conifer zone. I hypothesized that the lower elevation treatments will experience greater drought stress due to decreased soil moisture availability combined with increased evaporative demand created by warmer temperatures. These conditions should favor those species most tolerant of warm, dry conditions (i.e., *Pinus ponderosa* and *Calocedrus decurrens*) (Minore 1979). Among the firs, drier conditions should favor *Abies concolor* over *Abies magnifica* (Ustin et al. 1984, Tappeiner and Helms 1971).

The second discrete treatment is light availability in low light (closed canopy) vs. high light (canopy gap) areas at each elevation. The most shade tolerant species (*Abies concolor* and *Abies magnifica*) (Burns and Honkala 1990) are expected to have the highest growth rates in the shade treatments, although all species are expected to exhibit greater growth and higher survival in high light environments as long as there is sufficient soil moisture. This experimental design allowed me to test the hypothesis that the seedling demography of the study species is affected by the relative shade and drought tolerances of these co-occurring species. Additionally, comparison of the effects of elevation, light, and their interactions on seedling survival and growth can provide an indication of these species' potential relative success in climates predicted to be warmer, and possibly drier, in the future.

The second experiment was conducted at a single elevation and was designed to investigate the effects of light and soil moisture availability on seedling predawn leaf water potential, growth and survival. No comprehensive study of the comparative physiological ecology of Sierran conifer seedlings has been published. Therefore, it is difficult to predict the relative responses of these species to varying climate conditions. I do expect, however, that growth of all species will be greatest under conditions of high light and adequate soil moisture (i.e., positive interaction of water and light). When soil moisture is low, those species most able to tolerate drought stress are expected to have highest survival and growth rates. This situation is predicted to occur in the conifer zone of the Sierra Nevada within the next century, when average temperature is predicted to increase 2-4°C, and will be accompanied by a corresponding increase in vapor pressure deficit (VPD). These conditions should favor those species most tolerant of warm, dry conditions (i.e., *Pinus ponderosa*, and *Calocedrus decurrens*) (Minore 1979). Among the firs, drier conditions should favor *Abies concolor* over *Abies magnifica* (Ustin, et al. 1984, Tappeiner and Helms 1971).

These generalizations will, however, be affected by local site conditions. For example, competition for soil moisture from shrubs and herbs can reduce ponderosa pine seedling growth despite adequate light conditions (Shainsky and Radosevich 1986, Elliot and White 1987), and competition for light or other resources (including proximity to seed trees) can restrict seedling growth (Cochran 1972, McDonald 1976, Vance and Zaerr 1991). In shaded areas, release from drought stress (experimental water addition) should cause an increase in relative growth rate of each species, with a greater increase in the most shade tolerant species (*Abies concolor, Abies magnifica* var. *shastensis, Pinus lambertiana, and Calocedrus decurrens*) (see Figure 1).

CONCLUSION

The goal of these experiments was to compare seedling growth responses, both among species and within species across environmental gradients to aid in prediction of species success in a future, unknown set of environmental conditions. Future work will include integrating my results into a model of forest dynamics developed by Dr. Dean Urban for Sierran mixed conifer forests. These experiments will also complement the seedling demography studies that I have conducted as part of the National Park Service's Global Change Research Program for the Sierran biogeographic area. Other studies conducted within this program address such topics as sapling and mature tree demography, past climate and fire history, mature conifer physiology, and modeling of ecosystem response to global change. This type of integrated approach makes it possible to begin to address the impact of global change at many spatial and temporal scales.

The experiments described significantly extend current understanding of seedling physiology and population dynamics in Sequoia National Park, and are applicable to much of the extent of the forest type, from southern California to central Oregon. This study is unique in linking population- and community-level studies to investigations of the effect of global change on forests. The relevance of population biology to predicting the response of forests to climate change has been largely overlooked in global change studies even though many will readily admit that global change will lead to vegetation change.

CHAPTER 2

THE EFFECT OF ELEVATION AND LIGHT AVAILABILITY ON SURVIVAL AND GROWTH OF SIERRAN CONIFER SEEDLINGS

INTRODUCTION

The objective of these studies is to quantify the effects of elevation and light availability on survival and growth of Sierran conifer seedlings in a field setting. Despite the much-discussed theory of adaptive trade-offs in community ecology, field studies of simultaneous resource limitation are rare (Bazzaz and Morse 1991). Elevation was used as a discrete experimental treatment in this study, with plots established at three elevations within the mixed conifer zone. I hypothesized that the lower elevation treatments will experience greater drought stress due to decreased soil moisture availability combined with increased evaporative demand created by warmer temperatures. These conditions should favor those species most tolerant of warm, dry conditions (i.e., *Pinus ponderosa* and *Calocedrus decurrens*) (Minore 1979). Among the firs, drier conditions should favor *Abies concolor* over *Abies magnifica* (Ustin et al. 1984, Tappeiner and Helms 1971). The second discrete treatment is light availability in low light (closed canopy) vs. high light (canopy gap) areas at each elevation. The most shade tolerant species (*Abies concolor* and *Abies magnifica*) (Burns and Honkala 1990) are expected to have the highest growth rates in the shade treatments, although all species are expected to exhibit greater growth and higher survival in high light environments as long as there is sufficient soil moisture. This experimental design allowed me to test the hypothesis that the seedling demography of the study species is affected by the relative shade and drought tolerances of these co-occurring species. Additionally, comparison of the effects of elevation, light, and their interactions on seedling survival and growth can provide an indication of these species' relative success in climates predicted to be warmer, and possibly drier, in the future.

METHODS

Field Methods

Three sites were selected for this field experiment at elevations 1600, 1900, and 2200 m in Sequoia National Park, California, USA. All sites were located in the mixed conifer zone on the west slope of the Sierra Nevada at a 36.57 degrees north latitude. At the low and high elevation sites 12 plots were established, 6 plots at each elevation in a high light natural canopy gap and 6 plots in a low light closed canopy area. At the middle elevation, 6 plots were established -- 3 in a gap and 3 in an adjacent closed canopy area. Treatments are thus designated L1 (1600 m, shade), L2 (1600 m, sun), M1 (1900 m, shade), M2 (1900 m, sun), H1 (2200 m, shade) and H2 (2200 m, sun).

To insure that all sites were equivalent with respect to soil nitrogen availability, three-to-five soil samples were taken at each treatment site (total= 22 samples) to compare the potential nitrogen mineralization index (PNMI). A difference in nitrogen availability among treatments could affect seedling growth and confound the effects of elevation and light. Each sample was split in half and the first half was saturated with deionized water for 24 hours then extracted with 2.0 Molar (M) potassium chloride (KCl) solution. The second half was saturated with deionized water and incubated for 30 days at 25°C before extraction with 2M KCl solution. All samples were analyzed for ammonium and nitrate content and the difference between total nitrogen in the second sample (after incubation) and the initial amount (unincubated sample) is the potential nitrogen mineralization index (Hart et al. 1994). Analysis of variance, used to compare PNMI values among treatments (n=22), showed no significant difference in the PNMI values ($P>0.94$), indicating no significant differences in potential nitrogen mineralization rates among treatments.

Soil moisture release curves were constructed to convert gravimetric soil water content values (g water/g soil) into soil water potential values (MPa). An additional set of soil samples was collected at each site, and 12 separate soil moisture release curves were constructed for two soil depth categories (0-5 cm and 5-20 cm) in each of the six treatments. Six replicate soil samples of at least 25 g were collected and a composite sample was retained for each treatment area and sample depth. Soils were allowed to air dry and sieved through a 2-mm screen. The ceramic plate extraction method (Richards 1965) was used to estimate water potential-content curves for five replicates from each composite soil sample. Five potentials, -0.033, -0.1, -0.5, -1.0, and -1.5 MPa were determined in each sample. The five curves of gravimetric water content (g water•kg^{-1} soil) vs. soil water potential (MPa) were then plotted for each treatment-by-depth combination. For each set of curves, each axis was transformed to the natural log and linear regression was used to estimate the water potential-content relationship for each treatment-by-depth soil environment.

The soil moisture release curves thus created were used to estimate soil water potential from gravimetric soil samples. Treatment plots were sampled at four to six week intervals throughout each growing season. All soil samples for gravimetric soil moisture measurements were obtained from the center of the seedling transplant plot and separated into 0-5cm and 5-20 cm depth components. Field samples were weighed, oven dried at 105 °C to constant mass and re-weighed dry to determine the mass of water held per mass of dry soil.

Irradiance was estimated for each plot by hemispherical photography of the forest canopy. Photographs were taken using a 35-mm camera and a Nikkor 8-mm hemispherical lens mounted on a tripod. All photographs were taken at the center of each transplant plot, at a height of 0.5 m above the ground, with the camera leveled and oriented with the top of the camera toward the north (necessary for accurate analysis of the daily sun path). Kodak TMAX 100 black and white print film was used and the developed negatives were analyzed using the program CANOPY (Rich 1990). The direct site factor (DIRsf: the proportion of potential direct light at a site relative to a site in the open) and the diffuse site factor (DIFsf: the proportion of potential diffuse light at a site relative to a site in the open) were calculated by CANOPY based on the intersection of the sun's track with canopy openings (Rich 1990). Each photograph was analyzed 12 times and the median threshold level was used for the final set of photo analyses. Direct and diffuse site factors were combined into a global site factor (GSF) using the equation

$$GSF = 0.8(DIRsf) + 0.2(DIFsf).$$

These weightings are based on results from a solar radiation model run for these sites based on Bonan (1989) and Nikolov and Zeller (1992). Shade plots were located in areas where the GSF was less than 0.15 and sun plots were located where GSF was greater than 0.15 (Figure 2).

Seventy seedlings were planted in the ground in a randomized array in each plot. There were 10 individuals each of 7 species in each of 30 plots to total 2100 seedlings. The species used were the seven dominant canopy species making up the southern Sierra mixed conifer forest -- *Abies concolor* (white fir), *Abies magnifica* var. *shastensis* (red fir), *Calocedrus decurrens* (incense cedar), *Pinus jeffreyi* (Jeffrey pine), *Pinus lambertiana* (sugar pine), *Pinus ponderosa* (ponderosa pine), and *Sequoiadendron giganteum* (giant sequoia). See Table 1 for species common names and information on age and condition at the time of planting. Seedlings were obtained

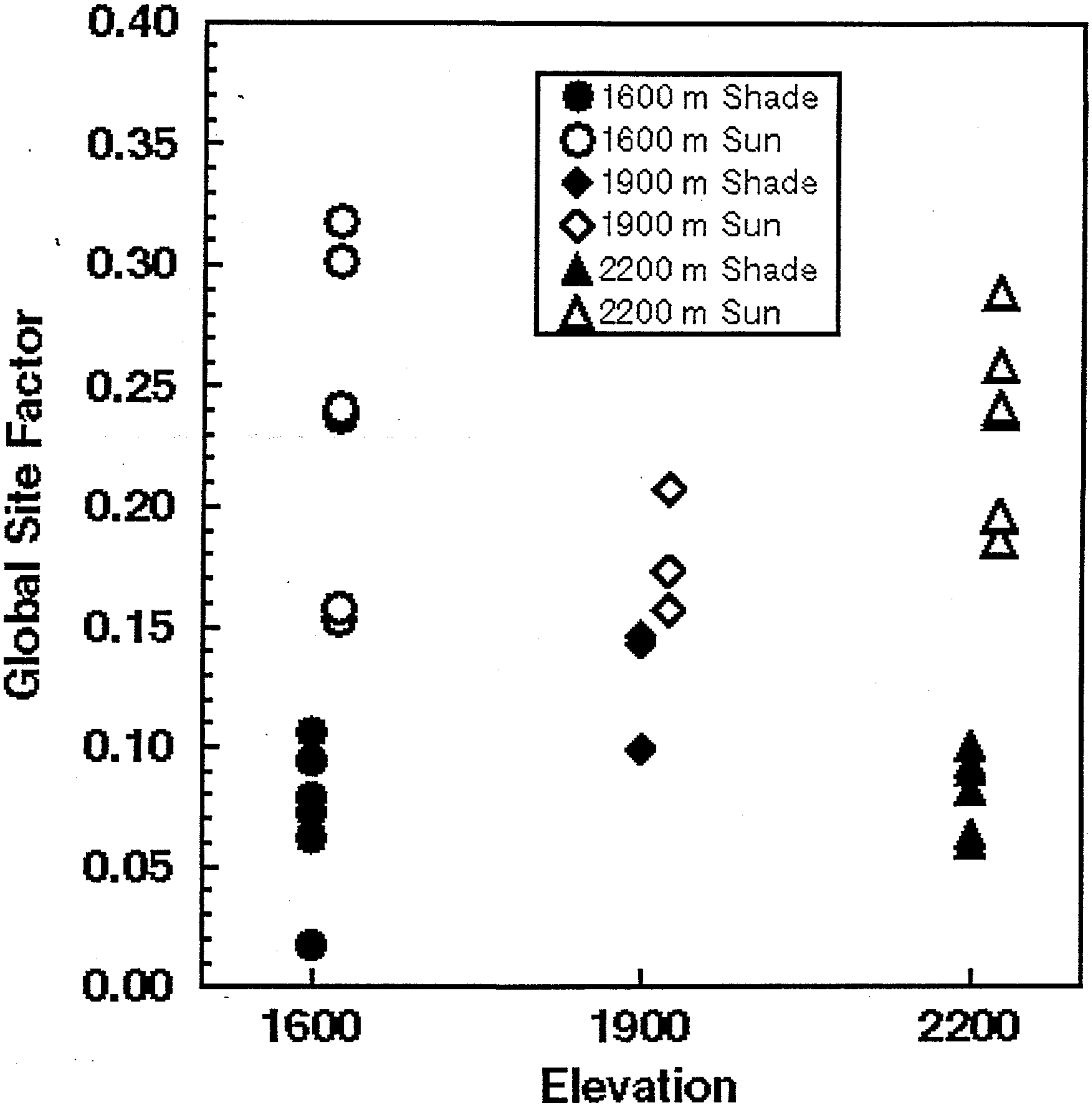

Figure 2. Light availability of transplant plots. Global site factor is an integrated light availability measure (80% direct light and 20% diffuse) determined using hemispherical photo analysis of each plot.

Species	Common Name	Code	Planting Age	Stock	Vigor
Abies concolor	White Fir	ABCO	2-0	Bare Root	High
Abies magnifica var. *shastensis*	Red Fir	ABMA	2-0	Bare Root	Low
Calocedrus decurrens	Incense Cedar	CADE	1-0	Bare Root	High
Pinus jeffreyi	Jeffrey Pine	PIJE	2-0	Bare Root	High
Pinus lambertiana	Sugar Pine	PILA	2-0	Bare Root	Medium
Pinus ponderosa	Ponderosa Pine	PIPO	1-0	Bare Root	Low
Sequoiadendron giganteum	Giant Sequoia	SEGI	1-0	Container	High

Table 1. Study Species. Planting age denotes number of years grown in USFS nursery seedling bed followed by number of years grown in a nursery transplant bed. Stock were all bare root except Giant Sequoia which were grown in 20 cm long tubes and planted along with the potting mix entwined in the root matrix. Vigor is a subjective determination that indicates the general condition of the seedlings at the time of planting.

from United States Forest Service (USFS) nursery stock grown from seeds collected from USFS areas adjacent to Sequoia National Park and within the same elevation and seed zone in which the experimental plots were located. Seedlings were planted between May 13-28, 1993 and watered initially to promote establishment. Wet seedling weights were recorded prior to planting and initial height and diameter measurements were made within a week of planting, as well as at the end of the growing season each year (fall 1993 and fall 1994). Height of all non-pine seedlings was measured from the root collar (Menes and Mohammed 1995) to the top of the highest live material. Pine seedling height was measured from the root collar to the top of the terminal bud. In long-needled species such as pines, loss of needles at the top of a seedling can result in a measured decrease in total height despite apical growth, so it was preferable to track height growth by the distance between the terminal bud and the root collar. Diameter measurements were always made just above the root collar. The seedling condition (alive or dead) was also noted at these measurement times and at the beginning of the second growing season (spring 1994).

Above- and below-ground parts of all living seedlings were harvested at the end of the second growing season (September 26-30, 1994). The harvested seedlings were refrigerated until they could be analyzed in the laboratory at Duke University. Roots and shoots were separated at the root collar, and roots were thoroughly washed, below- and above-ground portions dried at 70 °C to constant weight and each portion weighed to the nearest 0.1 gram.

Data Analysis Methods

Four plant responses, each a separate measure of success; survival, height, diameter, and biomass growth (total biomass as well as root and shoot growth separately), were evaluated in this analysis. Survival data were analyzed using analysis of variance on the proportion surviving (p) in each plot (SAS Institute, 1989) with elevation and light defined as class variables where

$$p = F(\text{elevation, light, elevation*light}).$$

In this analysis, p was transformed using

$$p' = \arcsin\sqrt{p}.$$

Confidence limits (95%) were calculated for the proportions surviving using the method demonstrated in Zar (1984)..

The influence of the initial size of the seedlings was investigated in two ways. First, a Spearman rank correlation (SAS Institute 1989) was performed with the seven species ranked according to their initial height, initial diameter and initial fresh weight (3 separate rankings). These ranks were compared to the six rankings generated by survival rates in the six treatments. Results indicated that species ordering with respect to initial diameter and fresh weight were not correlated with species rankings of survival in any treatment. The ranking of initial height was, however, significantly

($P<0.05$) or marginally significantly ($P<0.10$) correlated with the species ranking of survival for all treatments. The next step, therefore, was to calculate the average initial height of each species in each plot and use this as a covariate in the analysis of survival proportions. Thus, the final survival analysis was performed using analysis of covariance where

$$p' = F(\text{Elevation, Light, Elev}*\text{Light, Initial Height})$$

Height, diameter and biomass growth were calculated as the percent increase during the measurement period where

$$\%\ \text{Height Growth} = \left(\frac{\text{Final Height} - \text{Initial Height}}{\text{Initial Height}}\right) \times 100.$$

"Height" was substituted with "diameter" or "biomass" (total, root, or shoot) in the equation to calculate the percent change in these growth parameters. Percent growth was used so that all growth measures would be comparable to each other and not confounded by initial size.

Initial dry biomass of each seedling was estimated from the initial fresh weight using species-specific regressions calculated from a random subsample of 10 seedlings. Seedlings of each species were taken from the pool of seedlings at the time of planting, weighed wet, roots washed, dried at 70 °C to constant weight and then re-weighed dry. Linear regression parameters for the wet to dry weight relationships are shown in Table 2. Accurate estimation of initial biomass of *S. giganteum* was not possible since these were container grown seedlings which were planted into the ground along with the potting mixture. The initial fresh weight could not be reliably determined since the variability in weight of the potting mixture (82.4 +/- 9.5 g) outweighed the average fresh weight of the seedlings (13.2 +/- 5.4 g).

	ABCO (n=10)	ABMA (n=10)	CADE (n=10)	PIJE (n=10)	PILA (n=10)	PIPO (n=10)
SLOPE	0.3540	0.3207	0.2933	0.3920	0.3055	0.3099
IN'CPT	-0.2128	-0.0795	-0.2299	-1.2957	0.6165	-0.1377
R-SQ.	0.9670	0.8539	0.9855	0.9595	0.9674	0.9763

Table 2. Linear regression parameters for estimation of initial dry biomass of transplanted seedlings. The form of the model is Y=A+BX, where Y=Dry weight (g), A=Intercept, B=Slope, and X=Fresh weight (g). All regression models are significant (P<0.0001) and all slopes are significant (P<0.0001).

For each of the growth parameters, it was first determined whether replicate plots could be combined (or if there were significant plot effects within any of the treatments). This was done using analysis of covariance with the initial height, diameter, or biomass as the covariate (Proc GLM; SAS Institute 1989) followed by analysis of variance to identify significant differences between plots in the slope of the growth response and in the absolute growth response among plots within the same treatment group. Analyses showed similar responses within treatments (P>0.10), so replicate plots were combined for all further analyses. Biomass and height growth analyses were conducted for the entire experimental period (spring 1993 to fall 1994). Diameter growth analyses were conducted on the annual increment fall 1993 to fall

1994 since there was significant shrinkage in stem diameter during the first summer after planting. This is a common response in seedling outplanting caused by loss of stem capacitance in adapting to the dry field environment.

Using combined replicate plots, main effects for elevation and light plus their interaction were tested using analysis of covariance where

% Growth = F (Light, Elevation, Light*Elevation interaction)

The initial measure (height, diameter, or dry biomass) was used as the covariate. Due to a significant effect of the covariate in most species, comparison of elevation and light effects, based on adjusted means and standard errors, were performed using the LSMEANS statement in the Proc GLM procedure (SAS Institute 1989).

Allometric analysis of biomass allocation patterns was performed using analysis of covariance where

% Root Growth = F (Treatment, % Shoot Growth, Treatment * % Shoot Growth)

Figure 3 presents an example of the allometric analyses. Significant interaction (non-parallel slopes) between the treatment (six combinations of elevation and light) and percent shoot growth (the covariate) terms indicates differences in biomass allocation patterns among treatments. Linear regression was used to determine the slope of the regression for each treatment and species using

% Root Growth = % Shoot Growth

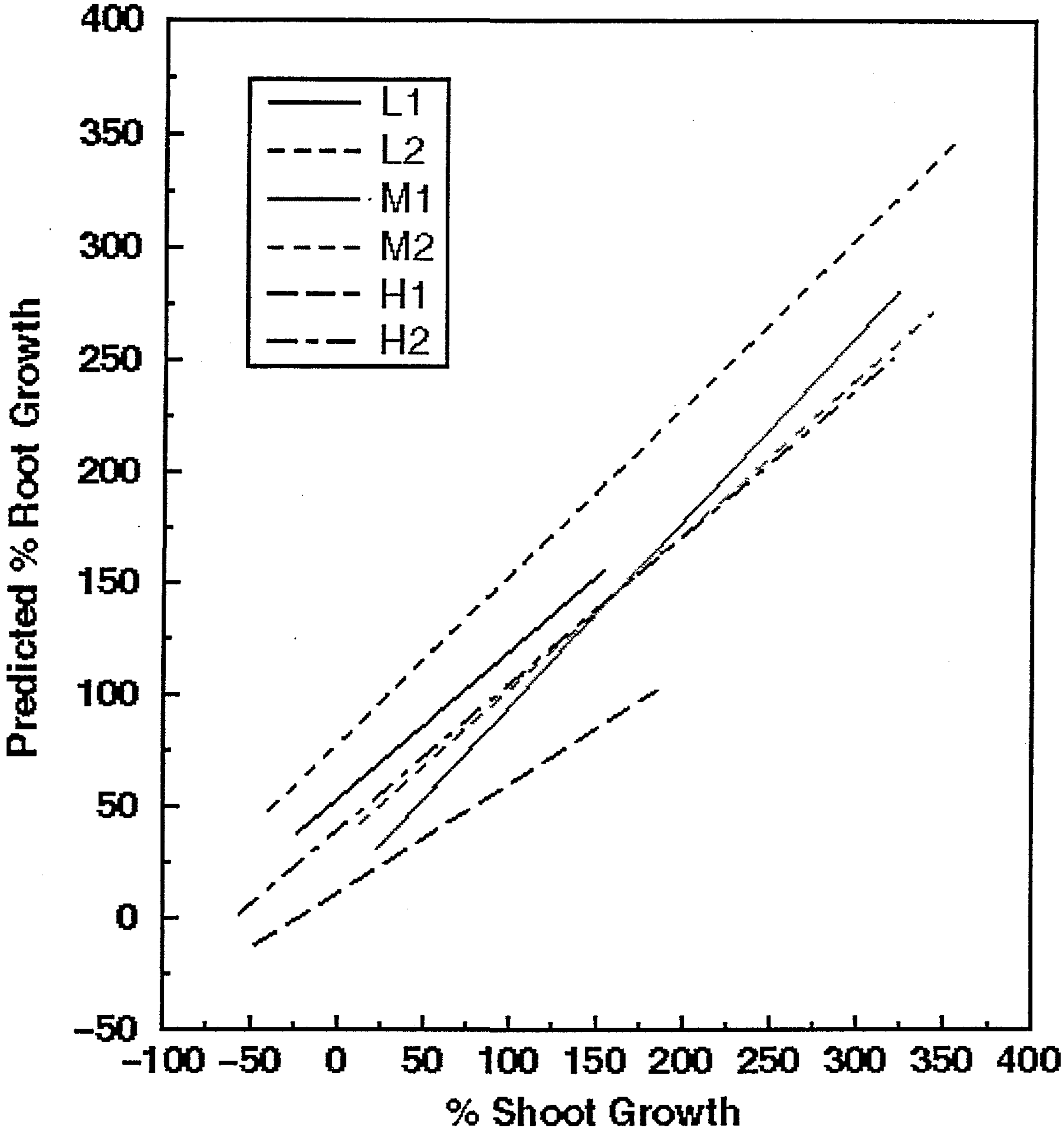

Figure 3. Example of allometric analysis for *Calocedrus decurrens* (CADE). L1=1600 m, shade, L2=1600 m, sun, M1=1900 m, shade, M2=1900 m, sun, H1=2200 m, shade, H2=2200 m, sun.

The slope of this regression is the dimensionless allometric coefficient 'K' (Bowler and Press 1993). 'K' represents the average biomass partitioning trend over the experimental period and measures the relative balance in root and shoot relative growth rates. If treatment slopes are parallel, significant differences between treatments (different intercepts) indicate differences in root growth rate among treatments.

RESULTS

Soil Moisture

Soil water potential values, plotted by treatment, are shown in Figure 4 for 1993 and Figure 5 for 1994. Values were estimated from water content-water potential curves constructed for each treatment-by-soil depth. The limit of the curves is -1.5 MPa since the highest pressure used in creating the content-pressure curves was 15 bars. The only significant difference in soil water potential between light treatments occurred in July 1994 in the surface (0-5 cm depth) soil samples at 1900 m elevation. In this case, the soil water potential was much lower (all <-1.5 MPa) in the sun plots than in the shade plots. Likewise, there was little variation in soil water potential among elevations within each light treatment. Significant gradients in soil water potential among elevations did develop in

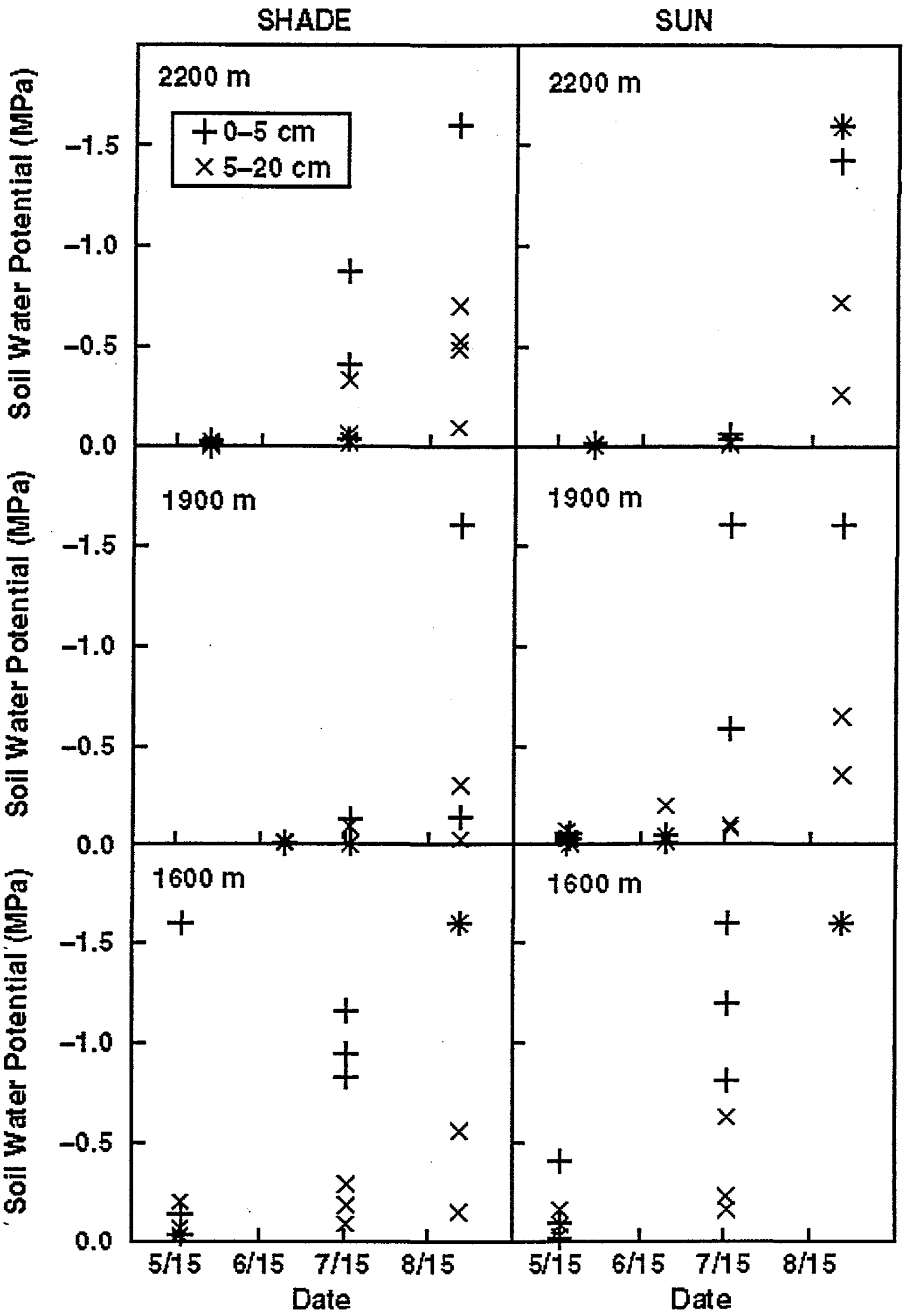

Figure 4. Soil water potential measurements for 1993. Points plotted at -1.6 MPa indicate values less than -1.5 MPa for which the actual soil water potential could not be estimated (limit of curves is -1.5 MPa).

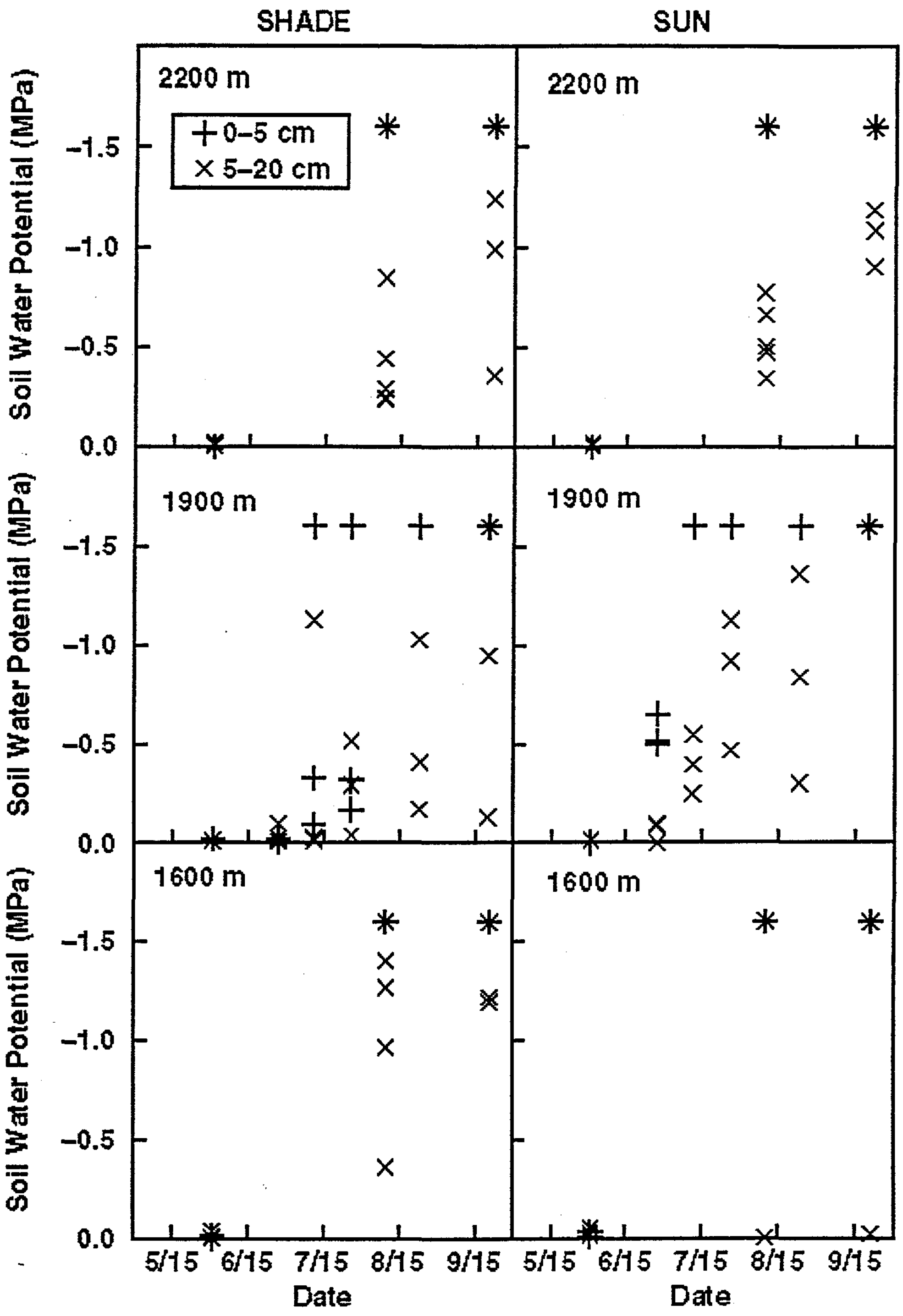

Figure 5. Soil water potential measurements for 1994. Points plotted at -1.6 MPa indicate values less than -1.5 MPa for which the actual soil water potential could not be estimated (limit of curves is -1.5 MPa).

the surface soil samples in the shade plots in July 1993 and in the deep soil samples in the sun plots in August 1994.

While there were virtually no differences in soil water potential among elevations or between light treatments, there were notable variations in soil water potential with depth and time. The deep samples in all treatments maintained average soil water potentials above -1.5 MPa throughout the growing season in both 1993 and 1994. The surface samples, however; became uniformly dry beyond -1.5 MPa in a predictable pattern. In 1993, this threshold was reached in the surface samples by the late summer (August) only in the lowest elevation plots (1600 m). In 1994, all surface samples were less than -1.5 MPa by the August sampling dates. The drier surface soil conditions at the middle and high elevation plots in 1994 are related to lower winter precipitation in 1994 relative to 1993 (Table 3). Daily precipitation measurements made near the 1900 m site were obtained from the National Biological Service research field station at Sequoia National Park (personal communication).

Survival

The proportion of surviving seedlings as well as the upper and lower 95% confidence intervals at each census period are listed in Table 4. Patterns of survival for each species are shown in Figures 6-10. Figures 6-8 demonstrate the effect of

Month	1992	1993	1994
January		39.33	4.79
February		27.95	22.92
March		16.04	4.10
April		2.15	14.52
May		2.62	4.64
June		6.08	0
July		0	0.64
August		0	0
September		0	4.39
October	15.03	2.95	
November	0.05	8.23	
December	19.54	5.91	

Season	1992-1993	1993-1994
October - May	122.71	68.06
June - September	6.08	5.03

Table 3. Precipitation near 1900 m site beginning 7 months before experimental period. All quantities are in centimeters water equivalent.

Species	Light	F93	95% CI	S94	95% CI	F94	95% CI
ABCO	Shade	0.600	0.724	0.283	0.414	0.133	0.246
			0.465		0.175		0.059
	Sun	0.483	0.616	0.350	0.484	0.300	0.432
			0.352		0.231		0.188
ABMA	Shade	0.333	0.467	0.017	0.089	0.000	0.060
			0.217		0.000		0.000
	Sun	0.217	0.342	0.083	0.184	0.050	0.139
			0.121		0.028		0.010
CADE	Shade	0.733	0.839	0.717	0.825	0.333	0.467
			0.603		0.586		0.217
	Sun	0.770	0.868	0.770	0.868	0.770	0.868
			0.645		0.645		0.645
PIJE	Shade	0.900	0.962	0.833	0.917	0.400	0.535
			0.795		0.715		0.276
	Sun	0.932	0.981	0.864	0.940	0.300	0.432
			0.835		0.750		0.188
PILA	Shade	0.400	0.535	0.233	0.360	0.150	0.266
			0.276		0.134		0.071
	Sun	0.300	0.432	0.283	0.414	0.283	0.414
			0.189		0.175		0.175
PIPO	Shade	0.750	0.853	0.617	0.739	0.317	0.450
			0.621		0.482		0.203
	Sun	0.700	0.812	0.583	0.709	0.567	0.694
			0.568		0.449		0.432
SEGI	Shade	0.783	0.879	0.300	0.432	0.117	0.226
			0.658		0.189		0.048
	Sun	0.817	0.905	0.517	0.648	0.383	0.518
			0.696		0.384		0.261

Table 4 (a). Survival proportions and upper and lower 95% confidence limits for 1600 m treatments.

Species	Light	F93	95% CI	S94	95% CI	F94	95% CI
ABCO	Shade	0.933	0.992	0.767	0.901	0.567	0.745
			0.779		0.577		0.374
	Sun	1.00	1.00	0.871	0.964	0.742	0.881
			0.888		0.702		0.554
ABMA	Shade	1.00	1.00	0.733	0.877	0.633	0.801
			0.884		0.541		0.439
	Sun	0.900	0.979	0.467	0.657	0.267	0.459
			0.735		0.283		0.123
CADE	Shade	0.900	0.979	0.833	0.944	0.833	0.944
			0.735		0.653		0.653
	Sun	0.933	0.992	0.867	0.962	0.867	0.962
			0.779		0.693		0.693
PIJE	Shade	1.00	1.00	1.00	1.00	1.00	1.00
			0.881		0.881		0.881
	Sun	1.00	1.00	1.00	1.00	0.966	0.999
			0.881		0.881		0.822
PILA	Shade	0.875	0.965	0.656	0.814	0.531	0.709
			0.710		0.468		0.347
	Sun	0.903	0.980	0.516	0.698	0.355	0.546
			0.742		0.331		0.193
PIPO	Shade	0.897	0.978	0.724	0.873	0.655	0.821
			0.726		0.528		0.457
	Sun	0.862	0.961	0.552	0.736	0.552	0.735
			0.683		0.357		0.357
SEGI	Shade	1.00	1.00	0.900	0.979	0.867	0.962
			0.884		0.735		0.693
	Sun	0.967	0.999	0.900	0.979	0.833	0.943
			0.828		0.735		0.653

Table 4 (b). Survival proportions and upper and lower 95% confidence limits for 1900 m treatments.

Species	Light	F93	95% CI	S94	95% CI	F94	95% CI
ABCO	Shade	0.984	0.999	0.869	0.942	0.836	0.918
			0.912		0.758		0.719
	Sun	0.900	0.962	0.750	0.853	0.667	0.783
			0.795		0.621		0.533
ABMA	Shade	0.763	0.864	0.339	0.474	0.186	0.309
			0.634		0.221		0.097
	Sun	0.850	0.929	0.567	0.694	0.450	0.584
			0.734		0.432		0.321
CADE	Shade	0.850	0.929	0.767	0.866	0.767	0.866
			0.734		0.640		0.640
	Sun	0.867	0.941	0.867	0.941	0.833	0.917
			0.754		0.754		0.715
PIJE	Shade	1.00	1.00	0.950	0.990	0.850	0.929
			0.940		0.861		0.734
	Sun	1.00	1.00	0.933	0.982	0.800	0.892
			0.940		0.838		0.677
PILA	Shade	0.867	0.941	0.500	0.632	0.400	0.535
			0.754		0.368		0.276
	Sun	0.700	0.812	0.400	0.535	0.267	0.397
			0.568		0.276		0.161
PIPO	Shade	0.867	0.941	0.433	0.568	0.233	0.361
			0.754		0.306		0.134
	Sun	0.917	0.972	0.700	0.812	0.467	0.600
			0.816		0.568		0.337
SEGI	Shade	0.933	0.982	0.867	0.941	0.767	0.867
			0.838		0.754		0.640
	Sun	0.983	0.999	0.917	0.972	0.750	0.853
			0.911		0.816		0.621

Table 4 (c). Survival proportions and upper and lower 95% confidence limits for 2200 m treatments.

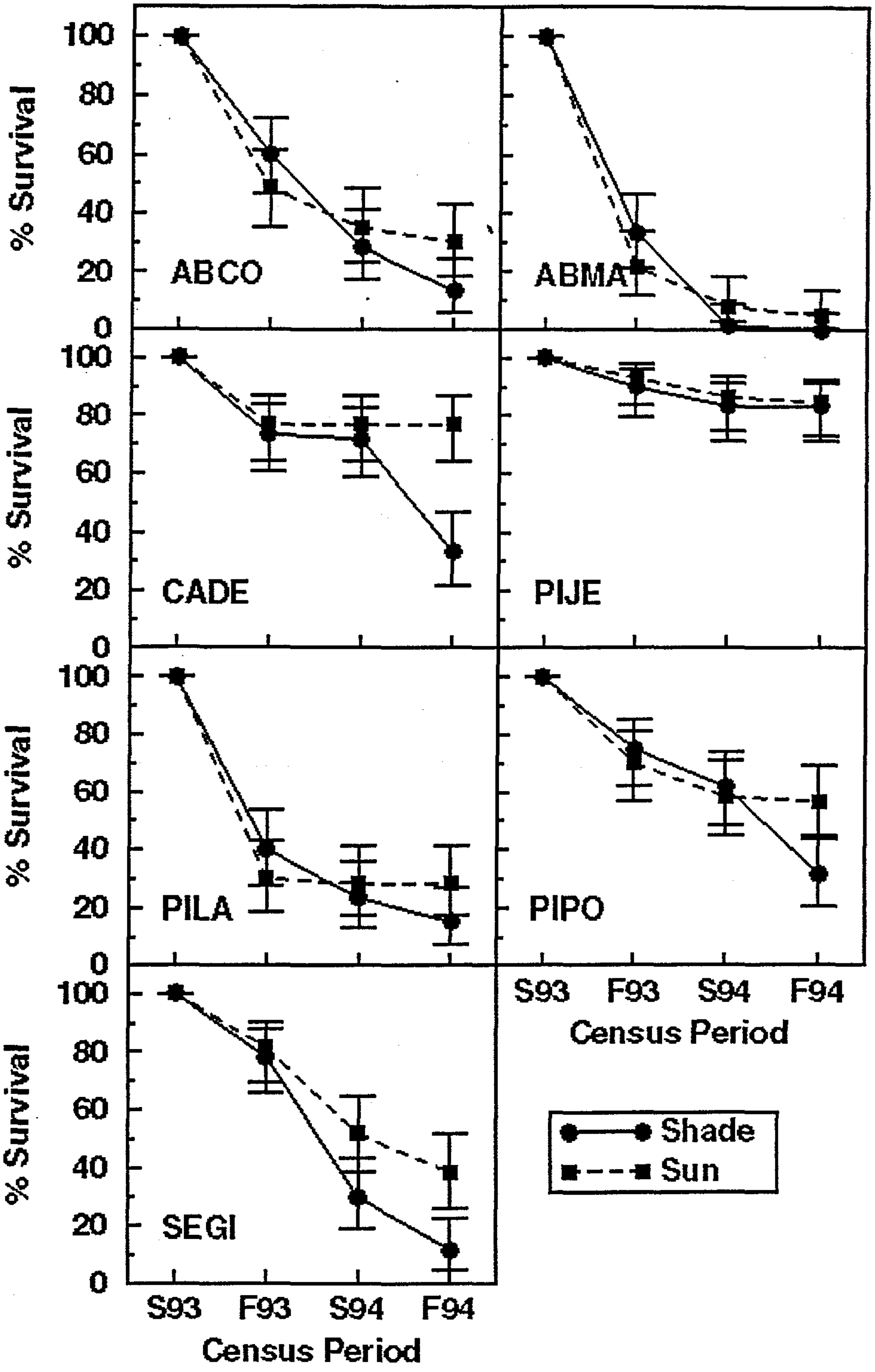

Figure 6. Survival proportions and 95% confidence limits for 1600 m treatments.

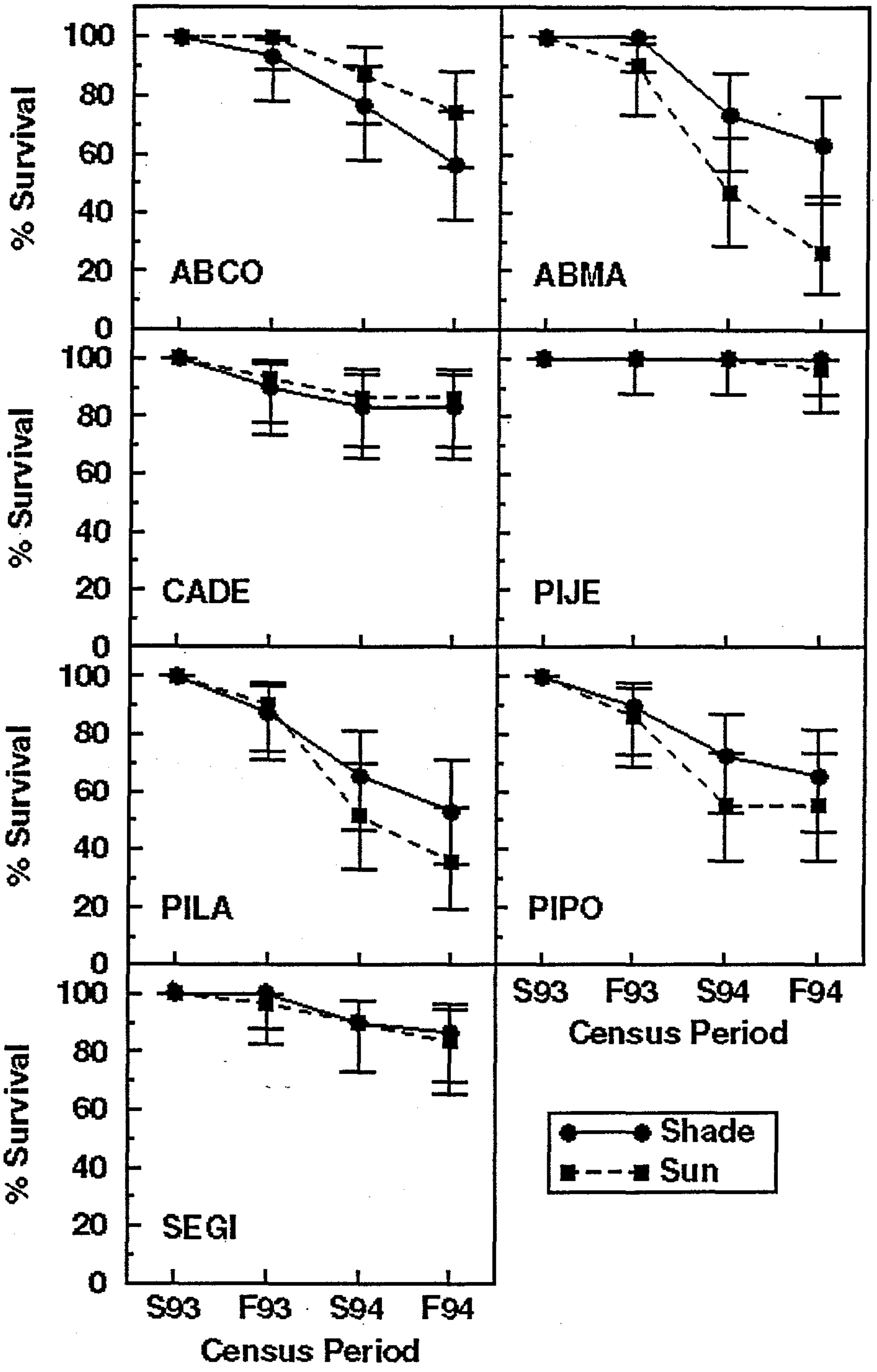

Figure 7. Survival proportions and 95% confidence limits for 1900 m treatments.

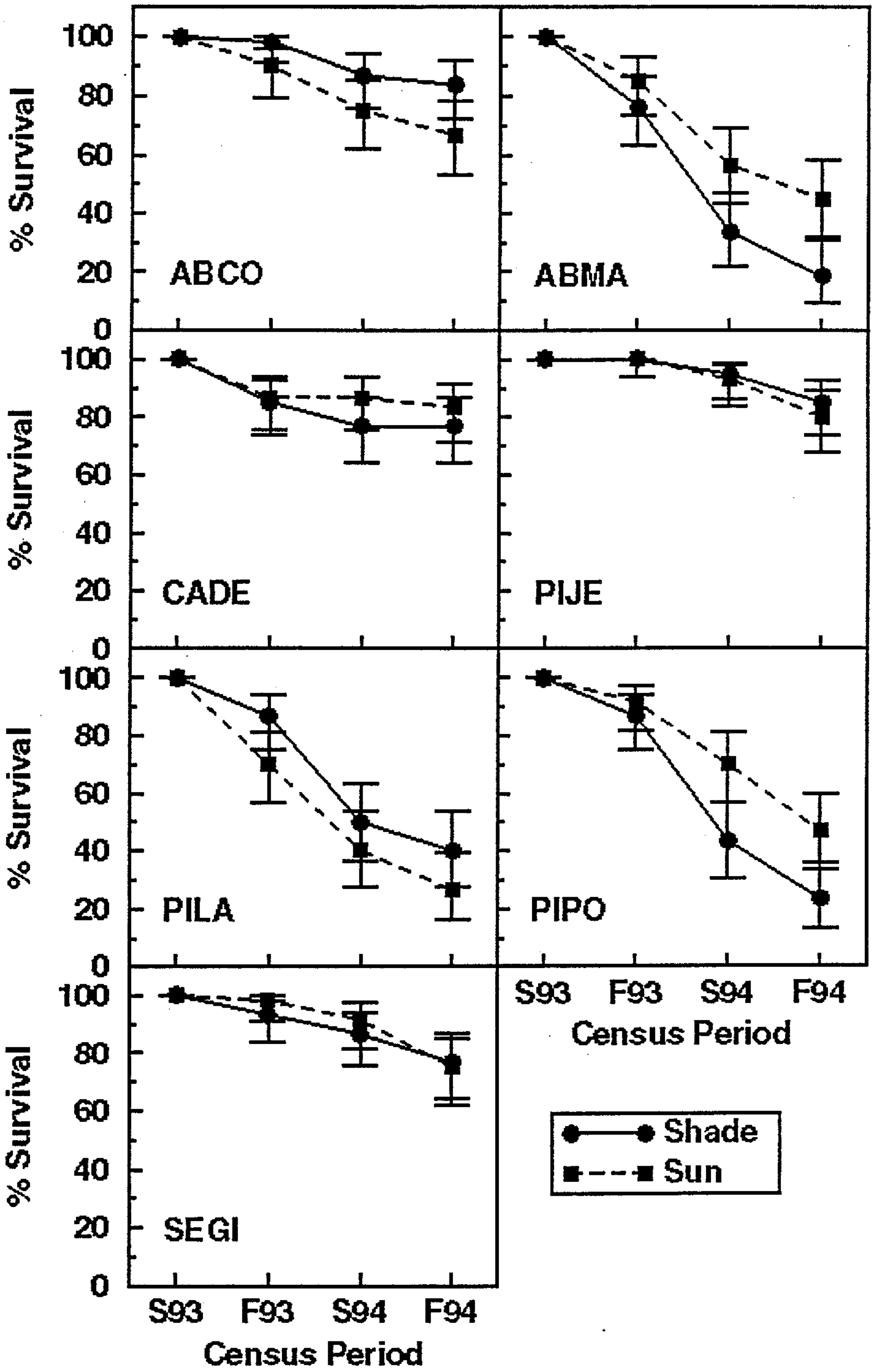

Figure 8. Survival proportions and 95% confidence limits for 2200 m treatments.

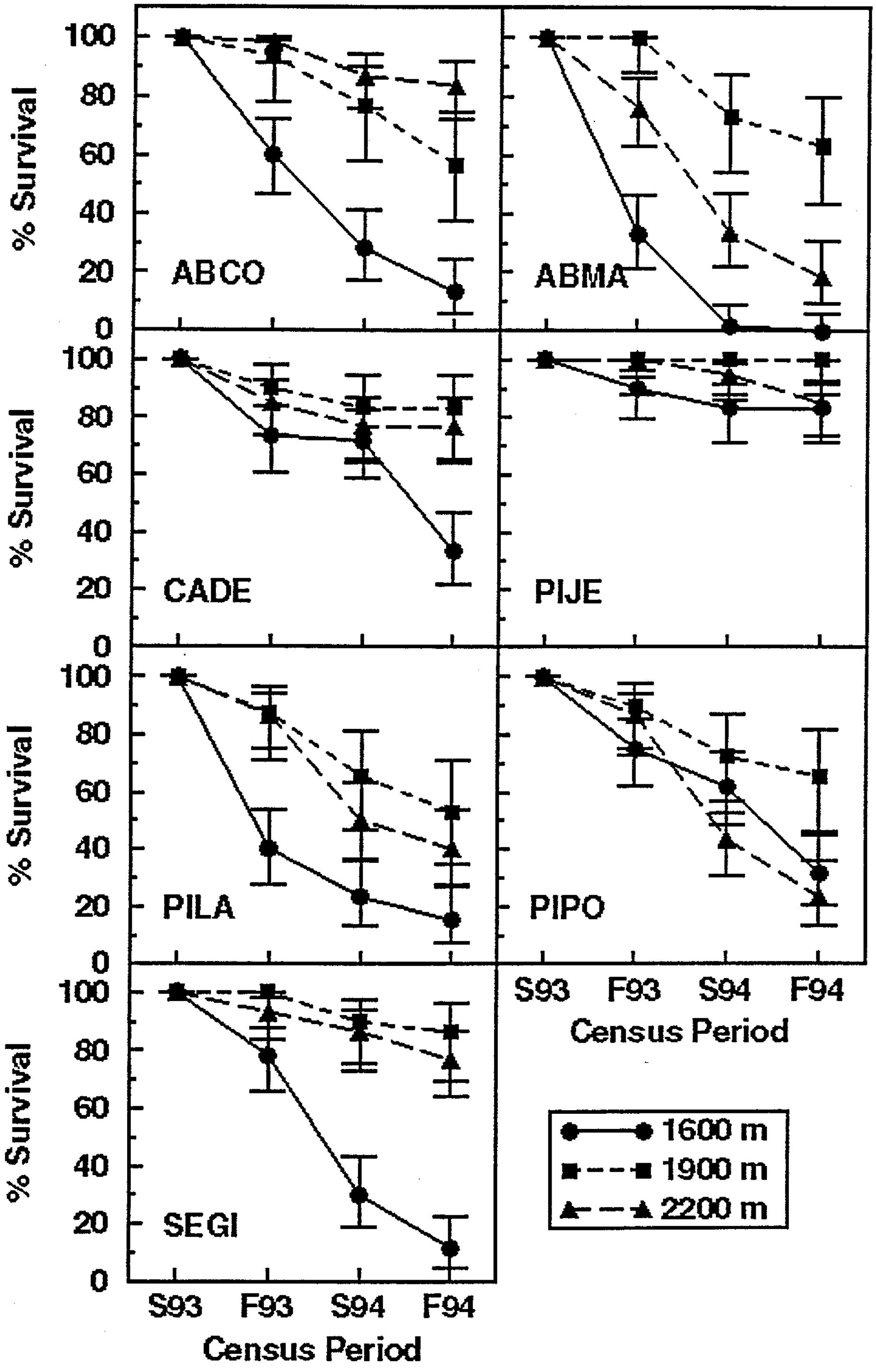

Figure 9. Survival proportions and 95% confidence limits for shade treatments.

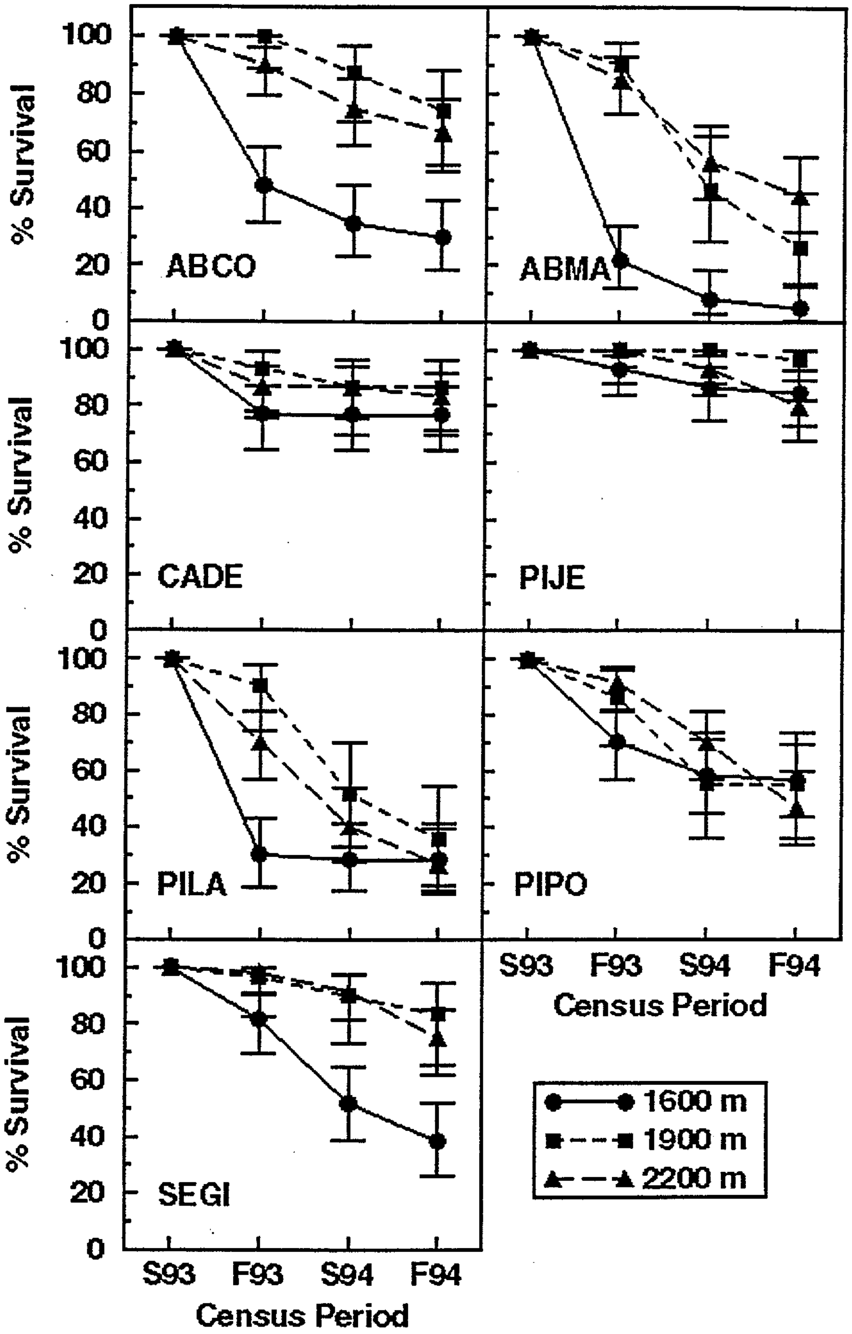

Figure 10. Survival proportions and 95% confidence limits for sun treatments.

Species	Elevation	Light	Elev*Light	Init. Height	R^2
ABCO	0.0001	0.3734	0.0282	0.1372	0.7641
ABMA	0.0032	0.9598	0.0818	0.9176	0.4963
CADE	0.0183	0.1076	0.2498	0.0264	0.5691
PIJE	0.2138	0.3897	0.9088	0.0370	0.3176
PILA	0.0720	0.9187	0.3807	0.1807	0.3530
PIPO	0.4044	0.6057	0.5777	0.0845	0.3375
SEGI	0.0001	0.3404	0.2526	0.6469	0.6668

Table 5. Analysis of covariance results (p-values) for proportion surviving. Proportions were transformed using [p' = arcsin (square root of proportion surviving)] prior to analysis of variance.

light on survival at each elevation, while figures 9 and 10 more clearly show the effect of elevation on survival within each light level.

Rank correlation of initial size with survival in each treatment indicated that only initial height was significant in survival. Initial height was, therefore, included as a covariate in the analysis of treatment effects on survival. Analysis of covariance results are reported in Table 5. There is a high degree of prediction (R^2 = 0.76-0.32) with this model for most species. Initial height was a significant factor ($P<0.05$) in the survival of *C. decurrens* and *P. jeffreyi*. It was also marginally significant ($P<0.10$) in survival of *P. ponderosa*. Inclusion of initial height as a covariate did not significantly change the pattern of main effects or interaction, relative to the analysis of variance model which did not include initial height in the survival analysis.

Significant interaction between elevation and light in determining survival occurred only in *A. concolor* at the level P<0.05. The interaction effect was marginally significant (P<0.10) in *A. magnifica* var. *shastensis*. The main effects of light and elevation must be interpreted cautiously when the interaction is significant. Among the other species, light is not a significant factor in overall survival in any species. Survival of *C. decurrens* and *S. giganteum* was significantly affected by elevation (P<0.05), while the response of *P. jeffreyi* was marginally significant (P<0.10). Notice that the three species whose survival was most poorly predicted by this model, *P. jeffreyi*, *P. lambertiana* and *P. ponderosa*, did not show significant effects of elevation or light on survival.

The effect of light within each elevation on the survival of each species is displayed in Figures 6-8. At low elevation (Figure 6) there are differences in survival at the time of harvest between light levels in *C. decurrens*, and *S. giganteum*, with lower survival in the shade plots. *A. concolor*, *P. lambertiana*, and *P. ponderosa* also had lower survival in the shade plots. These differences in survival were significant when proportion surviving was plotted +/- one standard error, but are within the 95 % confidence intervals. At medium elevation (Figure 7), no significant effect of light is detected using the 95 % confidence intervals, although *A. concolor* survival was lower in the shade plots, whereas *A. magnifica* var. *shastensis* and *P. lambertiana* had lower survival in the sun plots. *C. decurrens*, *P. jeffreyi*, *P. ponderosa*, and *S. giganteum* did not differ in survival between light treatments at this elevation. In the high elevation plots (Figure 8), there was again no significant difference in survival between sun and shade plots in any species. *C. decurrens*, *P. jeffreyi*, and *S. giganteum* had virtually identical survival rates in the sun and shade; *A. magnifica* var. *shastensis* and *P. ponderosa* had lower survival in the shade plots, and *A. concolor* and *P. lambertiana* had lower survival in the sun plots.

The primary effect of elevation within each light level (Figs. 9 and 10) is much reduced survival at 1600 m elevation for most species. This was especially marked for shade plots. In contrast, there is very little difference in percent survival between the medium (1900 m) and high (2200 m) elevation sites in either low or high light treatments.

In the shade plots (Figure 9), the only species that do not show a marked decrease in survival at the low elevation relative to the medium and high elevation treatments are *P. jeffreyi* and *P. ponderosa*. In the case of *P. jeffreyi*, there was very high survival at all elevations, partially due to the large size of the seedlings at the time of planting. *P. ponderosa* showed high mortality in the low and high elevation treatments, with the highest survival occurring in the medium elevation treatment.

In the sun plots (Figure 10), there was also a significant decrease in survival at the lowest elevation relative to the medium and high elevations (though not as great as the shade) in *A. concolor*, *A. magnifica* var. *shastensis*, and *S. giganteum*. Survival of

C. decurrens and *P. lambertiana* did not differ among elevations in the sun plots as they did in the shade plots. *P. lambertiana* did have high mortality at the low elevation relative to the other elevations in the first growing season, but mortality in the medium and high elevation treatments "caught up" by the end of the second growing season.

Growth

Plot effects within treatments were compared to determine whether replicate plots could be combined. In the height growth results, this test failed for *S. giganteum.* Further investigation showed the effect of the covariate (initial height) on height growth was different for treatments M2 and H1 than for all other treatments. These treatments were, therefore, removed from the analysis of variance of growth in order to maintain the statistical assumption that all replicates respond similarly with respect to the covariate. The resulting analyses indicated that replicate plots could be combined in all other treatments. Similarly, treatments L2 and M2 were removed from the analysis of diameter growth in *P. jeffreyi* and treatment L1 was removed for *P. lambertiana.* Treatment L1 in *A. magnifica* var. *shastensis* was deleted from all analyses because all individuals in this treatment were dead at the end of the experimental period.

Analysis of covariance results are given in Table 6. Results of LSMEANS analysis for height, diameter, and total biomass are reported in Table 7 and plotted in Figures 11-13.

Height growth

There was a highly significant ($P<0.01$) effect of the covariate (initial height) on all species, and a significant ($P<0.05$) interaction between elevation and light in all species except *P. ponderosa* ($P>0.71$). No estimate of interaction was possible for *S. giganteum* due to the reduced number of treatments included in the analysis.

Light was highly significant ($P<0.01$) and elevation was somewhat significant ($P<0.06$) in height growth of *P. ponderosa.* All other species had significant interaction between light and elevation. Main effects must be interpreted cautiously when the interaction term is significant. In such cases it is best to compare separately the effect of elevation within each light level and the effect of light within each elevation.

Percent height growth in the sun plots was greater than or equal to percent height growth in the shade plots for all species. Whether or not the growth difference between light treatments is significant differs among species and elevations. The general trend is for significantly greater height growth in the high-light plots at the

	n	Species	Elevation	Light	Elev*Light	Covariate
Height	157	ABCO	0.2571	0.0001	0.0001	0.0001
	68	ABMA	0.6361	0.7874	0.0499	0.0001
	210	CADE	0.0001	0.0002	0.0298	0.0001
	256	PIJE	0.0001	0.0001	0.0001	0.0001
	92	PILA	0.0245	0.2411	0.0203	0.0028
	127	PIPO	0.0594	0.0001	0.7198	0.0001
	100	SEGI(1)	0.0441	0.4206	--	0.0001
Diameter	157	ABCO	0.2292	0.3386	0.0288	0.1452
	68	ABMA	0.2937	0.0093	0.1845	0.0797
	214	CADE	0.0320	0.0143	0.0891	0.0001
	176	PIJE(2)	0.8806	0.2633	--	0.0001
	85	PILA(3)	0.1879	0.2354	0.7695	0.0056
	130	PIPO	0.0693	0.8514	0.6689	0.0019
	172	SEGI	0.8851	0.5755	0.0843	0.0003

Table 6 (a). Analysis of covariance results (p-values) for height and diameter growth parameters. (1)Height, SEGI - M2 & H1 removed, (2)Diam, PIJE- L2 & M2 removed (3)Diam, PILA - L1 removed

	n	Species	Elevation	Light	Elev*Light	Covariate
Mass	157	ABCO	0.0019	0.0001	0.0089	0.045
	68	ABMA	0.1742	0.3828	0.0076	0.0145
	212	CADE	0.0003	0.0022	0.0005	0.0001
	255	PIJE	0.0001	0.0030	0.0006	0.0001
	94	PILA	0.1277	0.5102	0.098	0.9176
	129	PIPO	0.3910	0.0001	0.0092	0.0289
Root	157	ABCO	0.1341	0.0020	0.2358	0.2363
	68	ABMA	0.2034	0.1436	0.1825	0.2386
	213	CADE	0.0001	0.0001	0.0002	0.0008
	255	PIJE	0.0001	0.0036	0.0072	0.0001
	94	PILA	0.2507	0.0459	0.0581	0.1344
	129	PIPO	0.0948	0.0001	0.0713	0.0149
Shoot	157	ABCO	0.0001	0.0008	0.0014	0.0410
	68	ABMA	0.3109	0.8002	0.0040	0.0171
	213	CADE	0.0001	0.0199	0.0039	0.0001
	255	PIJE	0.0023	0.0133	0.0021	0.0281
	94	PILA	0.1101	0.7987	0.1435	0.5995
	129	PIPO	0.5174	0.0001	0.0001	0.0653

Table 6 (b): Analysis of covariance results (p-values) for mass growth parameters - total mass, root mass, and shoot mass. *S. giganteum* is not shown since initial fresh weight could not be reliably determined.

Treatment	L1		L2		M1		M2		H1		H2	
	X	SE	X	SE	X	SE	X	SE	X	SE	X	SE
Height												
ABCO	9.9	5.8	27.4	3.9	14.0	4.1	8.6	3.5	0.8	2.4	27.5	2.6
ABMA	--	--	95.3	27.9	76.9	11.0	53.8	17.0	50.4	14.9	80.8	9.3
CADE	-1.7	3.9	13.8	2.6	31.1	3.4	30.7	3.4	8.5	2.5	22.3	2.4
PIJE	14.1	2.5	20.9	2.4	23.6	3.2	18.7	3.2	-11.7	2.4	18.0	2.5
PILA	21.6	5.4	22.1	3.4	30.7	4.4	26.0	5.0	7.9	3.4	25.4	4.2
PIPO	29.2	9.4	65.5	6.9	42.6	9.5	66.3	10.7	12.9	10.7	51.3	7.6
SEGI	3.7	6.5	13.7	3.3	21.0	3.1	22.4	3.2	6.5	2.3	18.7	2.4
Diameter												
ABCO	1.5	5.6	6.7	3.8	2.9	3.9	1.5	3.3	13.6	2.2	1.0	2.5
ABMA	–	–	14.1	10.7	9.2	4.3	2.3	6.6	22.8	5.7	2.2	3.6
CADE	33.3	3.9	35.0	2.6	35.0	3.5	22.3	3.4	30.3	2.6	22.4	2.5
PIJE	10.6	1.9	14.5	1.9	9.3	2.4	9.1	2.5	10.1	1.9	5.6	1.9
PILA	26.8	5.7	24.0	4.1	17.9	4.3	15.3	5.2	21.4	3.5	16.1	4.4
PIPO	21.5	4.6	24.6	3.4	14.7	4.5	10.6	5.0	15.8	5.3	18.8	3.9
SEGI	13.1	6.6	23.4	3.7	24.9	3.4	16.0	3.5	24.2	2.6	16.5	2.7
Biomass												
ABCO	-34.6	8.1	2.1	5.4	-34.1	5.6	-34.9	4.8	-28.6	3.2	-11.1	3.6
ABMA	--	--	-6.9	15.7	-19.3	6.2	-33.4	9.6	-25.9	8.2	1.5	5.2
CADE	49.9	13.6	111.9	8.6	131.8	12.1	107.3	11.6	58.0	8.7	101.8	8.4
PIJE	10.9	3.0	26.4	3.0	12.6	3.9	4.4	4.0	-5.3	3.0	11.9	3.0
PILA	1.7	7.2	2.6	5.2	2.5	5.4	-4.8	6.6	-16.9	4.4	-0.9	5.4
PIPO	-11.4	9.9	31.6	7.4	-5.3	10.0	-0.5	10.7	-27.7	11.9	42.1	8.2

Table 7. Mean percent growth and standard error, listed by parameter - height, diameter, and biomass. *S. giganteum* is not shown in the biomass category since initial fresh weight could not be reliably determined.

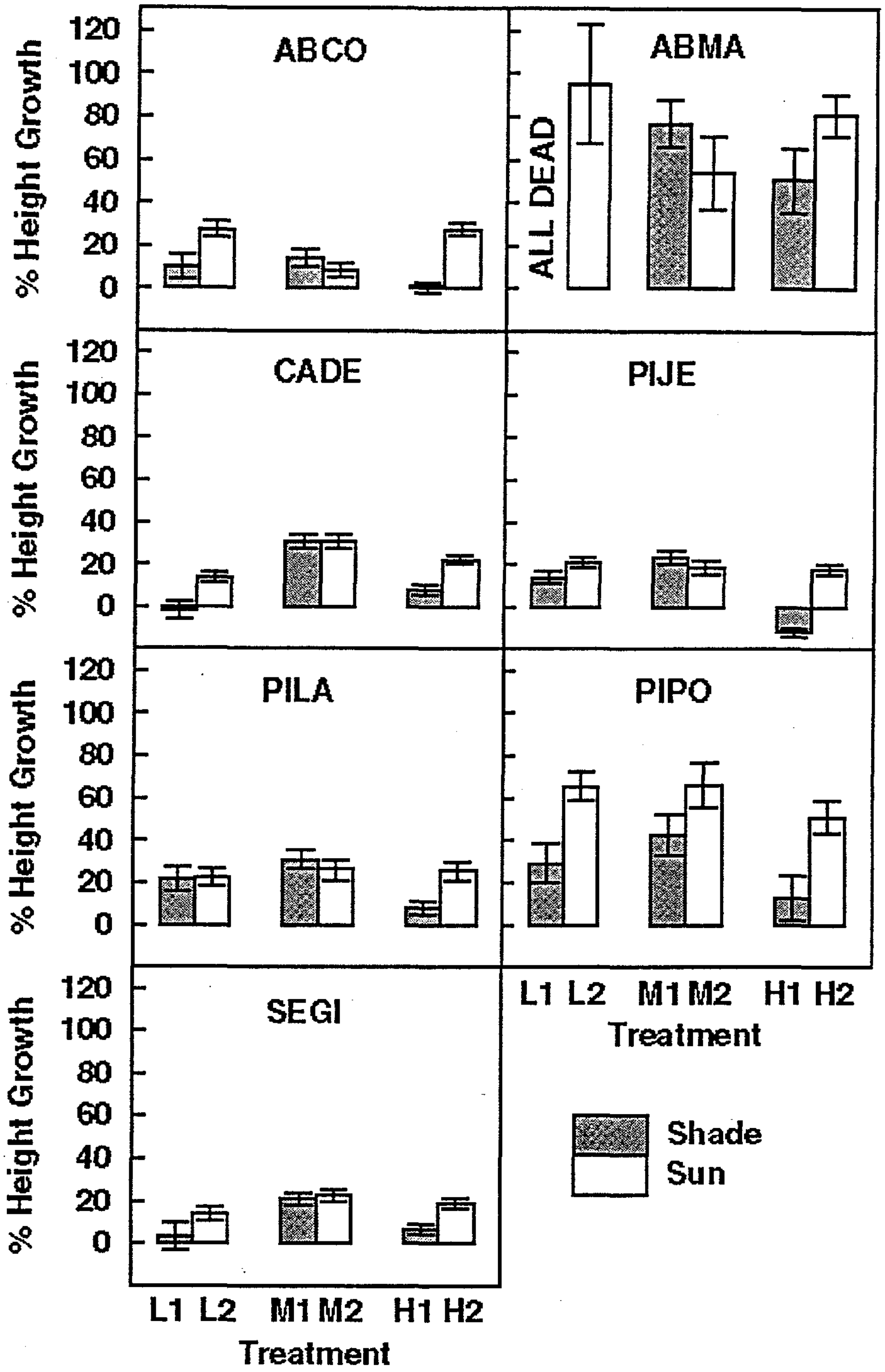

Figure 11. Mean percent height growth +/- one standard error. L1 = 1600 , shade, L2 = 1600 m, sun, M1 = 1900 m, shade, M2 = 1900 m, sun, H1 = 2200 m, shade, H2 = 2200 m, sun.

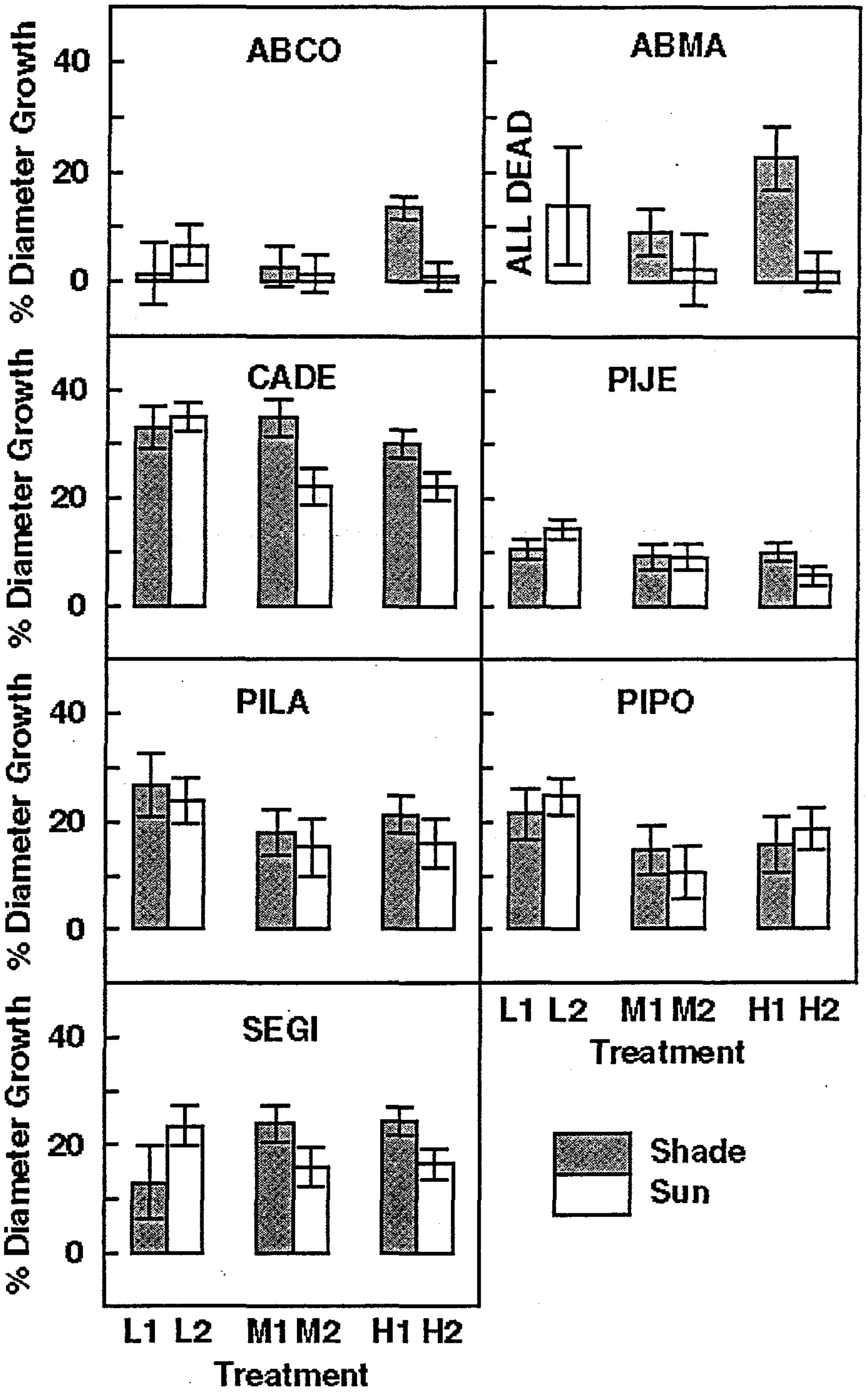

Figure 12. Mean percent diameter growth +/- one standard error. L1 = 1600 , shade, L2 = 1600 m, sun, M1 = 1900 m, shade, M2 = 1900 m, sun, H1 = 2200 m, shade, H2 = 2200 m, sun.

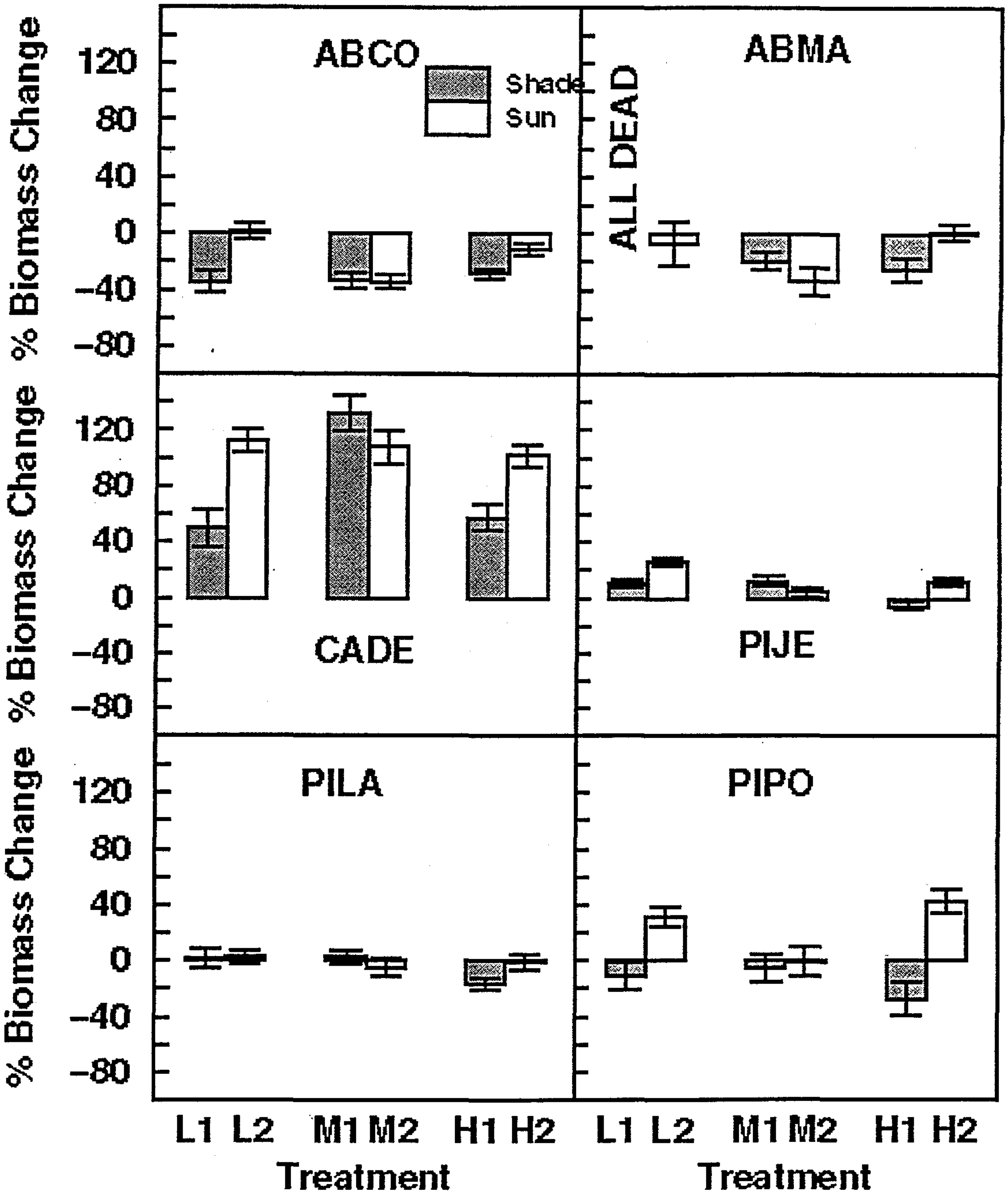

Figure 13. Mean percent mass change +/- one standard error. L1 = 1600 , shade, L2 = 1600 m, sun, M1 = 1900 m, shade, M2 = 1900 m, sun, H1 = 2200 m, shade, H2 = 2200 m, sun. *S. giganteum* is not shown since initial fresh weight could not be reliably determined.

low and high elevations, but not at the middle elevation (Figure 11). At the low elevation sites, greater height growth was seen in the high-light plots in all species except *P. lambertiana* and *S. giganteum*. Comparisons for *A. magnifica* var. *shastensis* were not possible because all individuals had died by the end of the experiment, but analysis of height growth during the first growing season showed, like *S. giganteum*, a non-significant trend toward higher growth in the high light plots. Greater height growth in the high light plots was also seen at the high elevation site in all species except *S. giganteum*, for which the H1 treatment was removed. Examination of height growth in *S. giganteum* during the first growing season showed significantly greater height growth in the high light plots at the high elevation.

The seedling height growth response to light was not as pronounced at the middle elevation as at the low and high elevations. The only significant difference occurred in *P. ponderosa*, where there was greater height growth in the high light plots (note that this is the only species that did not have significant interaction between light and elevation). For all other species, there was a trend, albeit nonsignificant, for greater height growth in the shade plots.

The effect of elevation within each light level can be seen in Figure 11 by comparing height growth bars of the 3 shade treatments or of the 3 sun treatments within each species. The lowest percent height growth in the shade treatments occurred at the highest elevation for most species, but complete comparisons were not possible for *A. magnifica* var. *shastensis* and *S. giganteum*. For *C. decurrens* the high elevation showed greater percent height growth than the low elevation.

Within the high light treatment there were 3 patterns of responses. The first type of response was seen in the 3 pine species which did not show an effect of elevation on height growth in the sun plots. A second type of response was observed in the 2 fir species which had reduced growth in the middle elevation sun plots, compared to the low and high elevation sun plots. *C. decurrens* and *S. giganteum* represented a third response group in which seedlings grown in the high light treatments had the highest percent growth in the middle elevation, with decreased growth in the high and low elevation plots.

Diameter growth

There were fewer significant differences in diameter growth responses than in height growth responses to light and elevation treatments (Figure 12). When a significant effect of light on diameter growth was evident, the greater growth occurred in the shade plots (*A. concolor*, *A. magnifica* var. *shastensis*, *C. decurrens*, and *S. giganteum* at high elevation and *C. decurrens* and *S. giganteum* at the middle elevation). A similar trend, while not significant, resulted in greater percent diameter growth in shade plots at the high elevation in *P. jeffreyi* and *P. lambertiana* and at the middle elevation in *A. concolor*, *A. magnifica* var. *shastensis*, *P. lambertiana*, and *P.*

ponderosa. The opposite trend, also not significant, was seen in the low elevation plots, where greater percent diameter growth was found in the sun plots in *A. concolor*, *C. decurrens*, *P. ponderosa*, and *S. giganteum*.

A significant effect of elevation within the low light treatments occurred only in *A. concolor* and *A. magnifica* var. *shastensis*, where the greatest percent diameter growth was seen in the high elevation treatment. In the high light treatments, significant differences among elevations were observed only in *C. decurrens*, where the diameter growth was significantly greater in the low elevation plots than in the medium or high elevation plots and in *P. ponderosa*, where the low elevation treatments also showed significantly greater growth than the middle elevation, but not more than the high elevation treatments.

Biomass growth

Estimates of percent biomass change (Figure 13) were largely negative. This is most likely due to loss of biomass as a result of transplanting healthy nursery-grown seedlings into the experimental environments and, to a lesser extent, to an inadequate harvest of the below-ground biomass. Nonetheless, it is instructive to examine the trends in percent biomass change between elevations and light levels and compare them to the results seen in height and diameter growth.

The effect of light on percent biomass change within each elevation was generally similar to the response seen in percent height growth, i.e., there was greater (or less negative) growth in the high light plots, especially in the low and high elevation treatments (*A. concolor*, *C. decurrens*, *P. jeffreyi*, and *P. ponderosa* - low and high elevation; *A. magnifica* var. *shastensis* and *P. lambertiana* - high elevation only).

Significant differences in percent biomass change across elevations within the shade plots were seen only in *C. decurrens* and *S. giganteum*, where greater (or less negative) percent biomass growth was found in the middle elevation plots relative to the low and high elevation plots, and in *P. jeffreyi* and *P. lambertiana*, where greater/less negative growth occurred in the low and medium elevation plots.

Biomass growth in the sun plots responded somewhat differently from the shade plots. *A. concolor*, *A. magnifica* var. *shastensis* and *P. ponderosa*, which did not show significant differences in percent biomass growth among elevations in the shade plots, did show significantly less (or more negative) percent biomass change in the middle elevation plots relative to low and high elevation treatments. *P. jeffreyi* also exhibited this pattern, but a significant difference was not observed between medium and high elevation treatments in this species. This trend toward increased growth in the low and high elevations in the majority of species is consistent with the response seen in the height growth measurements.

The same pattern of greater growth in the high light environments at low and high elevations held true when total biomass growth was separated into root and shoot growth (Table 8, Figures 14 and 15). Results of allometric analyses are reported in table 9. *P. ponderosa* is the only species in which K, the allometric coefficient, differed significantly among treatments ($P<0.0001$). In this species, less root mass was allocated per unit shoot mass in treatments L1 and H1.

Treatment	L1		L2		M1		M2		H1		H2	
	X	SE	X	SE	X	SE	X	SE	X	SE	X	SE
Root Mass												
ABCO	-22.4	10.7	11.4	7.1	-24.9	7.4	-18.2	6.3	-21.0	4.2	-7.2	4.8
ABMA	--	--	25.7	17.5	-3.7	7.0	-2.5	10.7	-0.6	9.2	23.1	5.8
CADE	76.7	13.5	149.2	8.8	125.3	12.4	108.6	11.9	43.5	8.9	105.8	8.6
PIJE	31.5	3.3	51.8	3.3	26.2	4.3	21.8	4.4	14.3	3.3	25.0	3.4
PILA	11.4	8.1	27.9	5.8	15.7	6.0	9.3	7.4	-2.6	4.9	20.4	6.1
PIPO	-2.9	7.7	26.6	5.7	-6.0	7.7	-0.9	8.3	-20.8	9.3	21.3	6.3
Shoot Mass												
ABCO	-47.3	9.5	-7.8	6.3	-43.9	6.5	-52.8	5.6	-37.0	3.8	-15.3	4.2
ABMA	--	--	-25.1	18.3	-26.7	7.3	-50.7	11.2	-39.4	9.6	-10.9	6.1
CADE	37.0	14.8	94.0	9.4	132.9	12.9	108.1	12.7	66.1	9.5	100.6	9.1
PIJE	2.1	3.5	16.1	3.6	6.9	4.7	-2.4	4.7	-13.3	3.6	6.3	3.6
PILA	-3.8	7.7	-11.9	5.6	-5.3	5.7	-13.0	7.1	-25.0	4.7	-13.2	5.8
PIPO	-17.4	12.8	35.1	9.6	-4.7	13.0	-0.1	13.9	-32.6	15.6	57.0	10.6

Table 8. Mean percent growth and standard error for root and shoot growth. *S. giganteum* is not shown since initial fresh weight could not be reliably determined.

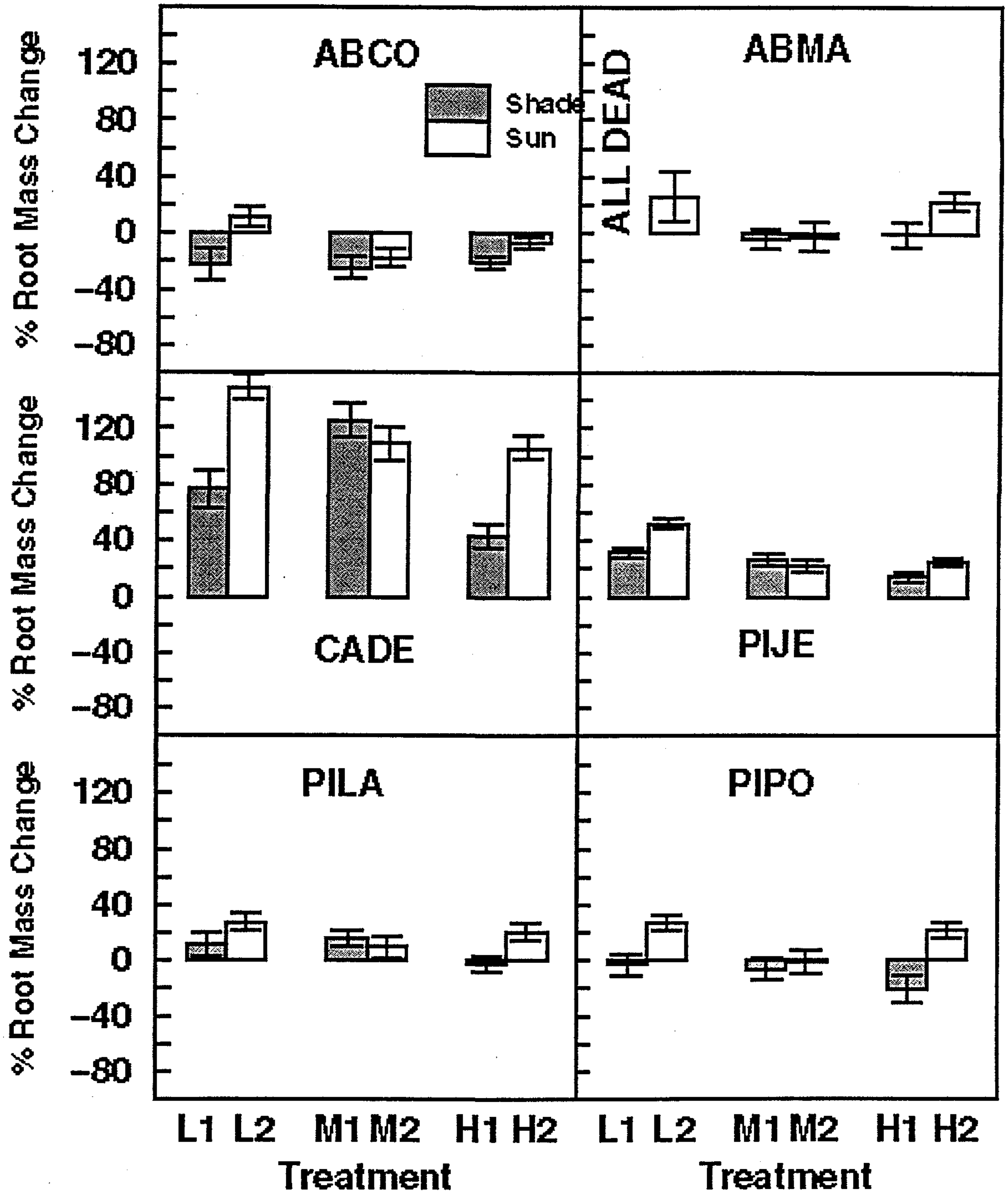

Figure 14. Mean percent root mass change +/- one standard error. L1 = 1600 , shade, L2 = 1600 m, sun, M1 = 1900 m, shade, M2 = 1900 m, sun, H1 = 2200 m, shade, H2 = 2200 m, sun. *S. giganteum* is not shown since initial fresh weight could not be reliably determined.

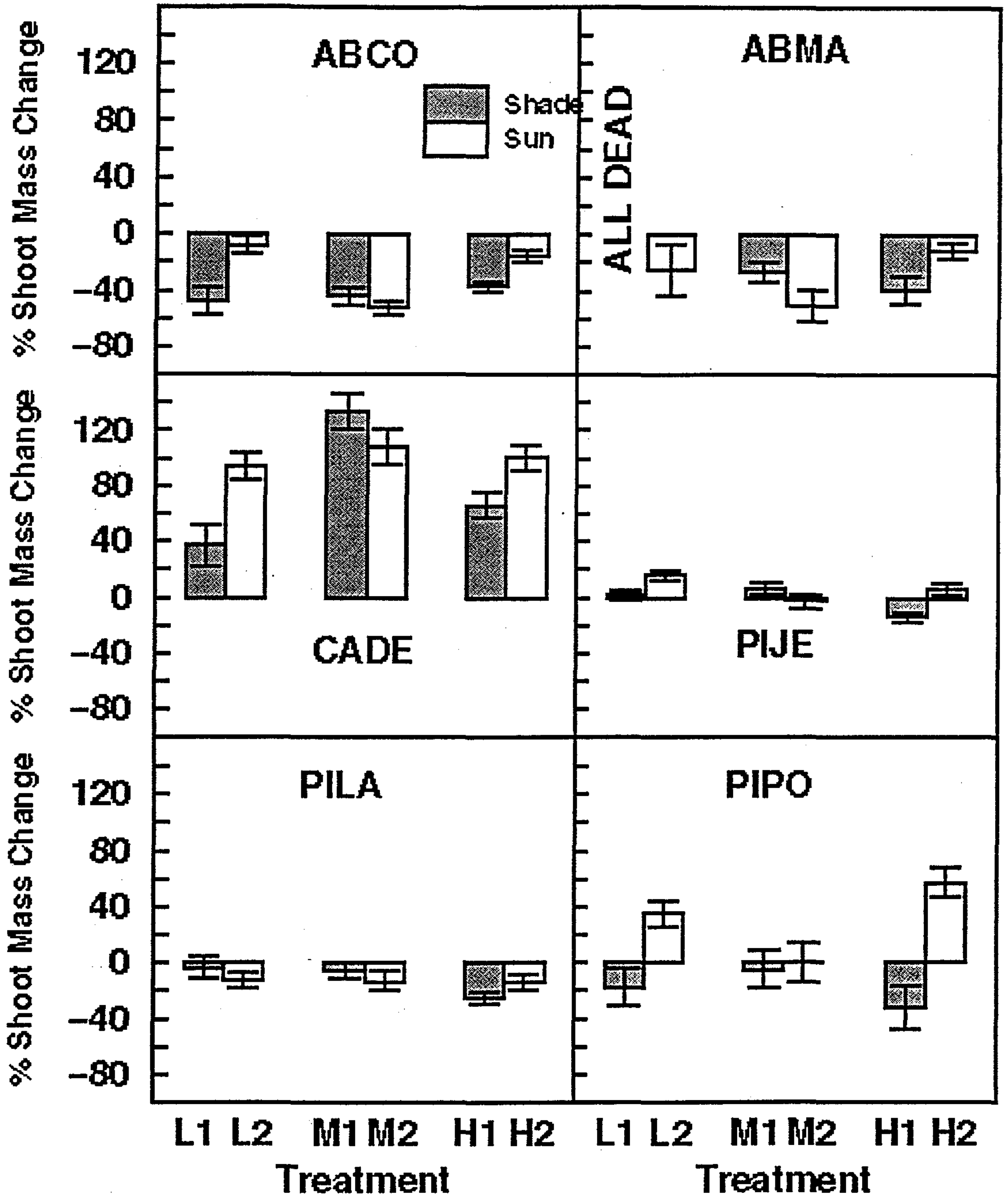

Figure 15. Mean percent shoot mass change +/- one standard error. L1 = 1600 , shade, L2 = 1600 m, sun, M1 = 1900 m, shade, M2 = 1900 m, sun, H1 = 2200 m, shade, H2 = 2200 m, sun. *S. giganteum* is not shown since initial fresh weight could not be reliably determined.

Trt	L1		L2		M1		M2		H1		H2	
	K	SE	K	SE	K	SE	K	SE	K	SE	K	SE
ABCO	-0.270	0.414	0.516	0.123	0.557	0.123	0.531	0.139	0.370	0.087	0.262	0.223
ABMA	--	--	0.462	0.068	0.196	0.183	-0.128	0.548	0.614	0.641	0.572	0.149
CADE	0.665	0.172	0.758	0.096	0.835	0.128	0.697	0.103	0.492	0.078	0.663	0.088
PIJE	0.528	0.159	0.448	0.170	0.278	0.180	-0.043	0.206	0.381	0.131	0.373	0.096
PILA	0.176	0.176	0.880	0.227	0.948	0.193	0.793	0.205	0.370	0.165	0.775	0.202
PIPO	-0.124	0.199	0.685	0.073	0.420	0.057	0.321	0.089	0.011	0.187	0.195	0.068

Table 9. Allometric analyses of root-shoot biomass allocation patterns. K is a dimensionless allometric coefficient calculated for each species and is the slope of the regression of percent change in root dry weight (Y) regressed on percent change in shoot dry weight (X). K represents an average partitioning trend over the experimental period and measures the relative growth rates. SE= Standard error. No values are reported for ABMA treatment L1 as all seedlings in this treatment died before harvest. *S. giganteum* is not shown since initial fresh weight could not be reliably determined.

DISCUSSION

As discussed in Chapter 1, each species' elevational range limits are constrained by physiological trade-offs between shade tolerance and drought tolerance (Smith and Huston 1989, Tilman 1988). Variations among species in their drought tolerance, shade tolerance, and temperature range are what allow so many species to coexist, forming the unique Sierra Nevada mixed conifer forest. Indeed, the fundamental importance of adaptive trade-offs was invoked by Clements in his classic papers on plant succession (Clements 1916) and plant competition (Cements et al. 1929). More recently, a number of studies have begun to link shade tolerance and drought tolerance to survival, and growth (Barton and Teeri 1993, Walters and Reich 1996, Kobe 1996, Kobe et al. 1995).

Gradients

The elevation and light treatments used in this study represent the natural environmental gradients in light and elevation found in Sierra Nevada mixed conifer forests. By planting seedlings of common genetic stock into six discrete treatments (3 elevations and 2 light classes), I was able to compare quantitatively the seedling-stage growth and survival of seven co-occurring species across the existing gradient and to investigate the consequences of adaptive trade-offs within this forest community.

Soil moisture samples taken throughout each summer growing season (Figs. 4 & 5) demonstrated no systematic soil moisture gradient among the different elevations or light levels. The elevation gradient, therefore, appears to be primarily a temperature gradient, with an average drop in temperature of 5.6 °C for every 1000 m increase in elevation (Stephenson 1988).

Light availability is treated as a discrete variable and is classed as high (GSF>0.15) or low (GSF<0.15). In reality, the irradiance values represent a continuum, with a median GSF of 0.15. Although it would be possible to perform the survival and growth analyses treating light as a continuous variable (using GSF values), this analysis assumes that the treatments were randomly selected. Sites were chosen to represent closed and open canopy areas which have naturally low and high light availability. The intent was to compare growth and survival within and among species in these contrasting light environments and to do this I used a fixed-effects model with both elevation and light as discrete variables.

The range of GSF values at the 1600 and 2200 m sites is greater than at 1900 m (see Figure 2). There is a bigger difference in understory light availability between light treatments at the low and high elevation sites than at the middle elevation site. Consequently, I expected the effects of light on growth and survival to be more pronounced in the low and high elevation treatments.

Survival

It is well recognized that nursery practices, including growth environment (nursery bed or container), seedling size and age affect seedling survival rate and performance after out-planting. The effects may differ among species. In this study, I assumed that under optimal conditions, all seedlings will exhibit similar survival rates. I plan to evaluate this assumption in future analyses by using published literature on the survival after out-planting of the species used in this study, as well as data from the United States Forest Service nursery at Placerville, California.

For most species, survival was much lower at the low elevation site than in the medium or high elevation sites. While overall soil water potentials were not significantly lower at the low elevation, the average soil water potential was lower in the low elevation plots than in the middle or high elevation plots at the time of planting (May 1993). This site (1600 m) was the warmest and the seedlings planted here probably experienced the highest evaporative demand. Although not a soil moisture availability gradient, elevation is functionally a drought gradient due to increased evaporative demand at lower elevation. Survival patterns among the species in the sun plots at 1600 m are an indication of their drought tolerance. Based on my results, I have ranked the study species from most drought tolerant to least - *P. jeffreyi>C. decurrens>P. ponderosa>S. giganteum>A. concolor=P. lambertiana>A. magnifica* var. *shastensis*. The Spearman rank correlation (SAS Institute 1989) of this drought tolerance ordering is highly correlated (P<0.01) to that of Minore (1979) and

Lassoie et al. (1985). *S. giganteum* was left out of the comparison since it was not ranked in Minore (1979) or Lassoie et al. (1985).

Despite the much reduced survival at 1600 m, the positive effect of light is reflected in significantly greater survival in the sun plots than in the shade plots at this elevation. The low elevation site is the warmest and seedlings grown in treatments L1 and L2 experienced greater evaporative demand -- effectively the most "drought stress" of the three elevations. Still, within this elevation, there is greater survival in the sun plots than in the shade plots. This illustrates the drought tolerance-shade tolerance trade-off. Species cannot be both highly drought tolerant and highly shade tolerant in this environment. The "double-whammy" of hot (dry) and shade did not favor any species. (*P. jeffreyi* did have high survival in all treatments since the seedlings were somewhat larger and more robust than the other species at the time of planting. Even so, survival in this species was lower at 1600 m than at 1900 m.)

Shade-intolerance leading to death is illustrated in the progression of increasing survival in shade plots from low to high to medium elevation - exactly the ranking of average GSF in shade - 1600<2200<1900 (Figure 2). Only *A. concolor* and *P. ponderosa* deviated from this pattern. In both species, survival was lower in the shade plots at 1600 m than at 1900 m, but in *P. ponderosa* survival was lowest at 2200 m, which is significantly above its current elevational range.

The effect of elevation on survival is much less pronounced in the sun plots. While survival in the extreme transpirational environment of 1600 m was lower than at 1900 and 2200 m in the less drought tolerant species (*A. concolor*, *A. magnifica* var. *shastensis*, *P. lambertiana*, and *S. giganteum*), the other species differed much less among elevations, with uniformly high survivorship in the most drought-adapted species of *C. decurrens*, *P. jeffreyi*, and *P. ponderosa*.

These results indicate that seedling survival is an important component in forest dynamics and is highly sensitive to both elevation and light availability. Studies of forest dynamics, including studies of response to global climate change, often focus on tree growth (Shugart 1984, Bazzaz 1990), minimizing the importance of survivorship in community dynamics. Kobe (1996) found survival to be of key importance in a study of eastern deciduous forest saplings. In the same study, Kobe, et al. (1995) found light availability to be a key factor in predicting species success and, in this forest which did not have a drought gradient, he found the important adaptive trade-off to be low light survivorship vs. high light growth. Very little quantitative seedling survivorship information is known from the Sierra Nevada. This is the first comparative field study of seedling survival to be performed on these seven conifer species.

Growth

Seedling growth responded more strongly to light availability than to elevation. In most species, height growth was greater in the sun than in the shade plots at 1600 m and 2200 m. Height growth could not be differentiated between sun and shade plots at 1900 m, probably because these plots had less difference in GSF. This mirrors the survival results and points out the importance of light availability to seedling success. If an individual seedling is able to survive, it is more likely to grow faster in a higher light environment, regardless of its shade tolerance.

Diameter growth increments were small and, therefore, the meaurements were not as sensitive to the experimental treatments. Nonetheless, when there was a significant difference in growth between light levels, greater diameter growth occurred in shade-grown plants. Perhaps shade-grown seedlings, lacking sufficient light to stimulate height growth, allocate their photosynthetic resources to diameter growth, building a more robust seedling that will be more likely to survive in low-light conditions.

Patterns of biomass growth in response to light and elevation were similar to those observed for height growth -- greater growth in the sun plots at low and high elevations, where the light availability was highest and most widely separated in GSF from the shade plots. The actual biomass changes were largely negative, due to root turnover and loss of above-ground biomass. The extremely dry summer conditions surely prohibited sufficient root regeneration to replace root mass lost after planting.

Previous studies have shown that resource competition and stressful environments often increase root growth. Allometric analysis showed that this did not occur in most species during this experiment. Perhaps these plants had neither the time nor the available soil moisture resources to fortify their below-ground biomass as expected. Only in *P. ponderosa* was there a treatment effect, resulting in relatively less root biomass growth in treatments L1 and H1. This is probably due to one or both of the following: *P. ponderosa* is simply a very shade-intolerant species and was unable to regenerate lost root biomass in the treatments with the lowest light availability. Alternatively, *P. ponderosa* produced relatively more root mass per shoot mass in the high light treatments. This is expected in plants grown in high light and low soil moisture which need the root surface area to absorb enough water to maintain function at high irradiance. In all other species, biomass allocation patterns were not affected by the elevation or light treatments.

Tolerance & Trade-offs

If they survived, seedlings in high light grew significantly more than seedlings in low light. Shade tolerance, defined as the capacity to survive at low irradiance (Shirley 1943), is an important characteristic in which the study species vary with elevation. Table 10 shows the shade tolerance rankings at each elevation as well as three published shade tolerance rankings for these species. Pairwise rank correlations (SAS Institute 1989) of the published shade tolerance rankings with survival rankings from the 3 elevations were not significant (P>0.15) -- in other words, no two rankings were sufficiently similar and the relative shade tolerances of the study species vary with elevation. Rank correlations of these shade tolerance rankings with published shade tolerance rankings of Burns and Honkala (1990), Minore (1979), and Baker (1949) were also not significant (P>0.10) in all cases. Two species, *A. magnifica* var. *shastensis* and *P. jeffreyi*, are consistently ranked differently in my results compared to any of the published shade tolerance rankings.

Rank	1600 m	1900 m	2200 m	B & H	Minore	Baker
1	PIJE	PIJE	ABCO, PIJE	ABCO, ABMA	ABC0	ABCO, CADE
2	CADE, PIPO	SEGI, CADE	CADE, SEGI	CADE, PILA	ABMA	ABMA, PILA, SEGI
3:	ABCO, PILA, SEGI	ABMA, PIPO	PILA	PIJE, PIPO, SEGI	PILA	PIJE, PIPO
4	ABMA	ABCO, PILA	ABMA, PIPO		CADE, SEGI*	
5					PIJE*, PIPO	

Table 10. Shade tolerance rankings from most shade tolerant (1) to least shade tolerant (5) at 3 study site elevations and from 3 published rankings; Burns and Honkala (1990), Minore (1979), and Baker (1949). (*) indicates that SEGI and PIJE were not ranked by Minore and their rankings were determined by comparison with the other two published shade tolerance rankings.

P. jeffreyi, traditionally considered to be shade-intolerant, is always ranked as highly shade tolerant in my results due to high survival in the shade at all elevations. Conversely, *A. magnifica* var. *shastensis* is consistently among the least shade-tolerant species in this experiment, although this species is traditionally considered to be quite shade tolerant. The *P. jeffreyi* seedlings were all relatively large, healthy seedlings at the time of planting, and their initial height was a significant covariate in survival. Initial height was not a significant factor in the survival of *A. magnifica* var. *shastensis*, even though the seedlings of this species were very small. Survivorship of *A. magnifica* var. *shastensis* was significantly affected only by elevation, suggesting drought tolerance was more important in survival than shade tolerance.

Just as survival in the shade is a possible definition for shade tolerance, survival in the sun can be used to represent drought tolerance. The high light environments experience greater evaporative demand making drought stress the key factor in seedling survival in the sun plots. Figure 16 shows shade tolerance (survival in the shade) versus drought tolerance (survival in the sun) at each elevation. Notice the slight shifts in tolerances and relative species arrangements among elevations. This indicates the importance of drought and shade tolerance trade-offs in determining species relative abundances along the elevational gradient studied.

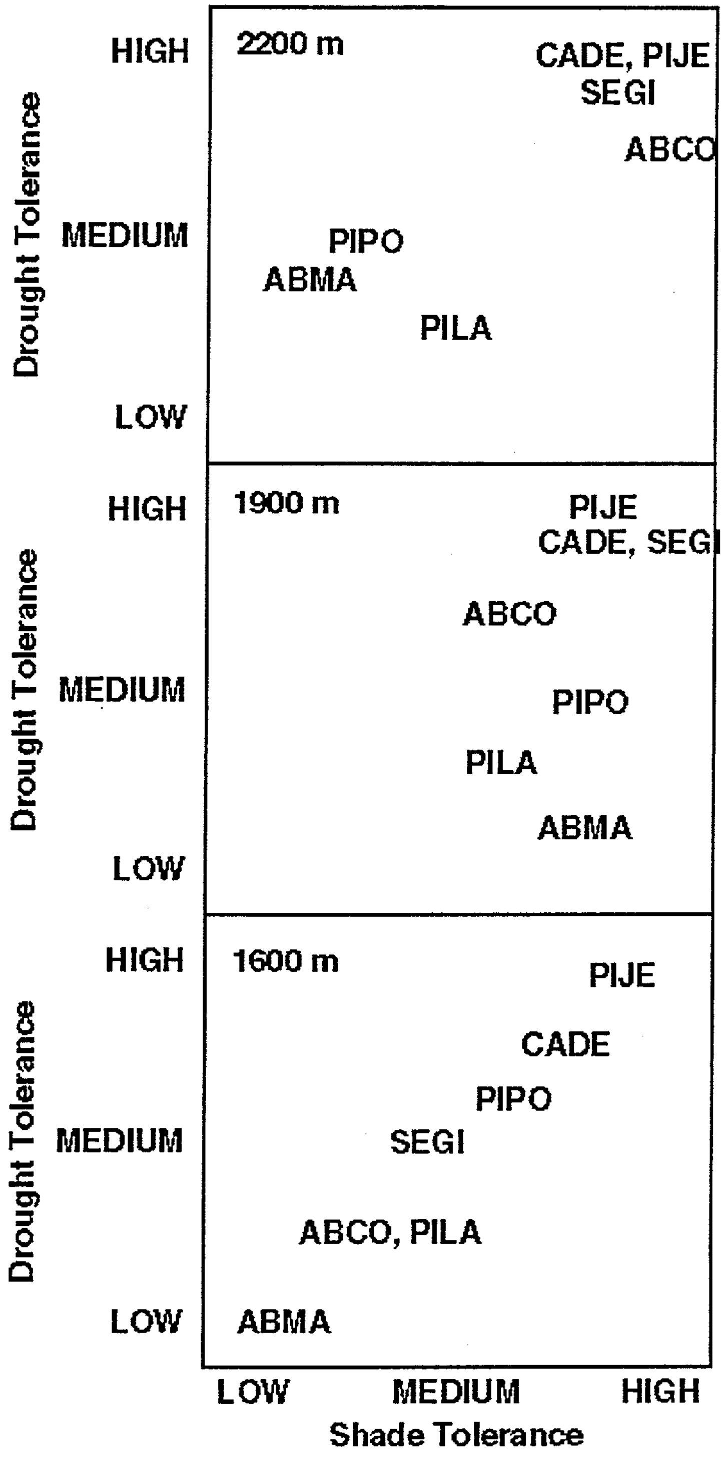

Figure 16. Shade tolerance (survival in shade) and drought tolerance (survival in sun) at 1600, 1900, and 2200 m. The low, medium, and high rankings are relative and based on survival results.

Perhaps a better way to interpret the adaptive trade-offs among species in this community is to consider the capacity of surviving seedlings for growth in their given environment. Competitive ability among these species begins with survival, but is then determined by relative growth rates among the surviving individuals. Survival-growth trade-offs at each elevation are shown in Figure 17 for shade-grown seedlings and in Figure 18 for sun. In these plots, the species are clumped or separated according to their relative competitive ability in each treatment. The patterns observed are structured by two major results already discussed: 1) greater growth rate in sun plots, and 2) lower survival at the lowest elevation.

Within each treatment, the trade-off of survival vs. capacity for growth structures the species' spatial arrangements in Figures 17 and 18. This may explain some species differences not seen in the shade tolerance comparisons alone. For example, *A. magnifica* var. *shastensis*, which was ranked, against expectation, as least shade tolerant at the highest elevation, now is revealed as having the highest percent height growth at all elevations (when it survives) - a clear example of the survival-growth trade-off. Another pattern worth noting is that the drought-adapted species *P. jeffreyi* and *C. decurrens* always group together except in the extreme treatment (L1), but *P. ponderosa*, expected to be equally drought tolerant, does not behave in the same way. *P. ponderosa* is separated from *P. jeffreyi* and *C. decurrens*

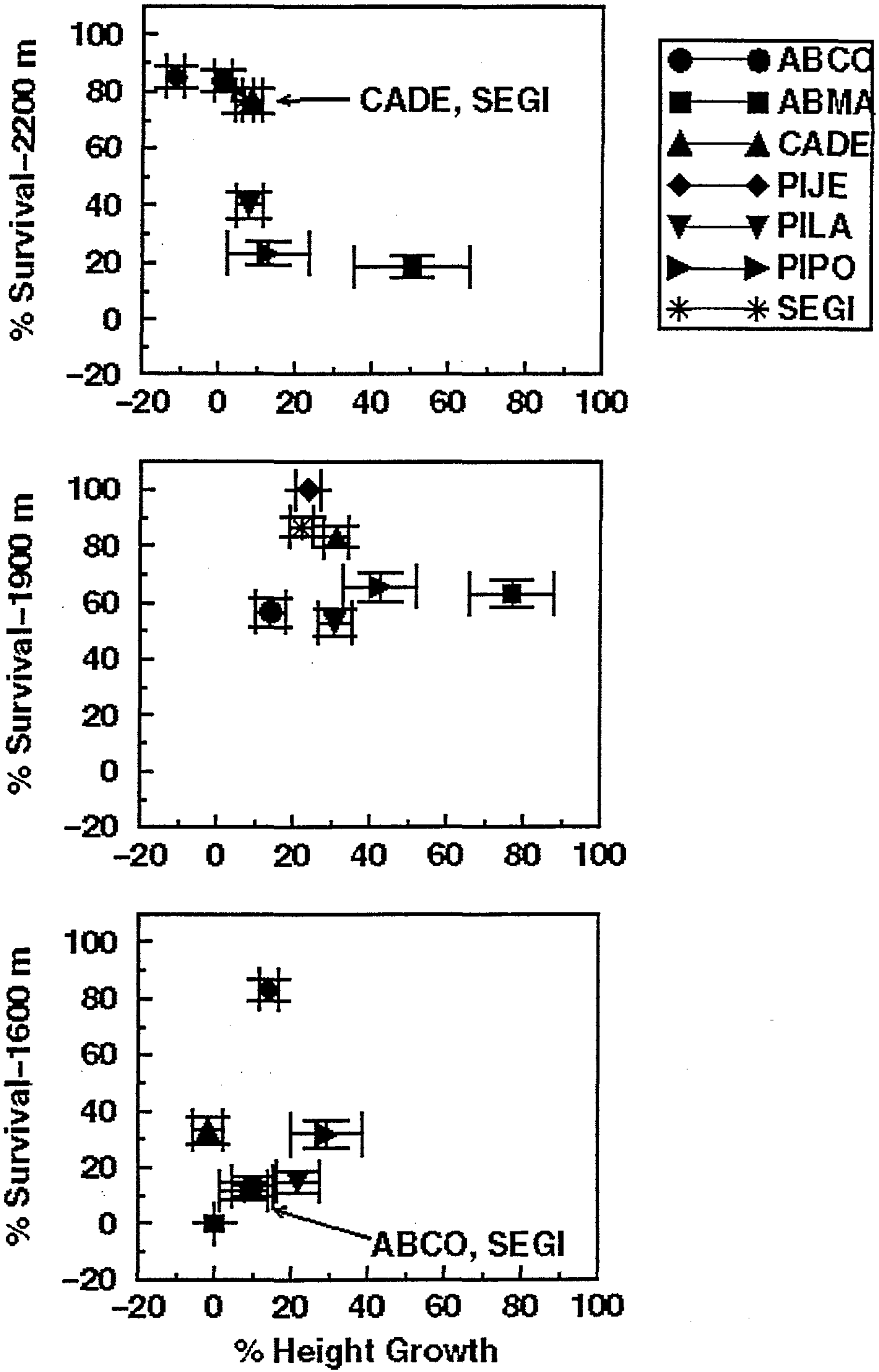

Figure 17. Survival-growth trade-off in the shade plots. Points are plotted as mean treatment response +/- one standard error.

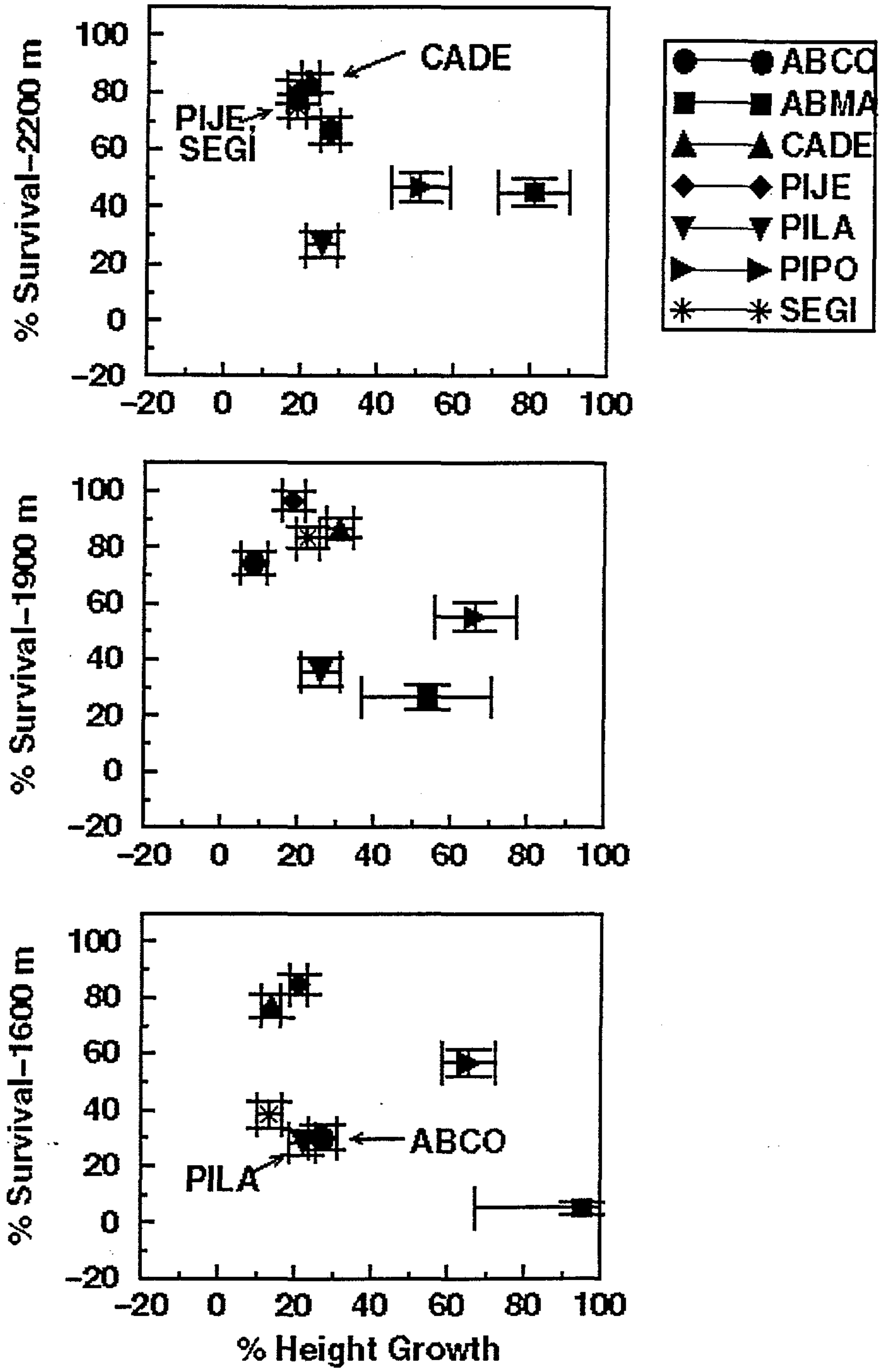

Figure 18. Survival-growth trade-off in the shade plots. Points are plotted as mean treatment response +/- one standard error.

in the sun plots by its increased growth, and in the shade by decreased survival. This indicates that *P. ponderosa* is less shade tolerant and has more capacity for rapid height growth than *C. decurrens* or *P. jeffreyi*. *P. lambertiana* seems to occupy the middle ground in most treatments, reflecting its intermediate shade and drought tolerances. It is not affected by the changing elevation in the sun plots, remaining in nearly the same position in all elevations. It is ranked lower in treatments M1 and H2 only because the other species have moved above it.

The changes in relative position with elevation may indicate future changes in community dynamics in response to global warming. As the climate warms, the effect on these species will be analogous to a lowering in elevation and the species relative abundances will likely change along the trajectory seen as elevation changes from high to low in Figures 18 and 19. For example, *A. magnifica* var. *shastensis* seedling survivorship will likely decrease, but those individuals that do survive will grow relatively well, especially in high light environments. *S. giganteum* survivorship would also be expected to decrease with climate warming, but its growth capacity is not likely to change. *C. decurrens*, on the other hand, will not be affected much in open sunny areas owing to its "weedy" characteristics of high survival and relatively rapid height growth in the sun, but it will be likely to decrease in survivorship in shade areas as the climate warms.

Few studies have addressed this elevational component of shade and drought tolerance in a field environment. In a greenhouse experiment, Barton and Teeri (1993) found that drought tolerance plays an important role in controlling the elevational positions of five pine species in the Chiricahua Mountains, with lower elevation species surviving longer and having less pronounced depression of plant water potential in an imposed greenhouse drought. Related field studies (Barton 1993) suggested that water stress controlled lower elevational limits by causing high mortality of young seedlings.

CONCLUSION

This study demonstrates the importance of survivorship and the survival-growth relationship in seeding dynamics. The seven conifer species studied respond differently to changes in elevation and light availability. Therefore, expected climate warming will not simply cause an upward elevational shift of the intact forest community, but rather changes in the relative abundances of each species as the seedling survival and growth of each of the co-occurring species change independently. Quantitative, comparative field studies such as this are necessary for understanding possible impacts of global climate change on plant communities and for successful management of forests in the coming decades.

CHAPTER 3

THE EFFECTS OF SOIL MOISTURE AND LIGHT AVAILABILITY ON SURVIVAL AND GROWTH OF SIERRAN CONIFER SEEDLINGS

INTRODUCTION

The objective of this experiment was to quantify the effects of light and soil moisture availability on predawn leaf water potential, growth and survival of Sierran conifer seedlings in a field setting. The species used are listed in Table 1. In general, relative differences in drought and shade tolerance among the study species, as shown in Figure1, were expected to govern the species' responses to the light and water treatments. As in chapter 2, this study involves multiple resource limitations in order to understand the relative shade and drought tolerance of the study species.

Experimental treatments include two levels of natural light availability (shade and sun) and four lengths of growing season, created by extending adequate soil moisture availability 0, 2, 4, or 8 week into the dry season within each light level. I hypothesized that growth and survival would be greatest in the high light treatments, as long as there was adequate soil moisture available. Therefore, as all species regenerate naturally at this elevation, I expected that the high light-long growing season treatment would have the highest growth and survival in all species.

METHODS

Field Methods

This field experiment was conducted at an elevation of 1900 m in the Giant Forest area of Sequoia National Park, California, USA. This site is located in the mixed conifer zone on the west slope of the Sierra Nevada at 36.57 degrees north latitude.

Twenty-four experimental plots were located in two natural light levels within the forest -- twelve in a high light natural canopy gap, and 12 in an adjacent closed canopy area. Irradiance was estimated for each plot by hemispherical photography of the forest canopy. Photographs were taken using a 35-mm camera and a Nikkor 8-mm hemispherical lens mounted on a tripod. All photographs were taken at the center of each transplant plot, at a height of 0.5 m above the ground, with the camera leveled and oriented with the top of the camera toward the north (necessary for accurate analysis of the daily sun path). Kodak TMAX 100 black and white print film was used and the developed negatives were analyzed using the program CANOPY (Rich 1990). The direct site factor (DIRsf: the proportion of potential direct light at a site relative to a site in the open) and the diffuse site factor (DIFsf: the proportion of potential diffuse light at a site relative to a site in the open) were calculated by CANOPY based on the intersection of the sun's track with canopy openings (Rich 1990). Each photograph was analyzed 12 times and the median threshold level was used for the final set of photo analyses. Direct and diffuse site factors were combined into a global site factor (GSF) using the equation

$$GSF = 0.8(DIRsf) + 0.2(DIFsf)$$

These weightings are based on results from a solar radiation model run for these sites based on Bonan (1989) and Nikolov and Zeller (1992). Shade plots were located in areas where the GSF was less than 0.15 and sun plots were located where GSF was greater than 0.15 (Figure 19).

Within each light level, four soil moisture treatments were established. In this Mediterranean climate, more than 90% of the annual precipitation arrives as snow in the winter, and the summer months are very dry (Table 3). Soil moisture was manipulated in this experiment by adding water to the experimental plots and extending the growing season during the treatment period.

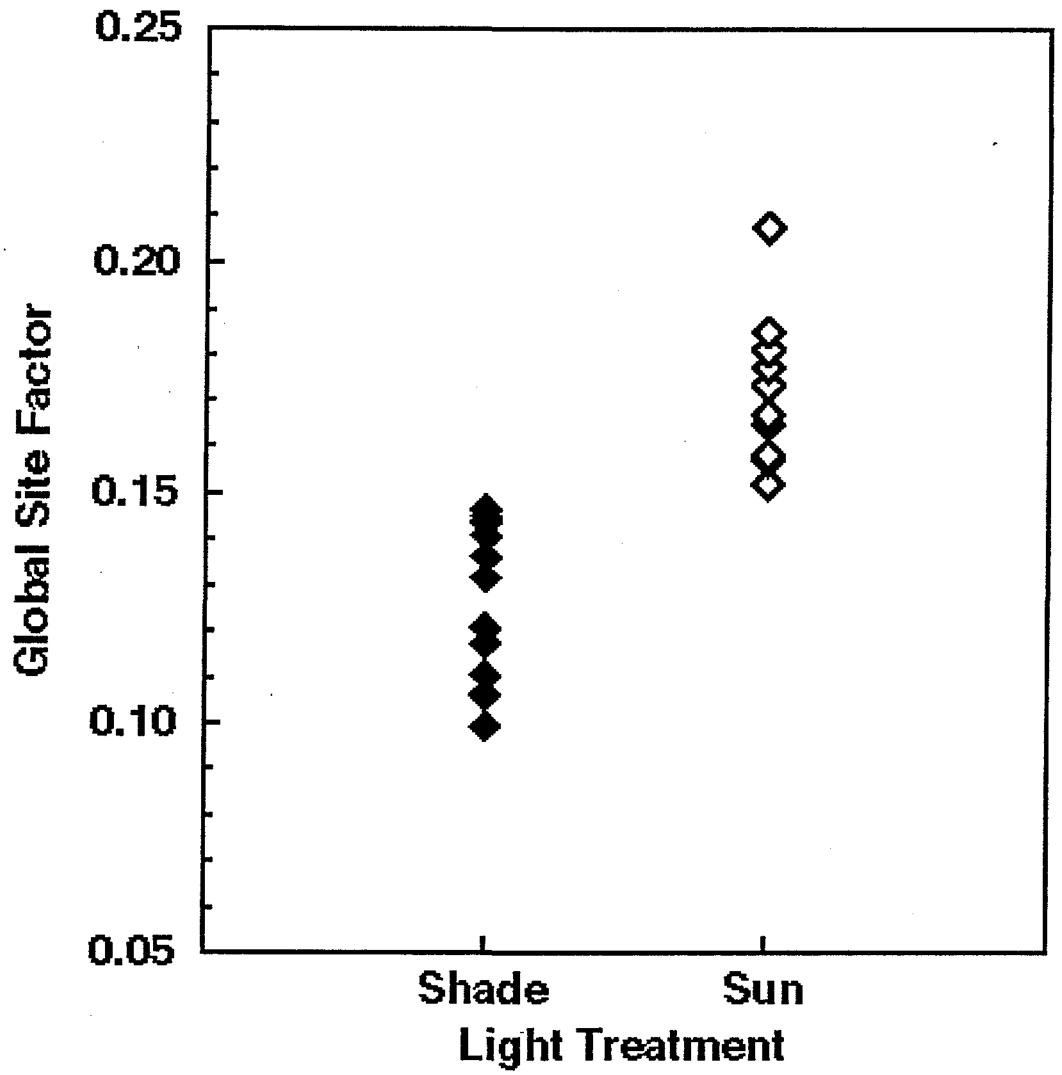

Figure 19. Light availability of transplant plots. Global site factor is an integrated light availability measure (80% direct light and 20 % diffuse) determined using hemispherical photo analysis of each plot.

I first established that the natural soil moisture availability did not differ between the sun and shade plot area. Soil samples were taken in each area and moisture of the 0-5 cm and 5-20 cm depths determined gravimetrically. Gravimetric water content values were converted to soil water potential using soil moisture release curves created for each soil depth (0-5 cm surface O horizon and 5-20 cm A horizon). Instantaneous soil water potential values were measured using a portable soil moisture probe (Soil Moisture Equipment Corp, Santa Barbara, CA, USA) throughout the duration of the water treatments.

Watering began when the natural soil water potential at 10-cm depth reached -0.05 MPa. Plots were then watered for the given experimental period and soil water potential was maintained at or above -0.05 MPa down to 20 cm depth. Of the 12 plots in each light level, 3 were not watered and served as the control plots, three were watered for 2 weeks, 3 for 4 weeks, and 3 for 8 weeks. Treatments are thus designated 0-1 (no water, shade), 0-2 (no water, sun), 2-1 (2 weeks water, shade), 2-2 (2 weeks water, sun), 4-1 (4 weeks water, shade), 4-2 (4 weeks water, sun), 8-1 (8 weeks water, shade), 8-2 (8 weeks water, sun).

Three-to-five soil samples were taken in each light treatment (9 samples total) to compare an index of the potential nitrogen mineralization (PNMI). A difference in nitrogen availability among treatments could affect seedling growth and confound the effects of soil moisture availability and light. Each sample was split in half and the first half was saturated with deionized water for 24 hours then extracted with 2.0 Molar (M) potassium chloride (KCl) solution. The second half was saturated with deionized water and incubated for 30 days at 25°C before extraction with 2M KCl solution. All samples were analyzed for ammonium and nitrate content and the difference between total nitrogen in the second sample (after incubation) and the initial amount (unincubated sample) is the potential nitrogen mineralization index (Hart et al. 1994). Analysis of variance, used to compare PNMI values among treatments ($n=9$), showed no significant difference in the PNMI values ($P>0.86$), indicating no significant differences in potential nitrogen mineralization rates among sites.

Seventy seedlings were planted in the ground in a randomized array in each plot. There were 10 individuals each of 7 species in each of 24 plots for a total of 1680 seedlings. The species used were the seven dominant canopy species making up the southern Sierra mixed conifer forest -- *Abies concolor* (white fir), *Abies magnifica* var. *shastensis* (red fir), *Calocedrus decurrens* (incense cedar), *Pinus jeffreyi* (Jeffrey pine), *Pinus lambertiana* (sugar pine), *Pinus ponderosa* (ponderosa pine), and *Sequoiadendron giganteum* (giant sequoia). See Table 1 for species common names and information on age and condition at the time of planting. Seedlings were obtained from United States Forest Service (USFS) nursery stock grown from seeds collected from USFS areas adjacent to Sequoia National Park and within the same elevation and seed zone in which the experimental plots were located. Seedlings were planted between May 13-28, 1993 and watered initially to promote establishment. Wet seedling weights were recorded prior to planting and initial height and diameter measurements were made within a week of planting, as well as at the end of the growing season each year (fall 1993 and fall 1994). Height of all non-pine seedlings was measured from the root collar (Menes and Mohammed 1995) to the top of the highest live material. Pine seedling height was measured from the root collar to the top of the terminal bud. In long-needled species such as pines, loss of needles at the top of the seedling can result in a measured decrease in total height even with apical growth, so it was preferable to track height growth by the distance between the terminal bud and the root collar. Diameter measurements were always made just above the root collar. The seedling condition (alive or dead) was also noted at these measurement times and at the beginning of the second growing season (spring 1994).

Pre-dawn leaf water potential was monitored in all species and treatments prior to the onset of watering each year and at the end of each watering treatment period. Sampling began several hours after sunset to allow tissue and soil water potentials to equalize, and was completed before sunrise. One seedling of each species was randomly selected for sampling from each replicate plot in each treatment. All pressures were measured using a Scholander pressure chamber (PMS Instrument Company, Corvallis, OR, USA). Leaf samples were cut using a sharp razor blade and inserted into the pressure chamber immediately. In order to sample the leaf water potential in these species with different leaf morphology, three sampling methods were used. For pines, a single fascicle (needle bundle) was cut at the leaf-branch interface, for incense cedar and giant sequoia a 4-cm section was cut from a branch tip, and for firs three individual needles were cut at the leaf-branch interface and inserted into the collar together.

Above- and below-ground parts of all living seedlings were harvested at the end of the second growing season (September 26-30, 1994). The harvested seedlings were refrigerated until they could be analyzed in the laboratory at Duke University. Roots and shoots were separated at the root collar, and roots were thoroughly washed, below- and above-ground portions dried at 70 °C to constant weight, and each portion weighed to the nearest 0.1 gram.

Temperature and relative humidity were monitored electronically throughout the experiment (30 minute averages during May through October and 60 minute averages during November through April) and used to calculate vapor pressure deficit (Figure 36).

Data Analysis Methods

Four responses, each a separate measure of success; survival, height, diameter, and biomass growth (total biomass as well as root and shoot growth separately), were used in this analysis. Survival data were analyzed using analysis of covariance on the proportion surviving in each plot (SAS Institute 1989) with elevation and light defined as class variables and average initial height as a covariate where

$$p' = F(\text{elevation, light, elevation*light, initial height}).$$

In this analysis, p was transformed using

$$p' = \arcsin\sqrt{p}.$$

Confidence limits (95%) were calculated for the proportions surviving using the method demonstrated in Zar (1984).

Height, diameter and biomass growth were calculated as the percent increase during the measurement period where

$$\text{\% Height Growth} = \left(\frac{\text{Final Height} - \text{Initial Height}}{\text{Initial Height}}\right) \times 100.$$

"Height" was substituted with "diameter" or "biomass" (total, root, or shoot) in the equation to calculate the percent change in these growth parameters. Percent growth was used so that all growth measures would be comparable to each other and not confounded by initial size.

Initial dry biomass of each seedling was estimated from the initial wet weight and a species-specific regression calculated from a random subsample of 10 seedlings of each species that were weighed wet, roots washed, dried at 70 °C to constant weight and then weighed dry. Linear regression parameters for the wet to dry weight relationships are shown in Table 2. Estimation of initial biomass of *S. giganteum* was not possible since these seedlings were container grown and were planted into the ground along with the potting mixture. Therefore the initial fresh weight could not be reliably determined since the variability in the weight of the potting mixture (82.4 +/- 9.5 g) outweighed the average fresh weight of the seedlings (13.2 +/- 5.4 g).

For each of the growth parameters, it was first determined whether replicate plots could be combined by using analysis of covariance with the initial height, diameter, or biomass as the covariate (Proc GLM; SAS Institute 1989) to identify significant differences in the slope of the growth response followed by analysis of variance to test for differences in growth response among plots within the same treatment group. Analyses showed similar responses within treatments, so replicate plots were combined for all further analyses. Biomass and height growth analyses were conducted for the entire experimental period (spring 1993 to fall 1994). Diameter growth analyses were conducted on the annual increment between fall 1993 and fall 1994 since there was significant shrinkage in stem diameter during the first summer after planting. This is a common response in seedling outplanting caused by loss of stem capacitance in adapting to the dry field environment.

Using combined replicate plots, main effects for elevation and light plus their interaction were tested using analysis of covariance where

$$\%\ \text{Growth} = F\ (\text{Light, Elevation, Light*Elevation interaction})$$

The initial measure (height, diameter, or dry biomass) was used as the covariate. Due to significant effect of the covariate in most species, comparison of elevation and light effects, based on adjusted means standard errors, was performed using the LSMEANS statement in the Proc GLM procedure (SAS Institute 1989).

Allometric analysis of biomass allocation patterns was performed using analysis of covariance as above where

% Root Growth = F (Treatment, % Shoot Growth, Treatment * % Shoot Growth)

and percent shoot growth is the covariate. Linear regression was used to determine the slope of the regression for each treatment and species using

% Root Growth = % Shoot Growth

The slope of this regression is the dimensionless allometric coefficient 'K' (Bowler and Press 1993). 'K' represents the average biomass partitioning trend over the experimental period and measures the relative balance in root and shoot relative growth rates. If treatment slopes are parallel, significant differences between treatments (different intercepts) indicate differences in growth rate among treatments.

Leaf Water Potential

Predawn leaf water potential measurements were analyzed using analysis of variance with main effects of light availability and the "dryness" of the treatment plot, or the number of weeks since it was last watered in the current year. Analyses were performed on pooled data from 1993 and 1994, as well as on each year's data individually.

RESULTS

Soil Moisture

Soil water potential values for the control plots in both shade and sun treatments are shown in figure 20. Values were estimated from water content-water potential curves constructed for each soil depth. The only significant difference in soil water potential between light treatments occurred in July 1994 in the surface (0-5 cm depth) soil samples. In this case, the soil water potential was much lower (all <-1.5 MPa) in the sun plots than in the shade plots.

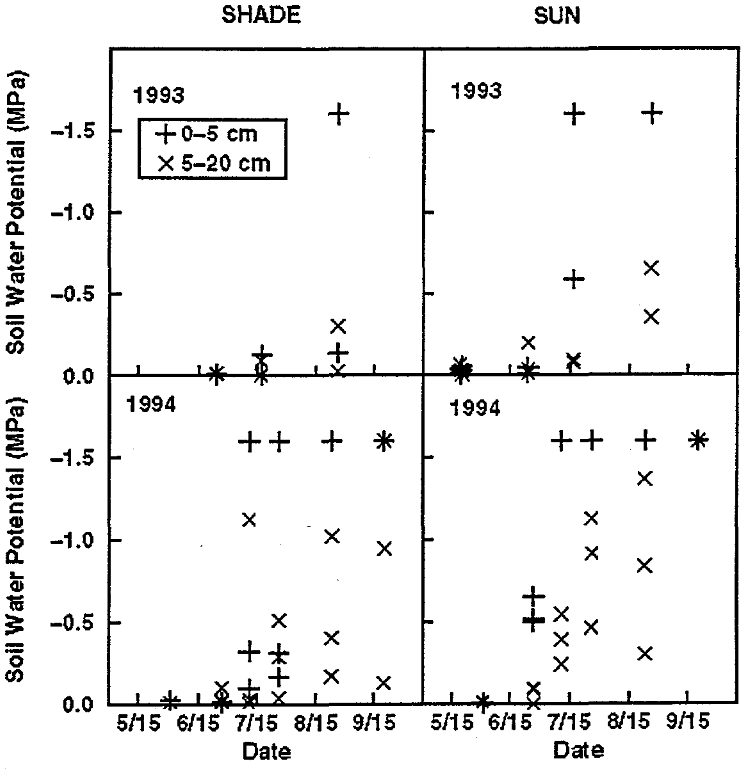

Figure 20. Soil water potential measurements.

While there was virtually no variation in natural soil water potential between light treatments, there were notable variations in soil moisture with depth and time. The deep samples in all treatments maintained average soil water potentials above -1.5 MPa throughout the growing season in both 1993 and 1994. The surface samples, however, became uniformly dry beyond the measured limit of -1.5 MPa in a predictable pattern. In 1993, this threshold was reached in some surface samples in July in the sun plots and in August in the shade plots. In 1994, surface samples were all less than -1.5 MPa by the July sampling dates in both light treatments. The drier surface soil conditions in 1994 are probably a consequence of the lower winter precipitation in 1994 relative to 1993 (Table 3). Daily precipitation measurements made near the 1900 m site were obtained from the National Biological Service research office (personal communication).

Light

Analysis of variance of hemispherical photo data showed significant differences ($P<0.0001$) between sun and shade plots in direct light received (DIRsf) but not in diffuse, or indirect light (DIFsf). Global Site Factor (GSF), calculated as

$$\mathrm{GSF} = 0.8(\mathrm{DIRsf}) + 0.2(\mathrm{DIFsf}),$$

was, of course, also significantly greater in the sun plots.

Survival

The proportion surviving as well as the upper and lower 95% confidence intervals at each census period are listed in Table 11. Patterns of survival for each species are shown in Figures 21-26. Figures 21-24 demonstrate the effect of light on survival in each soil moisture treatment, while Figures 25 and 26 more clearly show the effect of elevation on survival within each light level. Analysis of covariance results are reported in Table 12. The effect of the covariate (initial height) on survival was only significant in *P. lambertiana.* There is a moderate to low degree of prediction ($R^2<0.45$) with this model for all species except *P. lambertiana* ($R^2=0.6810$). Significant interaction between water and light did not occur in any species. Light is a significant factor in overall survival of *A. magnifica* var. *shastensis* and *P. ponderosa* ($P<0.05$). The water treatments affected overall survival only in *P. lambertiana.*

The effect of light within each soil moisture treatment on the survival of each species is displayed in Figures 21-24. In the control (0 weeks water) and 8-week water treatment plots there were no significant differences in survival between light levels at the time of harvest. There was a notable decrease in survival in the control treatment shade plots in *A. magnifica*, but the difference is not significant as shown with the 95 % confidence intervals. This effect of light on survival in *A. magnifica*

Species	Light	F93	95% CI	S94	95% CI	F94	95% CI
ABCO	Shade	0.933	0.992	0.767	0.901	0.567	0.745
			0.779		0.578		0.881
	Sun	1.00	1.00	0.871	0.964	0.742	0.881
			0.888		0.792		0.554
ABMA	Shade	1.00	1.00	0.733	0.877	0.633	0.801
			0.884		0.541		0.439
	Sun	0.900	0.979	0.467	0.657	0.267	0.459
			0.735		0.283		0.123
CADE	Shade	0.900	0.979	0.833	0.944	0.833	0.944
			0.735		0.653		0.653
	Sun	0.933	0.992	0.867	0.962	0.867	0.962
			0.779		0.693		0.693
PIJE	Shade	1.00	1.00	1.00	1.00	1.00	1.00
			0.881		0.881		0.881
	Sun	1.00	1.00	1.00	1.00	0.966	0.999
			0.881		0.881		0.822
PILA	Shade	0.875	0.965	0.656	0.814	0.531	0.709
			0.710		0.468		0.347
	Sun	0.903	0.980	0.516	0.698	0.355	0.546
			0.742		0.331		0.192
PIPO	Shade	0.897	0.978	0.724	0.873	0.656	0.821
			0.726		0.528		0.457
	Sun	0.862	0.961	0.552	0.736	0.552	0.736
			0.684		0.357		0.357
SEGI	Shade	1.00	1.00	0.900	0.979	0.867	0.962
			0.884		0.735		0.693
	Sun	0.967	0.999	0.900	0.979	0.833	0.944
			0.828		0.735		0.653

Table 11 (a). Survival proportions and upper and lower 95% confidence limits for control (0 weeks) water treatment.

Species	Light	F93	95% CI	S94	95% CI	F94	95% CI
ABCO	Shade	0.867	0.962	0.633	0.801	0.533	0.717
			0.693		0.439		0.343
	Sun	0.967	0.999	0.800	0.923	0.600	0.773
			0.828		0.614		0.406
ABMA	Shade	0.933	0.992	0.767	0.901	0.667	0.827
			0.779		0.577		0.472
	Sun	0.833	0.944	0.267	0.459	0.167	0.347
			0.653		0.123		0.056
CADE	Shade	0.867	0.962	0.833	0.944	0.833	0.944
			0.693		0.653		0.653
	Sun	0.933	0.992	0.933	0.992	0.933	0.992
			0.779		0.779		0.779
PIJE	Shade	1.00	1.00	1.00	1.00	1.00	1.00
			0.881		0.881		0.881
	Sun	1.00	1.00	1.00	1.00	1.00	1.00
			0.884		0.884		0.884
PILA	Shade	0.857	0.952	0.629	0.785	0.543	0.712
			0.697		0.449		0.366
	Sun	0.900	0.979	0.733	0.877	0.633	0.801
			0.735		0.541		0.439
PIPO	Shade	0.923	0.991	0.846	0.956	0.692	0.857
			0.749		0.651		0.482
	Sun	0.967	0.999	0.667	0.827	0.533	0.717
			0.828		0.472		0.343
SEGI	Shade	1.00	1.00	1.00	1.00	1.00	1.00
			0.884		0.884		0.884
	Sun	0.967	0.999	0.900	0.979	0.900	0.979
			0.828		0.735		0.735

Table 11 (b). Survival proportions and upper and lower 95% confidence limits for 2 week water treatments.

Species	Light	F93	95% CI	S94	95% CI	F94	95% CI
ABCO	Shade	0.953	0.999	0.905	0.988	0.806	0.946
			0.762		0.696		0.581
	Sun	0.975	0.999	0.700	0.834	0.625	0.773
			0.868		0.535		0.458
ABMA	Shade	0.950	0.999	0.900	0.988	0.850	0.968
			0.751		0.683		0.621
	Sun	0.850	0.943	0.300	0.465	0.275	0.439
			0.702		0.166		0.146
CADE	Shade	1.00	1.00	1.00	1.00	0.950	0.999
			0.832		0.832		0.752
	Sun	0.800	0.909	0.800	0.909	0.800	0.909
			0.644		0.644		0.644
PIJE	Shade	1.00	1.00	1.00	1.00	1.00	1.00
			0.832		0.832		0.832
	Sun	1.00	1.00	1.00	1.00	0.975	0.999
			0.912		0.912		0.868
PILA	Shade	0.700	0.881	0.400	0.639	0.300	0.543
			0.457		0.191		0.119
	Sun	0.950	0.994	0.650	0.794	0.525	0.685
			0.831		0.483		0.361
PIPO	Shade	1.00	1.00	1.00	1.00	0.895	0.987
			0.824		0.824		0.669
	Sun	0.900	0.972	0.575	0.730	0.400	0.567
			0.763		0.409		0.249
SEGI	Shade	1.00	1.00	1.00	1.00	1.00	1.00
			0.832		0.832		0.832
	Sun	0.925	0.984	0.725	0.854	0.725	0.854
			0.796		0.561		0.561

Table 11 (c). Survival proportions and 95% confidence limits for 4 weeks water treatments.

Species	Light	F93	95% CI	S94	95% CI	F94	95% CI
ABCO	Shade	0.975	0.999	0.825	0.927	0.775	0.892
			0.868		0.672		0.615
	Sun	0.950	0.999	0.950	0.999	0.850	0.968
			0.751		0.751		0.621
ABMA	Shade	0.952	0.994	0.690	0.824	0.619	0.764
			0.838		0.529		0.456
	Sun	0.950	0.999	0.700	0.881	0.450	0.685
			0.751		0.457		0.231
CADE	Shade	1.00	1.00	0.950	0.994	0.950	0.994
			0.912		0.831		0.831
	Sun	1.00	1.00	0.950	0.999	0.950	0.999
			0.832		0.751		0.751
PIJE	Shade	1.00	1.00	1.00	1.00	0.974	0.999
			0.910		0.910		0.865
	Sun	1.00	1.00	1.00	1.00	1.00	1.00
			0.832		0.832		0.832
PILA	Shade	0.900	0.972	0.650	0.794	0.500	0.662
			0.763		0.483		0.338
	Sun	0.952	0.999	0.714	0.887	0.619	0.819
			0.762		0.478		0.384
PIPO	Shade	0.875	0.958	0.725	0.854	0.700	0.834
			0.732		0.561		0.535
	Sun	1.00	1.00	0.684	0.874	0.474	0.711
			0.824		0.435		0.244
SEGI	Shade	1.00	1.00	0.949	0.994	0.949	0.994
			0.910		0.827		0.827
	Sun	1.00	1.00	1.00	1.00	1.00	1.00
			0.832		0.832		0.832

Table 11 (d). Survival proportions and 95% confidence limits for 8 week water treatments.

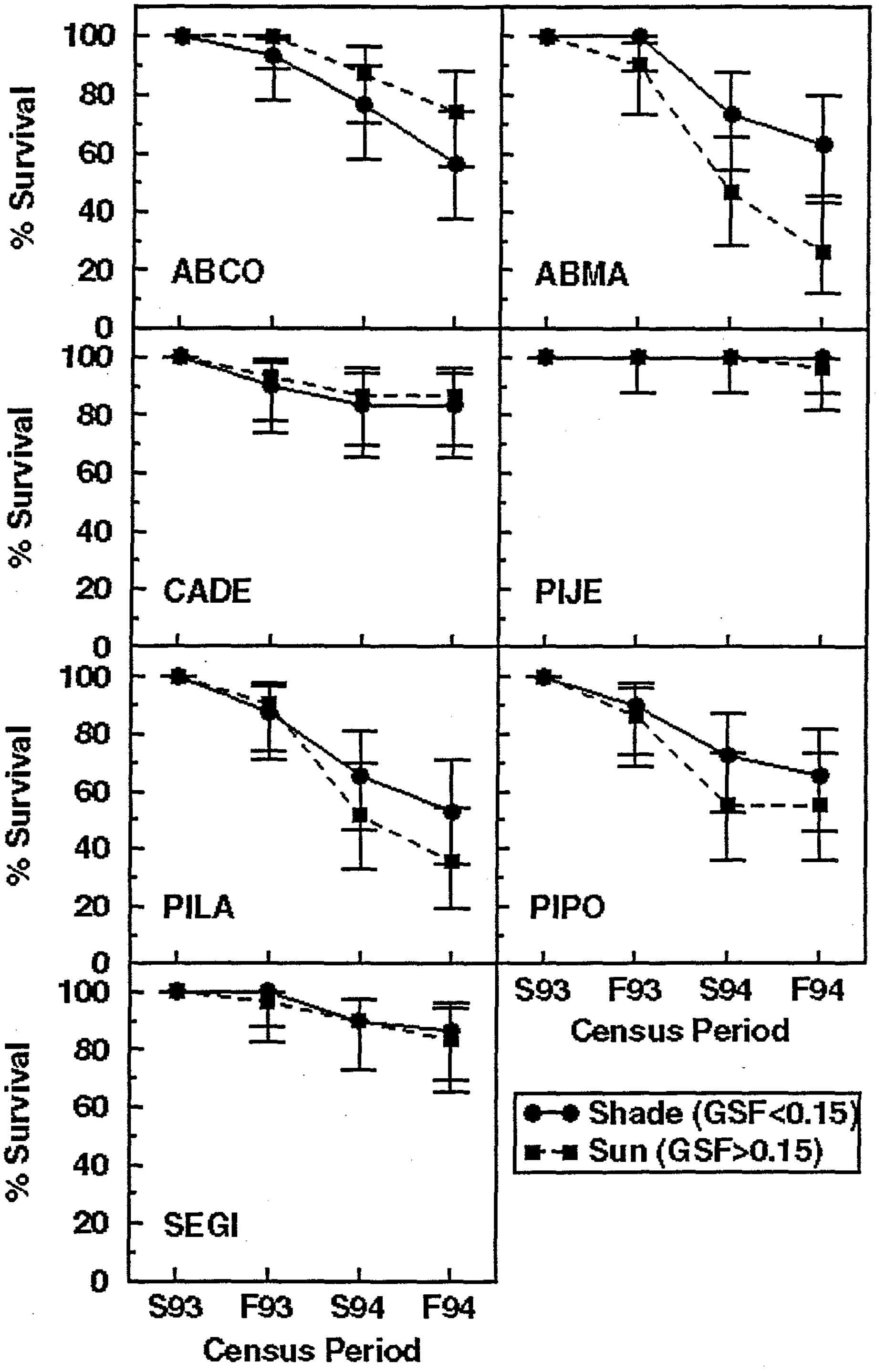

Figure 21. Survival proportions and 95% confidence limits for control (0 weeks water) treatments.

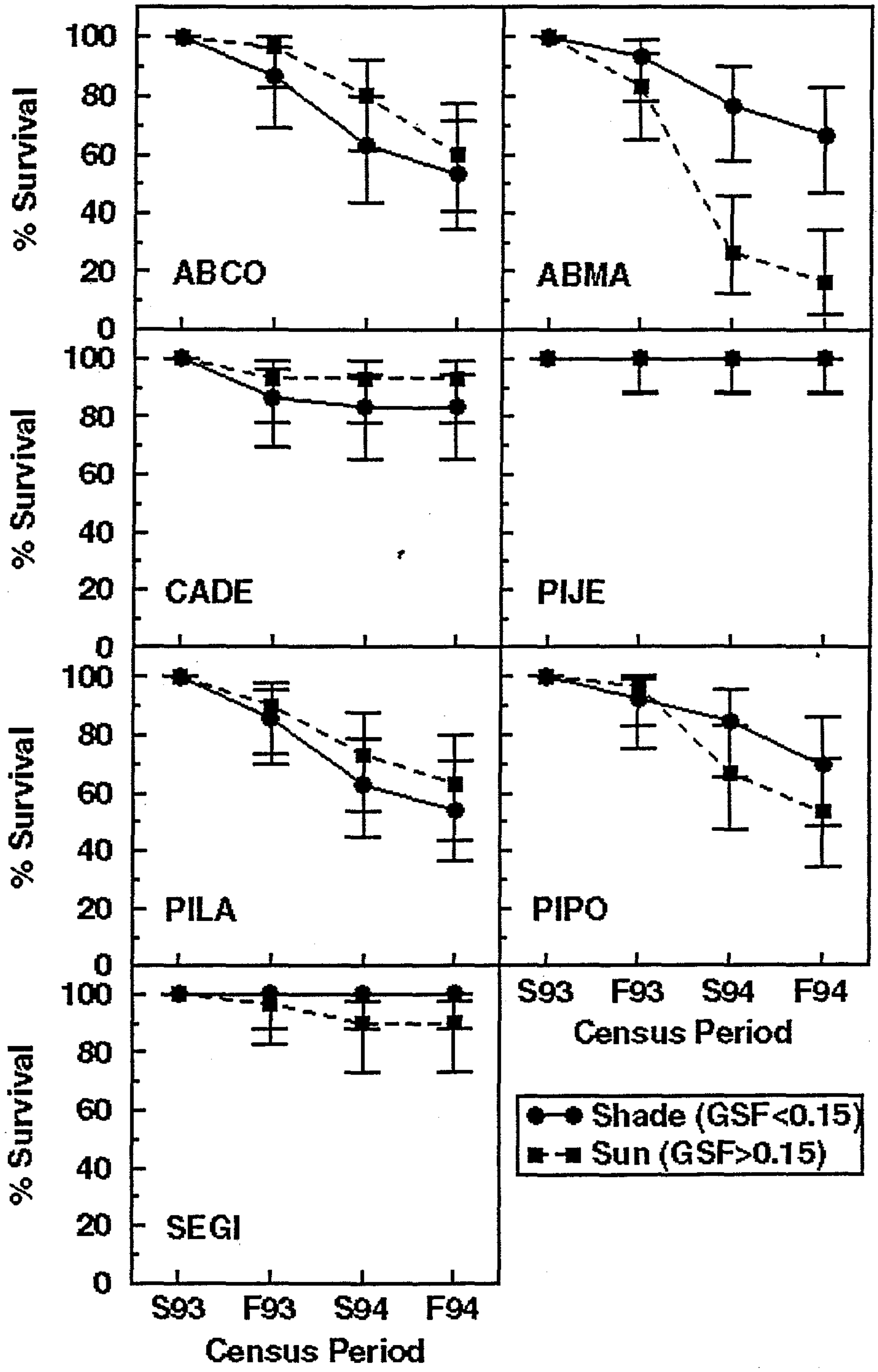

Figure 22. Survival proportions and 95% confidence limits for 2 week water treatments.

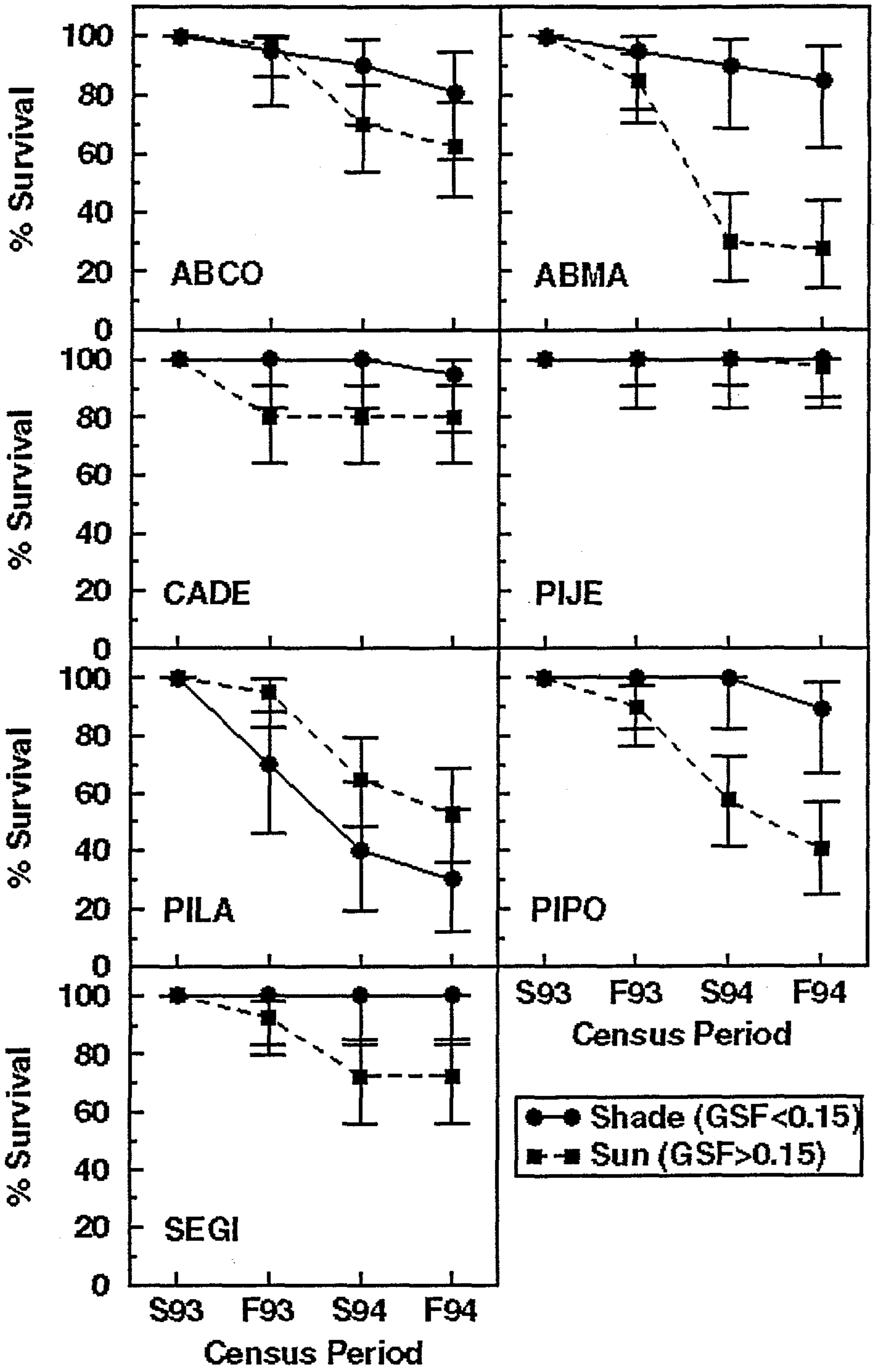

Figure 23. Survival proportions and 95% confidence limits for 4 week water treatments.

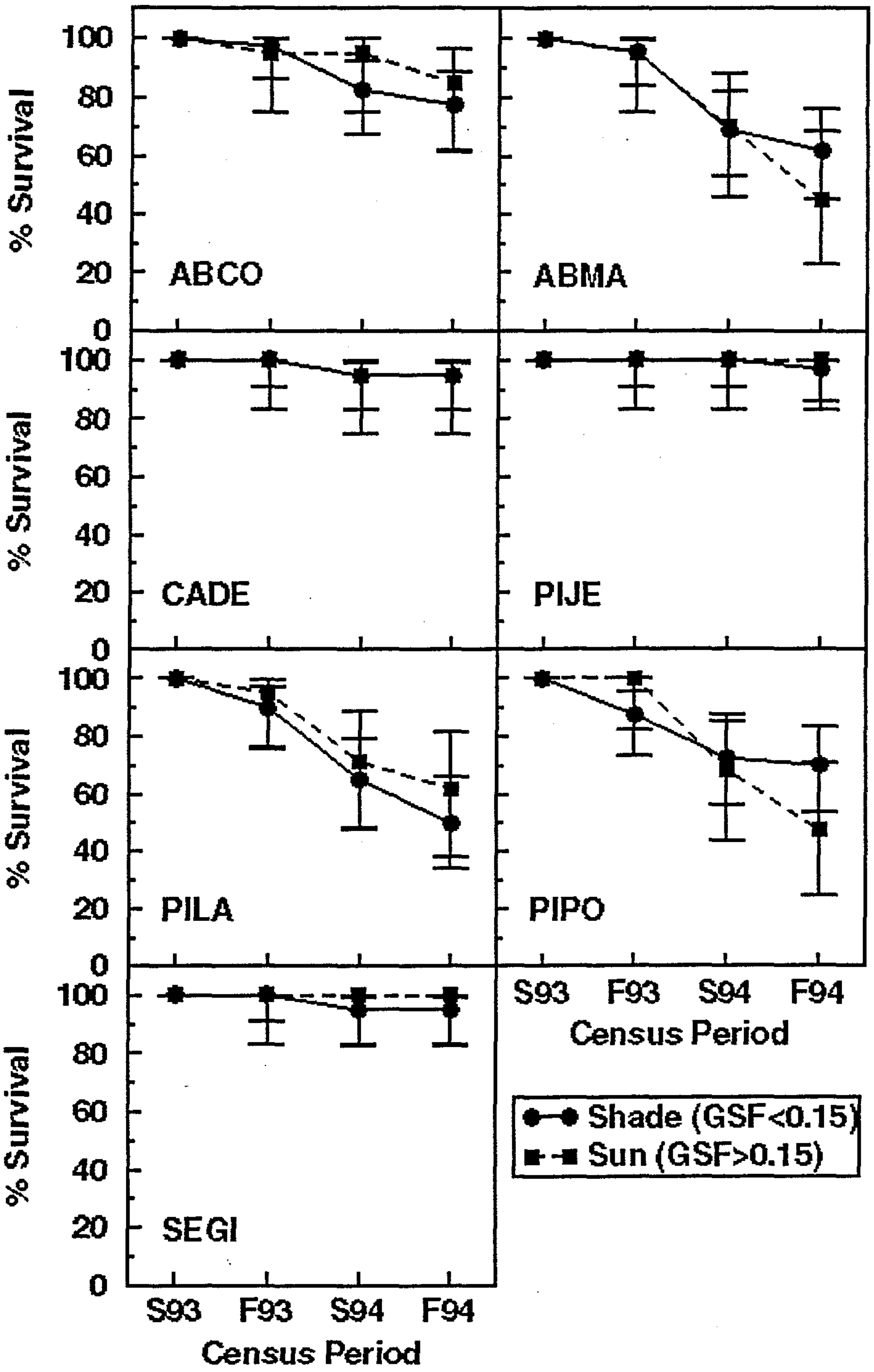

Figure 24. Survival proportions and 95% confidence limits for 8 week water treatments.

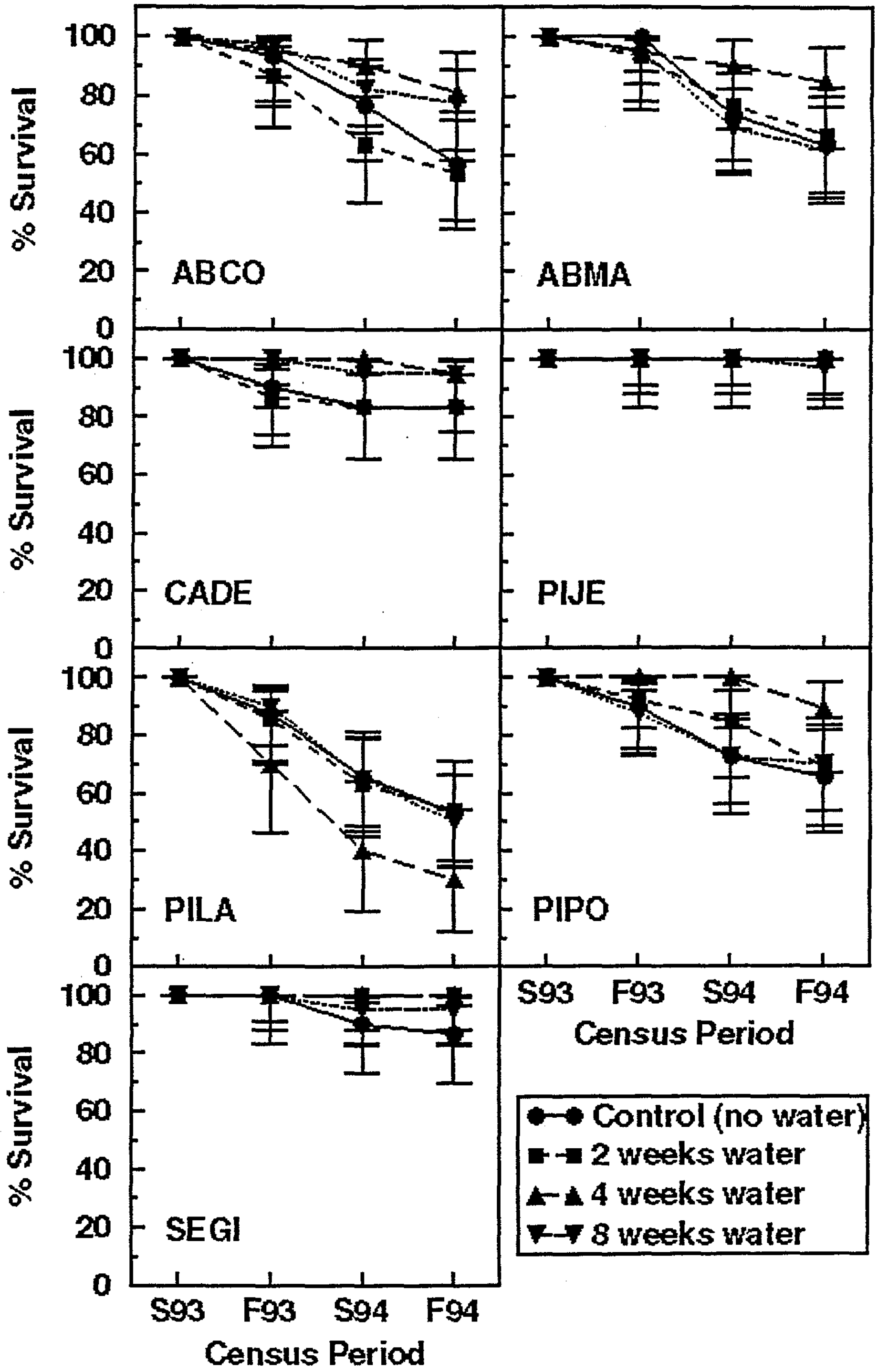

Figure 25. Survival proportions and 95% confidence limits for shade treatments.

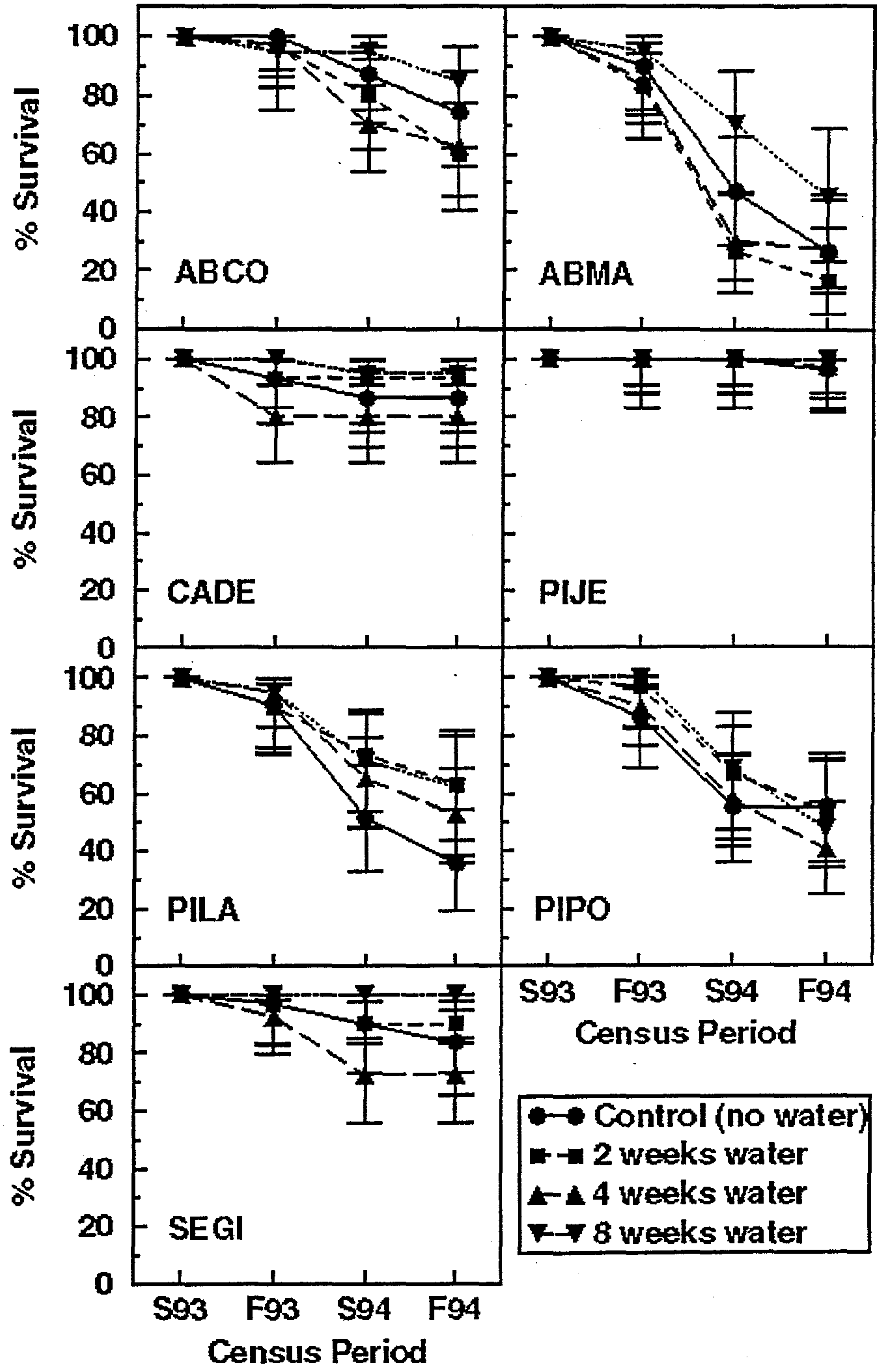

Figure 26. Survival proportions and 95% confidence limits for sun treatments.

Species	Water	Light	Water*Light	Init. Height	R^2
ABCO	0.4349	0.6378	0.6927	0.5690	0.23014
ABMA	0.8772	0.0339	0.6156	0.5666	0.4443
CADE	0.7671	0.9793	0.7524	0.6803	0.1501
PIJE	0.7158	0.7152	0.5381	0.2593	0.2439
PILA	0.0410	0.0394	0.3959	0.0004	0.6810
PIPO	0.9308	0.0261	0.4520	0.3576	0.3832
SEGI	0.3755	0.2141	0.2610	0.7272	0.4313

Table 12. Analysis of covariance results (p-values) for proportions surviving. Proportions were transformed using [p' = arcsin (square root of proportions surviving)] prior to performing the analysis of variance.

does become highly significant in the two- and four-week water treatments (Figures 22 and 23). *P. ponderosa* also had significantly lower survival in the sun plots in the 4-week water treatment, as did *S. giganteum*, although the 95% confidence intervals overlapped slightly in this species. The effects of light on survival in these three species *A. magnifica* var. *shastensis*, *P. ponderosa,* and *S. giganteum*, are the only significant main effects seen in the analysis of variance of the survival proportions (table 12). Water (soil moisture) was not a significant factor in the survival of any species, as shown in Table 12 and Figures 25 and 26.

Growth

Plot effects within treatments were compared to determine whether replicate plots could be combined. In the height growth results, this test failed for *S. giganteum*. Further investigation showed the effect of the covariate (initial height) on height growth was different for treatments 0-2 and 4-1 than for all other treatments, so these treatments were removed. The resulting analyses indicated that replicate plots could be combined in all other treatments. Similarly, treatment 4-1 was removed from the analysis of root growth in *P. jeffreyi*.

Analysis of covariance results are given in Table 13. Results of LSMEANS analysis for percent change in height, diameter, total biomass, root mass and shoot mass are reported in Table 14 and plotted in Figures 27-31.

	n	Species	Water	Light	Water*Lt	Covariate
Height	164	ABCO	0.0892	0.0175	0.1359	0.0002
	115	ABMA	0.0398	0.2148	0.0079	0.0001
	212	CADE	0.2578	0.0820	0.5395	0.0001
	233	PIJE	0.0246	0.1822	0.6771	0.0001
	124	PILA	0.9595	0.1552	0.7398	0.0001
	133	PIPO	0.2201	0.1884	0.0658	0.0001
	169	SEGI*	0.0731	0.4527	0.1641	0.0001
Diameter	164	ABCO	0.0187	0.1014	0.0009	0.0001
	115	ABMA	0.0639	0.1857	0.9025	0.0023
	212	CADE	0.4404	0.0001	0.5366	0.0001
	233	PIJE	0.8286	0.5382	0.9151	0.2521
	126	PILA	0.2185	0.1565	0.0643	0.0001
	139	PIPO	0.1415	0.0006	0.3586	0.0088
	214	SEGI	0.0004	0.7849	0.0184	0.0024

Table 13 (a). Analysis of covariance results (p-values) for height and diameter growth parameters. * Height, SEGI - Treatments 0-2 and 4-1 removed for this analysis.

	n	Species	Water	Light	Water*Lt	Covariate
Mass	164	ABCO	0.0005	0.0018	0.0221	0.1272
	114	ABMA	0.0271	0.0007	0.8816	0.5455
	211	CADE	0.5965	0.0001	0.0057	0.0001
	233	PIJE	0.3719	0.0001	0.0336	0.0001
	126	PILA	0.5518	0.0014	0.2139	0.183
	138	PIPO	0.0052	0.0001	0.0008	0.544
Root	164	ABCO	0.0002	0.2850	0.0350	0.0135
	114	ABMA	0.1509	0.1144	0.6445	0.0409
	211	CADE	0.8140	0.0001	0.0009	0.0009
	213	PIJE*	0.2447	0.0010	0.2189	0.0001
	126	PILA	0.5306	0.0380	0.6372	0.0511
	138	PIPO	0.1521	0.0156	0.0833	0.0566
Shoot	164	ABCO	0.0045	0.0003	0.0398	0.4485
	114	ABMA	0.0308	0.0001	0.9671	0.1365
	212	CADE	0.3649	0.0001	0.0176	0.0001
	233	PIJE	0.1279	0.0001	0.0654	0.2005
	126	PILA	0.6792	0.0014	0.1698	0.3876
	138	PIPO	0.0030	0.0001	0.0002	0.9585

Table 13 (b). Analysis of covariance results (p-values) for mass growth parameters - total mass, root mass, and shoot mass. * Root, PIJE - Treatment 4-1 removed for this analysis. *S. giganteum* is not shown since initial fresh weight could not be reliably estimated.

Treatment	0-1		0-2		2-1		2-2		4-1		4-2		8-1		8-2	
	X	SE	X	SE	X	SE	X	SE	X	SE	X	SE	X	SE	X	SE
Height																
ABCO	15.0	5.6	9.4	4.9	6.5	5.8	6.1	5.5	31.5	5.6	7.8	4.6	19.3	4.3	12.6	5.6
ABMA	76.8	11.3	53.7	17.4	71.5	11	38.7	22	57.1	11.9	102.5	14.8	62.1	9.6	20.2	16.5
CADE	31.2	2.9	30.9	2.8	29.4	2.9	26.6	2.8	31.5	3.3	28.8	2.6	38	2.4	29.4	3.4
PIJE	26.2	3.5	21.4	3.6	30.6	3.5	22.7	3.5	20.8	4.3	19.8	3.1	31.4	3.1	31.5	4.3
PILA	30.1	6.4	30.1	7.7	40.2	5.8	26	5.8	35.5	10.2	27.2	5.6	33.1	5.6	27.5	6.9
PIPO	48.2	9.5	71.5	10.8	58.1	9.5	28.4	11.3	59	9.9	43.2	10.2	47.8	7.7	31.1	13.5
SEGI	20.2	2.9	21.4	2.9	21.3	2.8	26.4	2.9	15	3.3	24.5	2.7	29.9	2.4	27	3.4
Diameter																
ABCO	2.7	3.3	1.5	2.8	0.9	3.4	9.9	3.2	18	3.4	1.3	2.7	13.6	2.5	7.7	3.3
ABMA	8.7	4.5	1.8	7	4	4.5	-5.7	4.8	14.9	4.8	14.1	6	14.7	3.9	9.6	6.6
CADE	33.9	3.8	21.5	3.7	40.6	3.8	22.5	3.6	31.6	4.4	24.4	3.4	37.9	3.2	27.6	4.4
PIJE	9.1	2.5	8.2	2.5	8.7	2.5	10.6	2.4	10.5	3	11.5	2.1	8	2.2	10.5	3
PILA	18.8	4.1	16.8	5.2	22.9	3.9	25.4	3.9	35.9	7	14.2	3.7	16.5	3.8	19	4.7
PIPO	14.1	4.1	10.1	4.5	22.4	4.2	13.7	4.5	29.6	4.4	10.4	4.5	28.6	3.4	15.6	6
SEGI	21.9	3	14.4	3.1	26.5	2.8	22	3.1	16.3	3.4	22	2.9	25.8	2.8	34.7	3.4
Biomass																
ABCO	-33.4	5	-34.5	4.3	-26.5	5.2	-32.4	4.9	-2.9	5.1	-31.2	4.2	-14.6	3.8	-22.5	5.1
ABMA	-18.5	5.8	-32.1	8.9	-8.1	5.7	-34.4	11.3	3.3	6.1	-13	8	-12.1	5	-31.6	8.5
CADE	131.1	10.6	106.5	10.2	164.7	10.4	67.4	9.9	164.2	12	91.4	9.2	161.6	8.5	91.9	12
PIJE	12.7	3.1	4.2	3.2	16.7	3.1	-8.2	3.1	15.5	3.8	-1.6	2.7	8.2	2.7	-1.3	3.8
PILA	3.2	4.9	-6.6	6.2	17.5	4.6	-7.8	4.6	8.4	8.2	-0.1	4.4	3.9	4.5	-3.3	5.6
PIPO	-8.7	7	-0.2	7.5	23.9	7.1	-26.6	7.5	35.6	7.3	0.6	7.8	4.4	5.7	-17.5	10

Treatment	0-1		0-2		2-1		2-2		4-1		4-2		8-1		8-2	
	X	SE	X	SE	X	SE	X	SE	X	SE	X	SE	X	SE	X	SE
Root Mass																
ABCO	-24.6	3.4	-17.8	3	-17.7	3.3	-20.6	3.3	-4.5	3.5	-16.8	2.8	-8.9	2.6	-10.4	3.5
ABMA	-3.3	6.5	-1.3	10	13.8	6.3	-5.4	12.6	19.4	6.9	13	9	11.5	5.5	-3.4	9.5
CADE	124.7	12.6	108	12.1	161.4	12.3	56.9	11.6	147	14.1	93	10.9	161.1	10.1	61.6	14.2
PIJE	26.3	4.9	22.2	5	35.3	4.9	14.6	4.8	51.2	5.9	26.9	4.2	36.9	4.3	22.4	6
PILA	15	5.9	8	7.4	27.9	5.5	10.3	5.5	21.3	9.8	10.1	5.3	13.5	5.4	10.3	6.7
PIPO	-8	4.9	-0.9	5.3	4.9	5	-10.1	5.3	10.7	5.2	-0.6	5.5	2.2	4	-15.7	7.1
Shoot Mass																
ABCO	-42.9	7.8	-52.3	6.7	-36	8	-44.9	7.6	-1.4	7.9	-46.7	6.4	-20.7	5.8	-35.5	7.9
ABMA	-25.8	6.5	-49.3	10	-20	6.3	-50.2	12.6	-5.5	6.8	-27.4	9	-25.4	5.5	-47.5	9.4
CADE	132.2	12	107.3	11.8	166.6	12	72.3	11.4	173.5	13.8	90.9	10.6	162.7	9.9	110.3	13.9
PIJE	6.9	3.9	-2.7	3.9	9.3	3.9	-17.8	3.8	4.2	4.6	-13.5	3.3	-2.6	3.4	-11.2	4.7
PILA	-3.9	5.5	-15.2	7	11.2	5.2	-18.4	5.2	0.9	9.3	-5.9	4.9	-1.6	5	-11.4	6.3
PIPO	-9.1	9.3	0.3	10	37.4	9.5	-38.5	10.3	53.4	9.8	1.4	10.4	6	7.6	-18.8	13.4

Table 14. Percent growth, mean and standard error, listed by parameter - height, diameter, total mass, root mass and shoot mass. Treatment codes are 0-1 = no water, shade; 0-2 = no water, sun; 2-1 = 2 weeks water, shade; 2-2 = 2 weeks water, sun; 4-1 = 4 weeks water, shade; 4-2 = 4 weeks water, sun; 8-1 = 8 weeks water, shade; 8-2 = 8 weeks water, sun. *S. giganteum* is not shown in the biomass categories since the initial fresh weight of this species could not be reliably estimated.

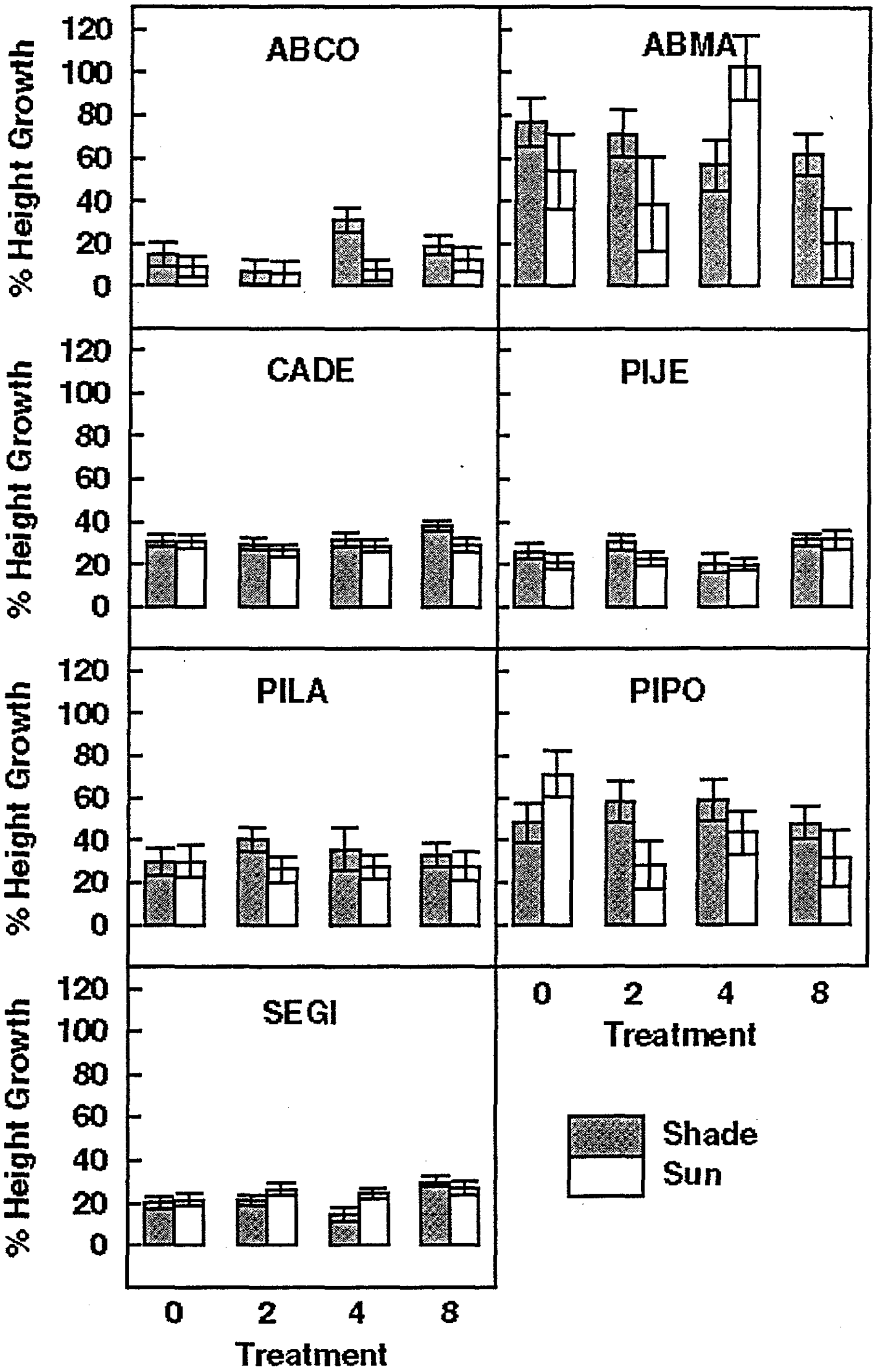

Figure 27. Mean percent height growth +/- standard error. Treatment 0 = control (no water addition, treatments 2,4, & 8 watered for 2, 4, or 8 weeks after natural soil moisture dropped below -0.05 MPa.

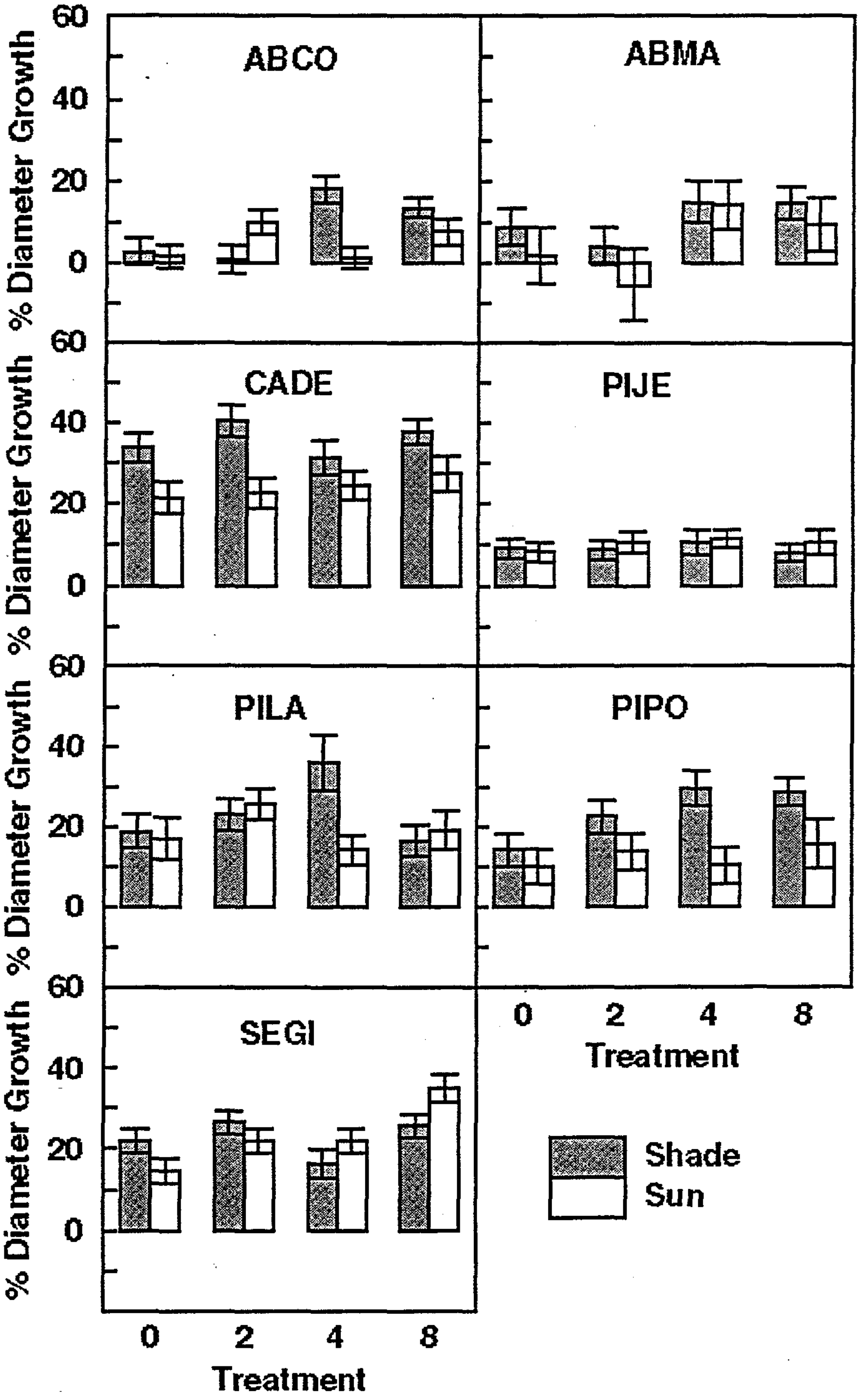

Figure 28. Mean percent diameter growth +/- standard error. Treatment 0 = control (no water addition, treatments 2,4, & 8 watered for 2, 4, or 8 weeks after natural soil moisture dropped below -0.05 MPa.

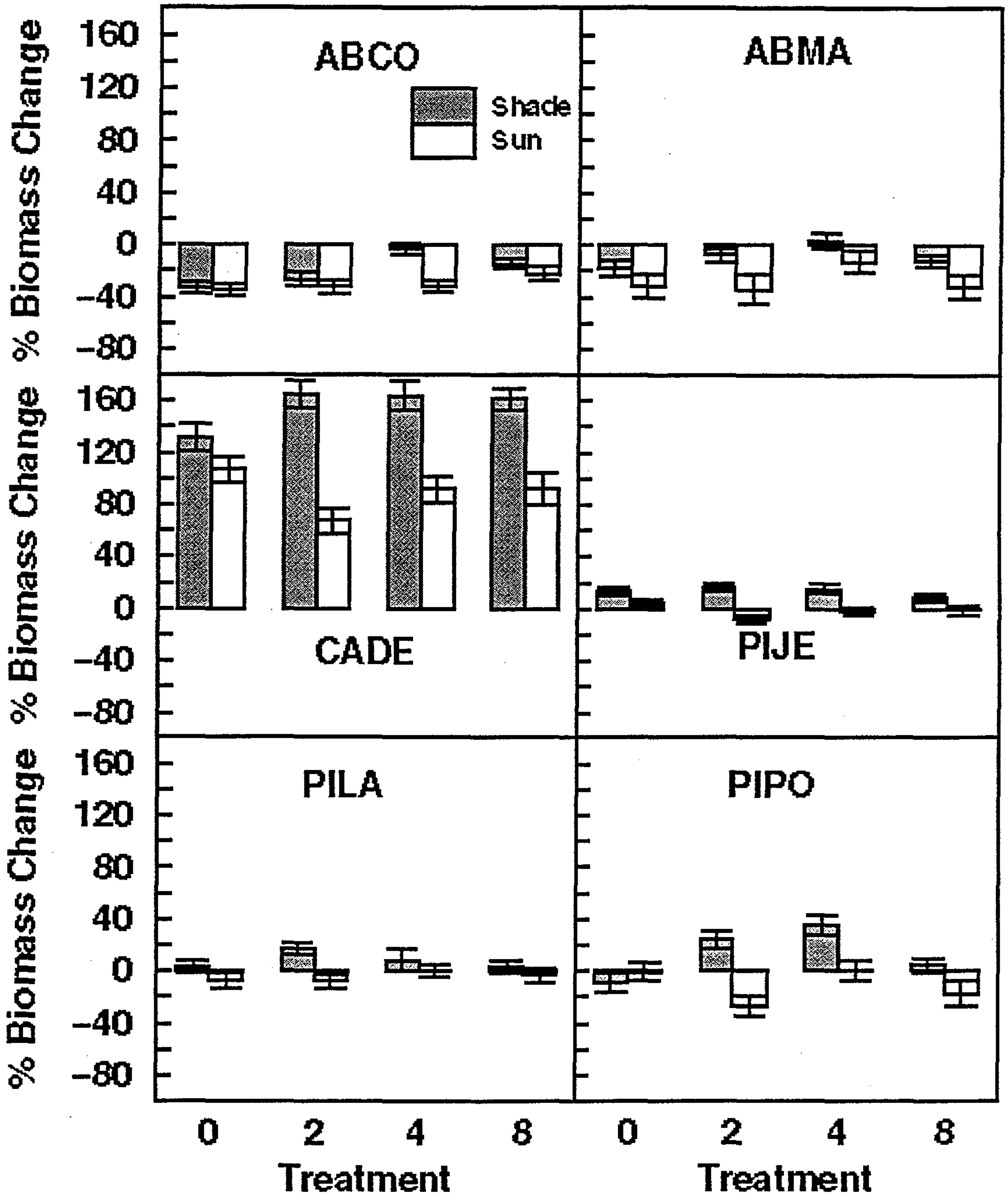

Figure 29. Mean percent total dry biomass change +/- standard error. Treatment 0 = control (no water addition, treatments 2,4, & 8 watered for 2, 4, or 8 weeks after natural soil moisture dropped below -0.05 MPa. *S. giganteum* is not shown since initial fresh weight could not be reliably estimated.

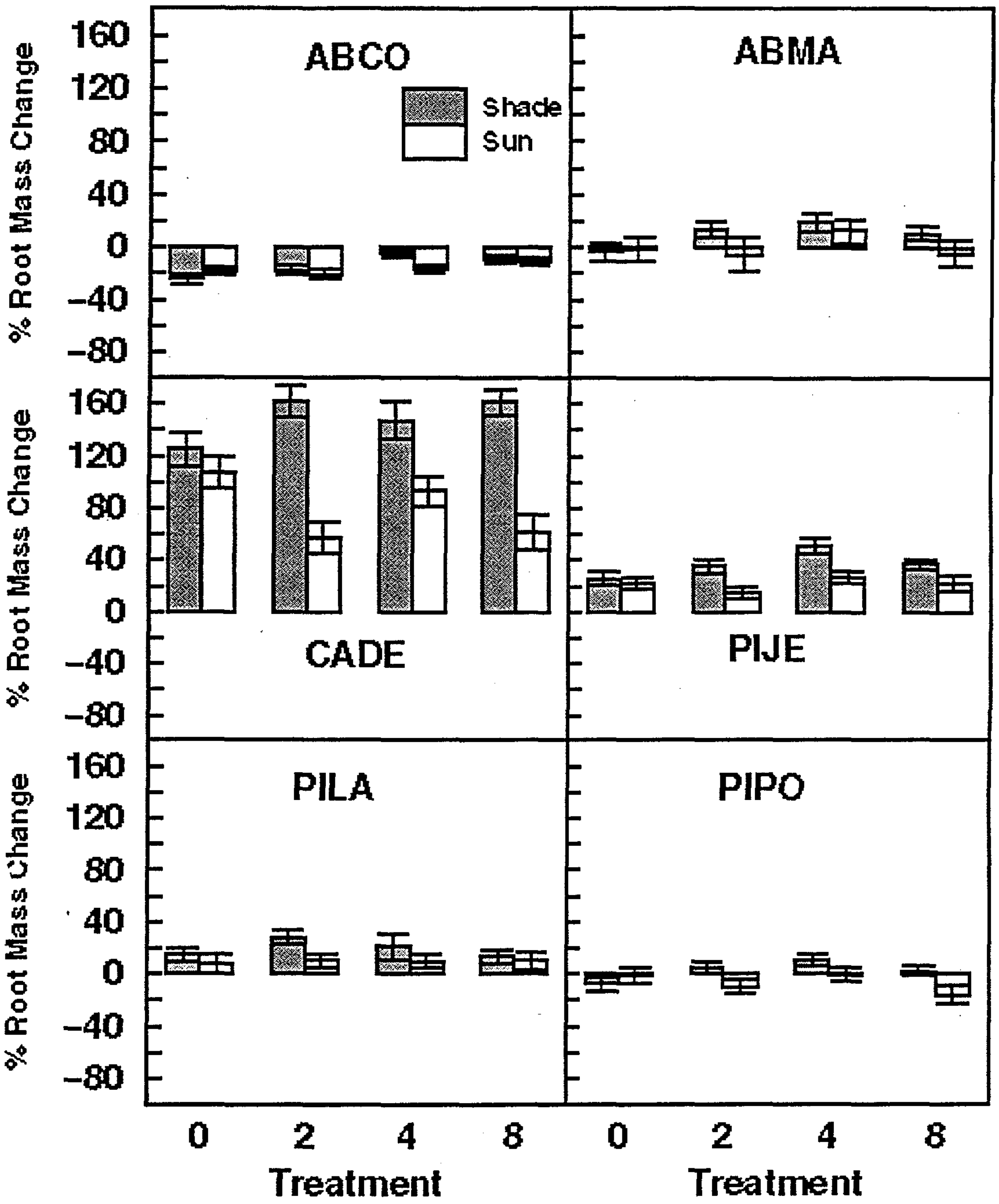

Figure 30. Mean percent dry root mass change +/- standard error. Treatment 0 = control (no water addition, treatments 2,4, & 8 watered for 2, 4, or 8 weeks after natural soil moisture dropped below -0.05 MPa. *S. giganteum* is not shown since initial fresh weight could not be reliably estimated.

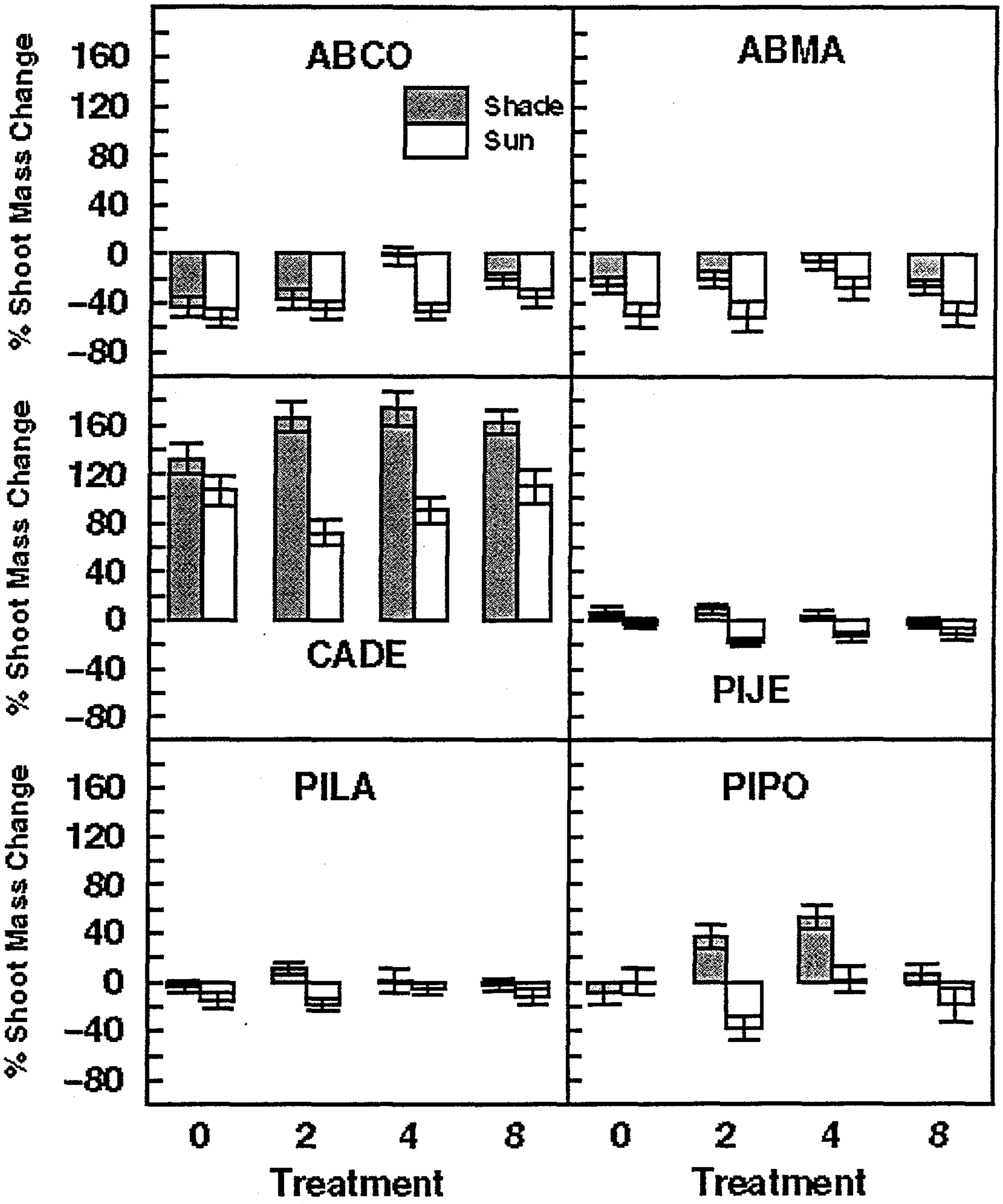

Figure 31. Mean percent dry shoot mass change +/- standard error. Treatment 0 = control (no water addition, treatments 2,4, & 8 watered for 2, 4, or 8 weeks after natural soil moisture dropped below -0.05 MPa. *S. giganteum* is not shown since initial fresh weight could not be reliably estimated.

Height growth

There was a highly significant ($P<0.001$) effect of the covariate (initial height) on the height growth of all species, and a significant ($P<0.05$) interaction between water and light in *A. magnifica*. Also, the interaction term for *P. ponderosa* is marginally significant ($P<0.10$). Main effects must be interpreted cautiously when there is significant interaction. Among the other species, light was a significant factor in height growth in *A. concolor* and *C. decurrens*, while water was a significant factor in height growth in *A. concolor*, *P. jeffreyi*, and *S. giganteum*.

P. ponderosa was the only species with a significant difference in height growth between light levels in the control (no water addition) plots, with greater height growth occurring in the sun plots (Figure 27). In the 2-week water treatment, *A. magnifica*, *P. jeffreyi*, *P. lambertiana*, and *P. ponderosa* all had decreased height growth in the sun plots, while *S. giganteum* had greater height growth in the sun plots. The greatest differences in height growth between light levels was seen in the 4-week water treatment, with greater height growth in the shade plots in *A. concolor* vs. greater height growth in the sun plots in *A. magnifica* and *S. giganteum*. Significant differences in height growth in the 8-week water treatment occurred in *A. magnifica* and *C. decurrens*, where there was greater height growth in the shade plots.

Diameter growth

There was a highly significant ($P<0.001$) effect of the covariate (initial diameter) on diameter growth in all species except *P. jeffreyi* , and significant ($P<0.05$) interaction between water and light in *A. concolor* and *S. giganteum*. Also, the interaction term for *P. lambertiana* is marginally significant ($P<0.10$). Main effects must be interpreted cautiously when there is significant interaction. Among the other species, light was a significant factor in diameter growth in *C. decurrens* and *P. ponderosa*, while water was a significant factor in diameter growth in *A. magnifica*.

Where significant effects of light on diameter growth (Fig 28) were observed growth was generally greater in the shade rather than in the sun. *C. decurrens* and *S. giganteum* were the only species with significant differences in diameter growth between light levels in the control (no water addition) plots, with greater diameter growth occurring in the shade plots (Figure 28). In the 2-week water treatment, *A. concolor* had lower diameter growth in the shade plots while *C. decurrens* and *P. ponderosa* had decreased diameter growth in the sun plots. As in height growth, the greatest differences in diameter growth between light levels was seen in the 4-week water treatment, with greater diameter growth in the shade plots in *A. concolor*, *P. lambertiana*, and *P. ponderosa*. Significant increases in diameter growth in the shade plots given 8 weeks of supplemental water occurred in *A. concolor, C. decurrens*, and *P. ponderosa* while in the sun plots there was greater diameter growth in *S. giganteum.*

Biomass growth

Estimates of percent biomass change (Figure 29) were largely negative. This is most likely due to loss of biomass as a result of transplanting healthy nursery-grown seedlings into the experimental environments and, to a lesser extent, the inability to harvest completely the below-ground biomass. Nonetheless, it is instructive to examine the trends in percent biomass change between treatments and to compare them to the results seen in height and diameter growth.

In contrast to height and diameter growth the effect of the covariate (initial dry mass) on biomass change was only significant in *C. decurrens* and *P. jeffreyi.* Interaction between water and light was significant ($P<0.05$) in all species except *A. magnifica* and *P. lambertiana*. Therefore, these are the only two species in which main effects can be interpreted clearly. Both water and light were significant factors in the biomass change in *A. magnifica*, while mass change in *P. lambertiana* was significantly affected by light but not water.

Effects of light and water on biomass are shown graphically in Figure 29. Because there are significant interactions between water and light in determining the biomass growth of most species, effects of light must be considered only within each water treatment and, likewise, effects of water only within each light level. Where the effect of light is significant, there is greater (or less negative) mass growth in the shade plots -- *A. magnifica*, *C. decurrens* and *P. jeffreyi* - all water treatments, *A. concolor* - 4 weeks water, *P. lambertiana* - 2 weeks water, and *P. ponderosa* - 2, 4, and 8 weeks water.

Root and shoot biomass changes are shown in Figures 30 and 31. The decrease in total mass in several species is attributable to decreases in above-ground mass. Specifically, *A. magnifica* var. *shastensis*, *P.. jeffreyi*, and *P. lambertiana* had positive root growth, but total mass change was overwhelmed by loss of shoot mass. Both root and shoot mass decreased in *A. concolor*, but the decrease in shoot mass was greater than that in root mass. Overall patterns of biomass change in *P. ponderosa* (increased growth in shade treatments in 2 and 4 week water treatments) were also more pronounced in shoot mass than in root mass.

The analysis of covariance indicates that the effect of the covariate is more commonly significant in root mass growth than in shoot mass growth (Table 13). Significant interaction between light and water ($P<0.05$) occurred in root growth in *A. concolor* and *C. decurrens*, and marginally significant ($P<0.10$) in *P. ponderosa*. Among species without significant interaction, light was a significant factor in root growth in *P. jeffreyi* and *P. lambertiana*, while water was not a significant factor in root growth in any species.

Main effects and significant interactions between light and water in shoot growth followed the same pattern as in total biomass. *A. concolor*, *C. decurrens* and *P. ponderosa* had significant (P<0.05) interaction while interaction in *P. jeffreyi* was marginally significant (P<0.10). As in total mass, *A. magnifica* and *P. lambertiana* were the only two species without significant interaction, and shoot growth was significantly affected by both water and light in *A. magnifica*, while only light was a significant factor in shoot growth in *P. lambertiana*.

Allometric Analyses

Treatments differed significantly (P<0.05) in their allocation of biomass to roots vs. shoots in *A. concolor*, *C. decurrens*, and *P. lambertiana*, and marginally significant in *P. ponderosa* (P<0.10) (Table 15). In all of these species, the treatments that differed were the 4 and 8 weeks water treatments ('K' values or slopes of root vs. shoot mass allocation are reported in Table 16), and the difference was less biomass allocated to roots per shoot biomass than in the 0 (control) and 2 week water treatments. Two cases, *P. jeffreyi* and *P. lambertiana* in treatment 4-1, had negative K values, or a trend for less root mass allocated per shoot mass as the shoot size increases.

Species	ABCO	ABMA	CADE	PIJE	PILA	PIPO
p-value	0.0001	0.2099	0.0226	0.5075	0.0348	0.0790

Table 15. Analysis of covariance results (p-values) for test of differences among treatments in root:shoot biomass allocation. *S. giganteum* is not shown since initial fresh weight in this species could not be reliably estimated.

Table 17 shows significance of the main effects of water treatments, light, and their interaction on root:shoot biomass allocation in each species. The interaction term is significant in *C. decurrens* and *P. ponderosa.* Both light and length of adequate soil moisture availability were significant in *A. concolor* and *P. jeffreyi.*

Leaf Water Potential

Overall, (all species, both years), interactions between light and soil moisture were marginally significant ($P<0.10$) in determining the leaf water potential of *A. concolor* and *S. giganteum* (Table 18). The effect of light was significant ($P<0.05$) in *C. decurrens* and *S. giganteum* and marginally significant ($P<0.10$) in *P. ponderosa* . When the data were analyzed by individual year, it became apparent that most of the significant differences occurred in the second growing season, 1994. Note that in 1994, the interaction is significant in *P. ponderosa* and marginally significant ($P<0.10$) in *A. concolor, P. lambertiana,* and *S. giganteum.* As in the overall results, the effect of "dryness" (time since last watered) is not significant in 1994 (*P. ponderosa* may be significant but must be interpreted cautiously in light of the significant interaction term). The effect of light (GSF) is also significant in the same three species as in the

Trt	0-1		0-2		2-1		2-2		4-1		4-2		8-1		8-2	
	K	SE	K	SE	K	SE	K	SE	K	SE	K	SE	K	SE	K	SE
ABCO	0.56	0.12	0.51	0.14	0.59	0.12	0.52	0.21	0.15	0.03	0.19	0.10	0.46	0.09	0.56	0.11
ABMA	0.20	0.18	-0.13	0.55	0.60	0.17	1.37	1.21	0.49	0.27	0.51	0.26	0.79	0.13	0.42	0.27
CADE	0.84	0.13	0.70	0.10	0.70	0.18	0.71	0.13	0.31	0.18	0.51	0.13	0.23	0.24	0.16	0.07
PIJE	0.28	0.18	-0.04	0.21	0.34	0.36	0.37	0.19	-0.59	0.61	0.21	0.18	0.37	0.32	0.26	0.38
PILA	0.95	0.20	0.80	0.21	0.66	0.31	0.40	0.31	-0.61	1.25	0.15	0.20	0.77	0.19	0.10	0.10
PIPO	0.42	0.06	0.32	0.09	0.24	0.08	0.12	0.24	0.35	0.10	0.24	0.09	0.57	0.10	0.06	0.21

Table 16. Allometric analyses of root-shoot biomass allocation patterns. K is a dimensionless allometric coefficient calculated for each species and is the slope of the regression of percent change in root dry weight (Y) regressed on percent change in shoot dry weight (X). K represents an average partitioning trend over the experimental period and measures the relative growth rates. SE = Standard Error. *S. giganteum* is not shown since initial fresh weight in this species could not be reliably estimated.

Species	Water	Light	Water*Lt
ABCO	0.0535	0.0632	0.3866
ABMA	0.7117	0.5114	0.4464
CADE	0.6420	0.0001	0.0032
PIJE	0.0126	0.0314	0.5125
PILA	0.6241	0.7126	0.8285
PIPO	0.9086	0.2238	0.0444

Table 17. Analysis of variance results (p-values) for allometry - root:shoot biomass allocation. *S. giganteum* is not shown since initial fresh weight in this species could not be reliably estimated.

overall analysis -- *C. decurrens*, *P. jeffreyi*, and *S. giganteum*, but *S. giganteum* may be affected by the marginally significant interaction (P<0.10). In the first growing season (1993) there were few significant effects. Interaction was significant in *S. giganteum*, the main effect of "dryness" was not significant in any species in 1993, and the main effect light (GSF) was significant only in *P. ponderosa*.

The most striking results are illustrated in Figures 32-35. Overall, predawn leaf water potential values were lower in the sun plots than in the shade (when there was a difference between light treatments), and leaf water potential values were lower in 1994 than in 1993, especially in *A. concolor*, *A. magnifica*, and *S. giganteum grown in the sun*. Figure 32 shows leaf water potential values measured in 1993 by species. The only significant effect of light in 1993 occurred in *P. ponderosa*. Effects of

Species	n	GSF	DRY	GSF*DRY
1993 and 1994				
ABCO	145	0.1812	0.1593	0.0918
ABMA	137	0.8338	0.6679	0.2748
CADE	144	0.0063	0.9707	0.6894
PIJE	144	0.0101	0.3720	0.1338
PILA	142	0.2653	0.5756	0.2373
PIPO	144	0.0883	0.2140	0.1834
SEGI	144	0.0008	0.7587	0.0772
1993 only				
ABCO	61	0.2475	0.2535	0.3224
ABMA	59	0.9020	0.5846	0.6798
CADE	60	0.6698	0.9737	0.9532
PIJE	60	0.4508	0.2526	0.2001
PILA	59	0.8298	0.7033	0.7099
PIPO	61	0.0282	0.5119	0.6306
SEGI	60	0.1725	0.0916	0.0405
1994 only				
ABCO	84	0.1836	0.1630	0.0689
ABMA	78	0.4085	0.4662	0.1654
CADE	84	0.0040	0.9398	0.5891
PIJE	84	0.0140	0.4182	0.2000
PILA	83	0.4739	0.2742	0.0961
PIPO	83	0.4072	0.0041	0.0030
SEGI	84	0.0002	0.4834	0.0623

Table 18. Analysis of variance results (p-values) for leaf water potential measurements.

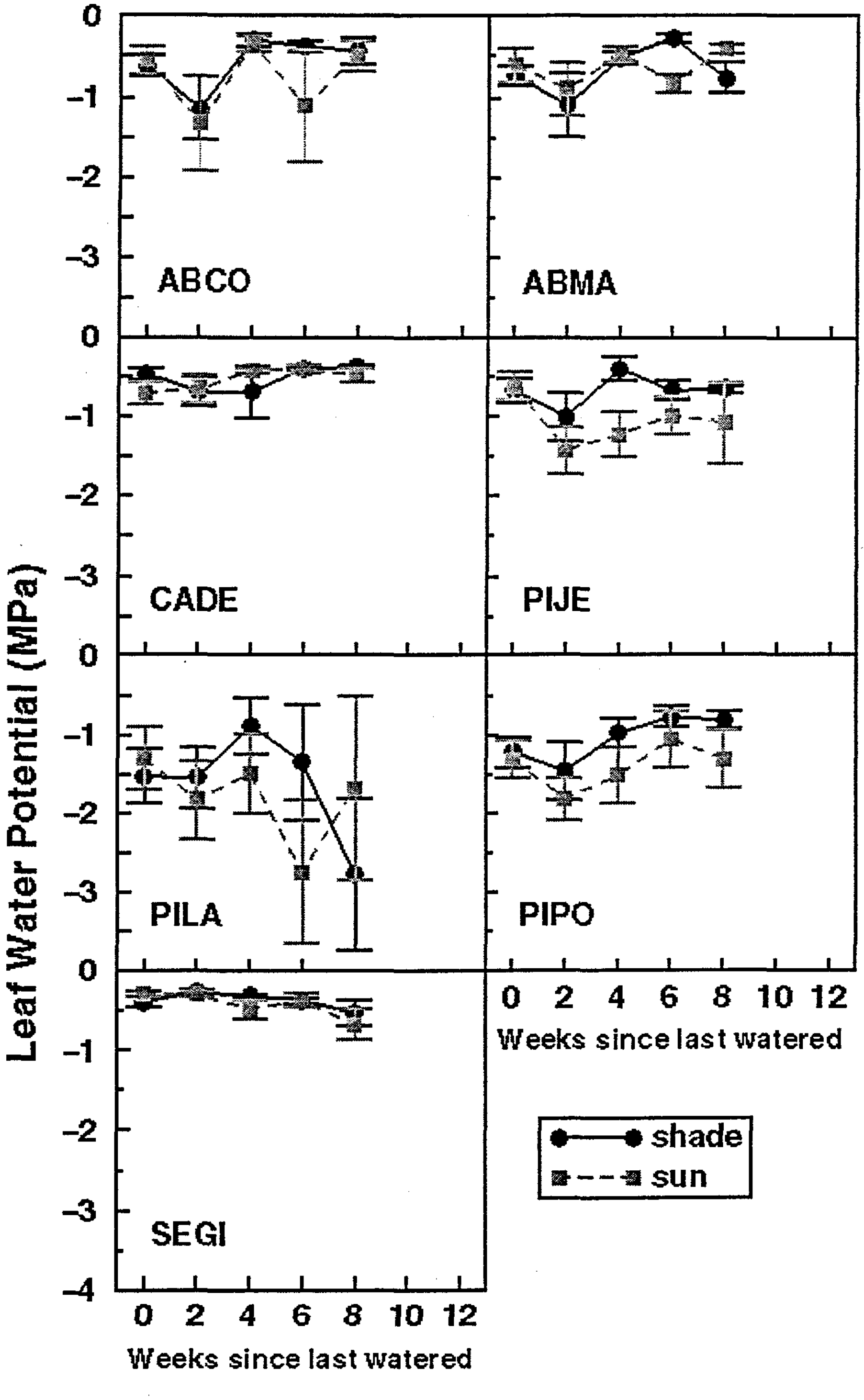

Figure 32. Predawn leaf water potential measurements for 1993.

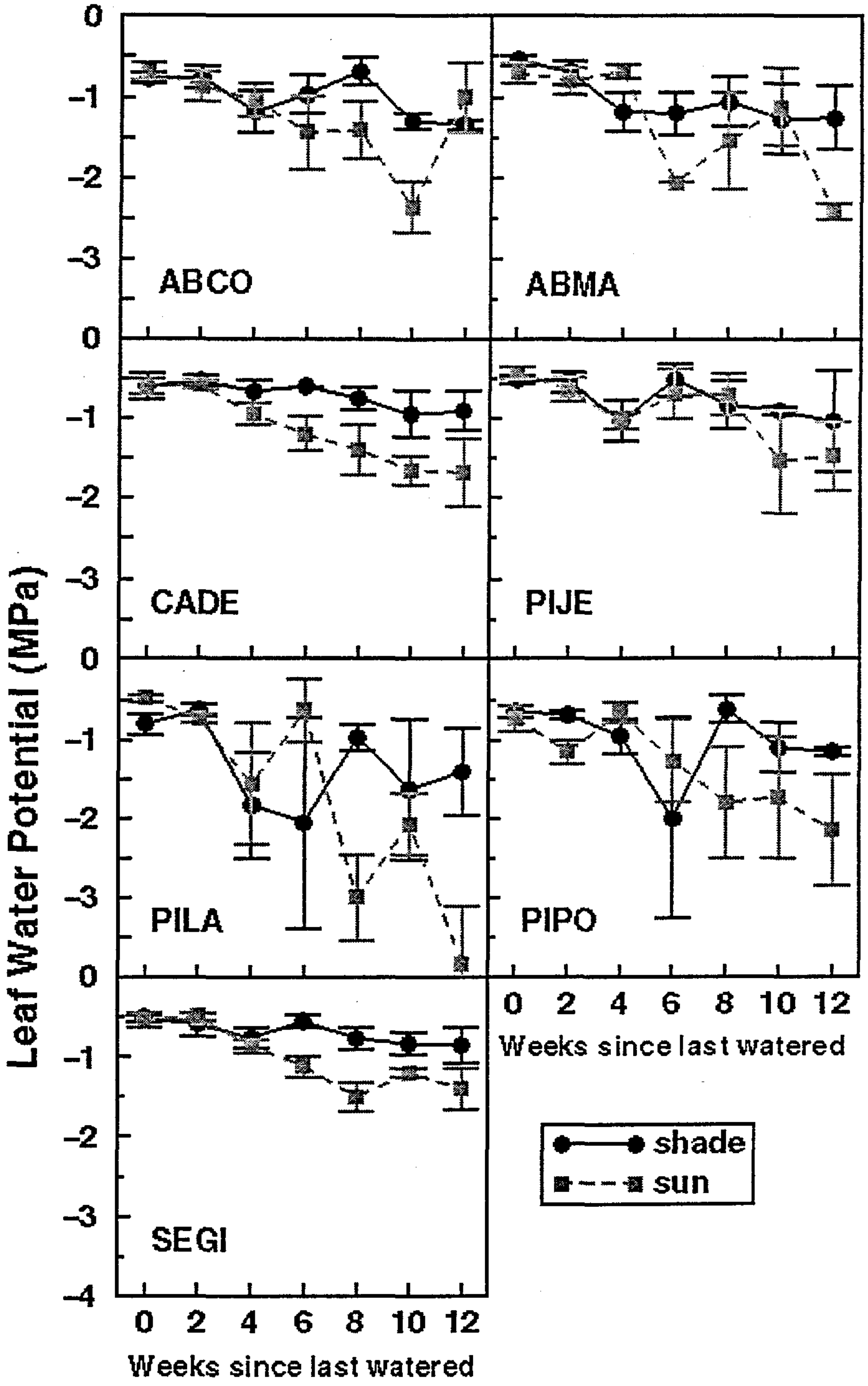

Figure 33. Predawn leaf water potential measurements for 1994.

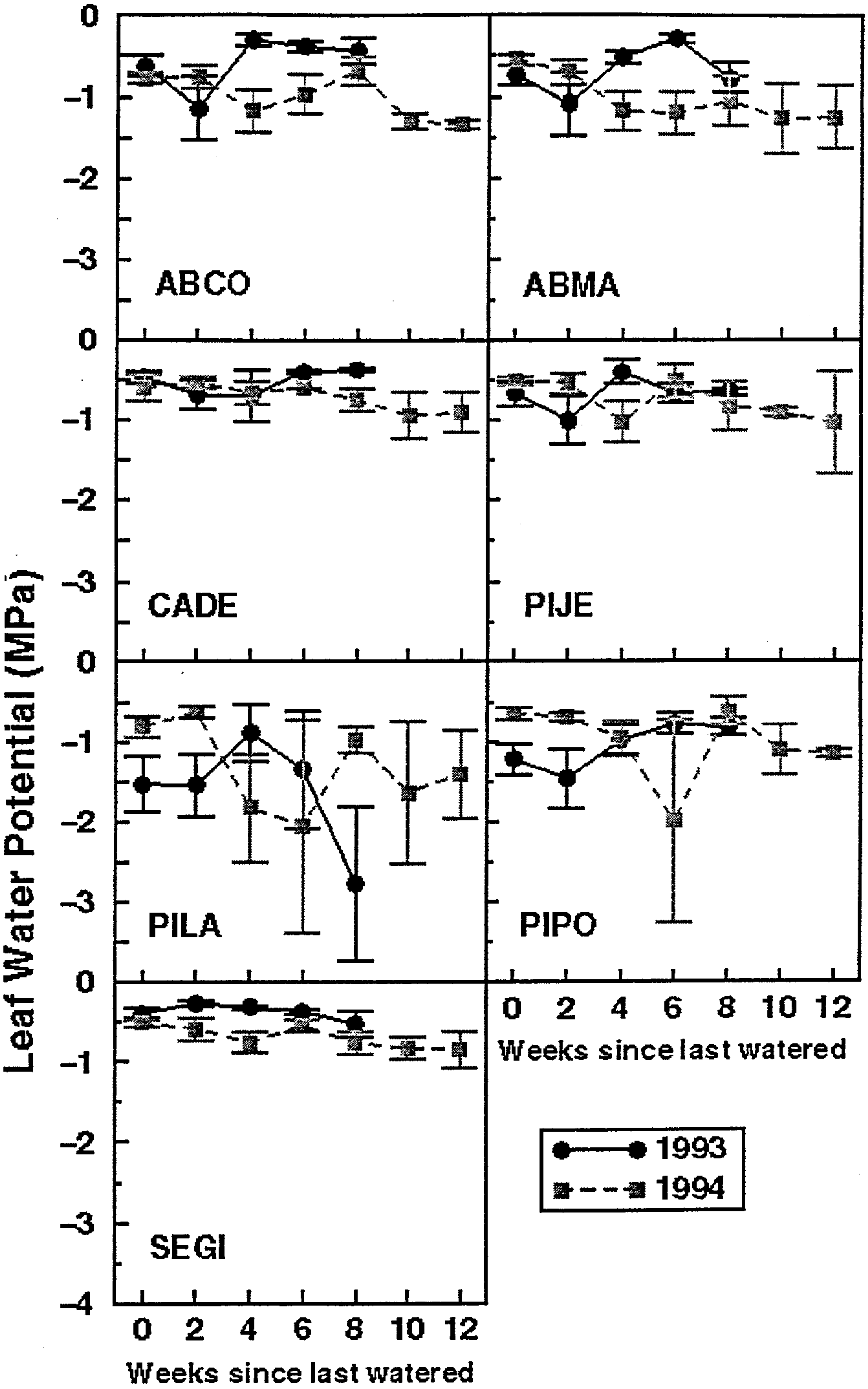

Figure 34. Predawn leaf water potential measurements for shade treatments.

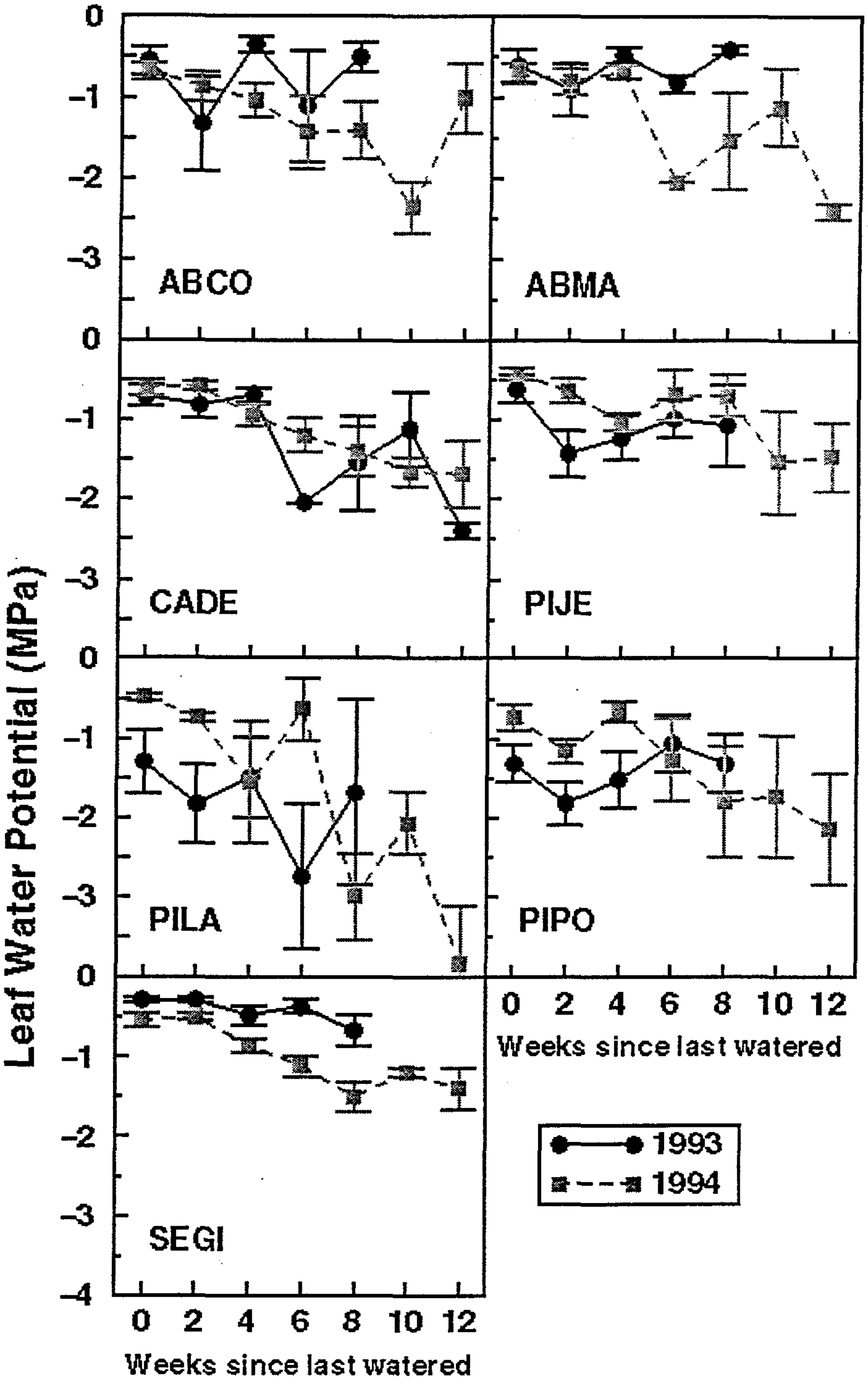

Figure 35. Predawn leaf water potential measurements for sun treatments.

"dryness" were not significant. More significant effects of light on leaf water potential occurred in 1994 (Figure 33). Note the lower predawn leaf water potential values in the sun plots for *C. decurrens*, *P. jeffreyi*, and *S. giganteum*. In the species with significant or marginally significant interaction between light and dryness (A. concolor, P. lambertiana, P. ponderosa, and S. giganteum), there is no clear trend separating the sun and shade treatment responses. Indeed, the interaction is apparent in the crossing of the lines plotting the sun and shade leaf water potential values over the drying curve. Figures 34 and 35 show that predawn leaf water potential values were lower in 1994, especially in the sun plots.

DISCUSSION

The multiple stresses experienced by seedlings in these experimental treatments lead to complex dynamics. The seedlings were subject to a range of above-ground resource availability (light) and below-ground resource availability (water and nutrients). The treatments used in this experiment address two of these factors -- light and soil moisture, or drought stress. By adding water and artificially extending the growing season in the treatment plots, I effectively delayed the onset of drought stress in the 4 and 8 week water treatments. Additionally, increased nutrient availability was probably associated with the water addition treatments.

The light treatments used represented the extremes of light availability found in this forest environment. The high light ("sun") treatments were all located in large canopy gaps and the low light ("shade") treatments in nearby closed canopy forest. While the interpretation of light effects focusses on irradiance, or light energy, the light environments of open and closed canopy areas also differ in light quality (wavelength composition), duration (daylength as well as sunfleck length and frequency) and radiation (heat energy). These are all important factors and the sum of them provides distinctly contrasting environments in which to compare growth and survival.

Predawn leaf water potential was lower in the sun plots than in the shade plots, and lower in 1994 than in 1993, especially in *A. concolor*, *A. magnifica*, and *S. giganteum*. This is most likely due to several factors. The driving force for transpiration, vapor pressure deficit, was higher in the summer months of 1994 (Figure 36) and the soil moisture reserves, determined by the snowfall during the previous winter, were much lower than during the previous year (Table 3). Thus, environmental factors alone would be expected to reduce the leaf water potentials in the sun plots during 1994 relative to 1993.

Tree responses to drought are manifested in a range of mechanisms that act at whole plant to subcellular levels. Typically, species are found to adopt one or both of the following strategies: 1) drought avoidance, characterized by high stomatal sensitivity to drought and/or deep roots allowing constant access to adequate soil moisture, and 2) drought tolerance, found in species with lower stomatal sensitivity but which have functional adaptations such as osmoregulation that allow maintenance of photosynthetic activity at lower water potentials (Levitt 1980). The scope of this study did not include the physiological measurements necessary to determine how the study species are regulating their drought responses -- avoidance, tolerance, or some combination of both through time -- but rather focussed on the integrated results as seen in seedling growth and survival.

Drought avoidance alone is not a reasonable strategy for Sierran conifer seedlings as these young trees have not yet developed extensive root systems and are growing in a climate with an extended dry season. These plants cannot "avoid" drought indefinitely by stomatal closure, but probably use this strategy early in the growing season when midday vapor pressure deficit peaks. They must then either have access to adequate soil moisture (root system development) or else develop functional adaptations that allow them to maintain a reduced photosynthetic level throughout the growing season. While physiological adaptations were not investigated here, biomass allocation was measured and results indicate that *A. concolor*, *C. decurrens*, *P. lambertiana*, and *P. ponderosa* employed the drought avoidance strategy of allocating relatively more biomass to roots vs. shoots in the drought-stressed treatments.

Many conifer species have been found to have high stomatal sensitivity to leaf water potential and are able to reduce transpirational water loss in drought stress conditions (Beerling et al. 1996, Picon et al. 1996). Lopushinsky (1969) and Lopushinsky and Klock (1974) demonstrated greater stomatal sensitivity in pines (*Pinus sp.*) than in firs (*Abies sp.*), providing a mechanistic explanation for greater drought tolerance in pines than in firs. Stomatal closure for many western conifers occurs at soil water potentials above -2.0 MPa (Lassoie et al. 1985, Smith 1985) and at approximately -1.8 MPa for *P. ponderosa* (Lopushinsky 1969 for seedlings, Running 1976 for saplings). DeLucia et al. (1988) measured September leaf water potentials in *P. ponderosa* as low as -1.12 and in *P. jeffreyi* as low as -1.36 in mature Great Basin pine stands. These studies demonstrate the ability of *P. ponderosa* and other pines to respond to drought stress by reducing stomatal conductance at quite low soil water potentials. The higher predawn leaf water potentials measured by DeLucia et al. (1988) suggest that these trees are deeply rooted and have a reliable water source.

A longer-term strategy to drought stress is osmotic regulation, or a decrease in osmotic potential greater than can be explained by concentration of solutes during dehydration, indicating accumulation of additional solutes (Turner and Jones 1980). Anderson and Helms (1994) showed clear evidence of osmotic adjustment in *P. ponderosa* throughout the summer drying cycle, but point out that the osmotic adjustment occurred at least partially as a result of factors other than moisture availability (e.g., accumulation of solutes with leaf aging or seasonal declines in photoperiod and temperature (Abrams 1988 and van den Driessche 1989). The pronounced differences in the late season leaf water potential may be due to lower ability to acclimate in the sun plots by the shade-tolerant (*A. concolor* and *A. magnifica*) and drought intolerant (*S. giganteum*) species.

The overall effect of water stress on predawn leaf water potential, measured as "dryness" or the time since last watered, was not significant in any species in 1993 or 1994. Rather, light level was the significant factor in predawn leaf water potentials measured in 1994 in *C. decurrens*, *P. jeffreyi*, and *S. giganteum* as seen in Figure 33 (although the interaction between light and dryness was marginally significant in *S. giganteum* so this result must be interpreted cautiously).

The reduced leaf water potential values measured in the sun plots must lead to reduced photosynthetic activity in these seedlings (Kozlowski et al. 1991), causing the observed decrease in growth in the sun plots relative to the shade plots. With few exceptions, smaller increments of growth were measured in the sun treatments than in the shade in all responses measured (height, diameter, total biomass, root mass, and shoot mass).

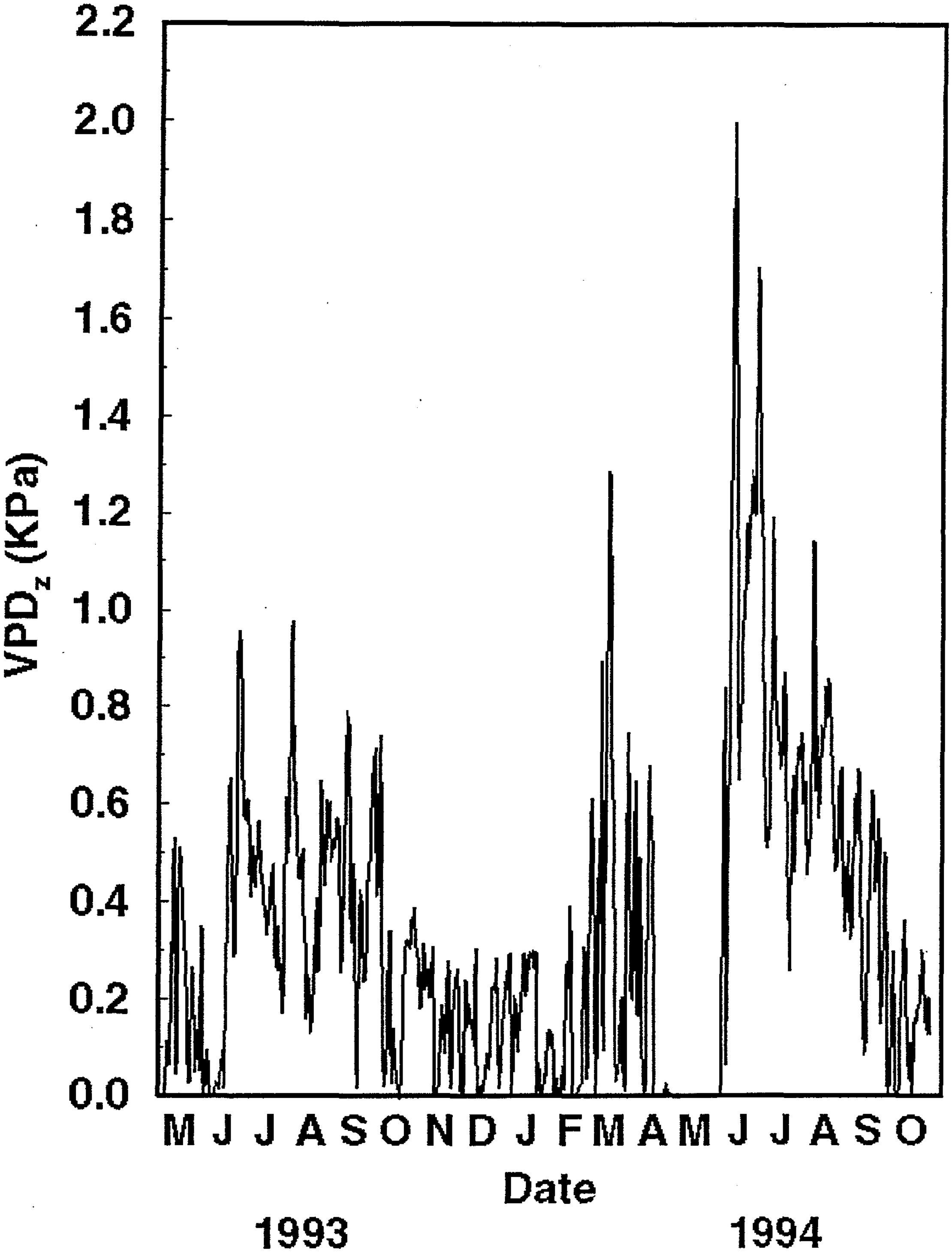

Figure 36. Vapor pressure deficit calculated from temperature and relative humidity measured at the 1900 m transplant experiment site.

Growth patterns were significantly affected by the covariate (initial size) in almost all species for height and diameter, but less so for mass changes. Main effects of water and light and the interaction between them are significant in a few species in each response measured, though the pattern is complex and differs among response variables. The effects of light and water on root and shoot growth do generally follow the same pattern as total biomass (Table 13), though the patterns of biomass allocation to roots vs. shoots differ among treatments in *A. concolor*, *C. decurrens*, *P. lambertiana*, and *P. ponderosa* (Table 15). In these species, the biomass allocation patterns of the 4- and 8-week treatments differ from the control and 2-week treatments by allocating less mass to root development per unit allocated to shoot development under most conditions (i.e., lower 'K' value, or shallower slope in root vs. shoot mass allocation) (Table 16).

The observed patterns of biomass allocation are probably due to the timing and severity of drought stress in the experimental treatments. The four dominant species of the lower elevation forest (*A. concolor*, *C. decurrens*, *P. lambertiana*, and *P. ponderosa*) all responded to drought stress by allocating relatively more biomass to roots than to shoots in the more drought-stressed treatments of 0 and 2 weeks water (both sun and shade). This is a common response in drought environments where additional root surface area is necessary to absorb enough water to maintain physiological activity. The exact mechanism and timing of events are not clear, however, and were not addressed in this study.

There is evidence that these conifers probably allocate growth to roots and shoots in an alternating fashion throughout the growing season (Burr et al. 1989, Drew and Ledig 1980, Krueger and Trappe 1967, Ross 1932, Stone and Jenkinson 1970) with an early season root growth period prior to shoot elongation and then a second peak in root growth following bud set (Jenkinson 1975). It is believed that this alternating pattern of root and shoot growth is a result of competition for energy reserves within the plant, or perhaps represents feedback mechanisms that maintain an adaptive balance between organ systems (Drew and Ledig 1980).

McMillin and Wagner (1995) tested effects of water stress on biomass partitioning in *P. ponderosa* seedlings and found that drought stress during shoot growth resulted in higher fine root: current year foliage ratios. This is another interpretation of the results found in *A. concolor*, *C. decurrens*, *P. lambertiana*, and *P. ponderosa* grown in the 0 and 2 weeks water treatments. The earlier onset of drought may have inhibited shoot elongation and root growth was proportionately increased, leading to greater root:shoot allocation in the 0 and 2 weeks water treatments relative to the 4 and 8 week water treatments.

Following the argument outlined above, it is possible that drought stress induced during the second spurt of root growth (approximately July in this system) would cause reduced root growth per unit of shoot growth, as seen in the 4 and 8 week water treatments. While biomass allocation patterns did not differ among treatment combinations in *A. magnifica* and *P. jeffreyi*, there were significant differences in root:shoot allocation in the 4 and 8 week water treatments in *A. concolor*, *C. decurrens*, *P. lambertiana*, and *P. ponderosa*. These are all drought tolerant species, but perhaps were not able to adapt to the timing of drought which occurred so late in the season. These species consequently allocated fewer resources to root vs. shoot throughout the growing season. Alternatively, the decreased root:shoot ratios in the less water-stressed treatments are simply a consequence of less need for additional water-absorbing roots in these treatments.

Finally, differences in biomass partitioning have been shown to be affected by drought intensity. Waring (1991) pointed out that partial drought creates conditions in evergreeens where photosynthesis continues but shoot elongation is inhibited. With reduced shoot growth, sugar concentrations increase in the phloem, the flux of carbon to the roots is disproportionately increased. The result is lower leaf water potential along with higher root:shoot biomass allocation.

Although light and soil moisture availability had significant impacts on the leaf water potential, biomass partitioning and growth responses, light was the only significant factor in the ultimate survival of *A. magnifica*, *P. ponderosa*, and *S. giganteum*. The largest differences in survival among light levels in these species occurred in the 2- and 4- week water treatments, with significantly lower survival in the sun plots. Especially in the 4- week water treatment, it appears that the shock of drought induced at the height of the dry season led to higher mortality in the sun treatments. It seems that the seedlings that never received any additional water responded more strongly to drought stress than to light, since no species differentiated between light treatments with respect to survival in the control water treatment. At the other extrerme, seedlings given 8 weeks of additional water also did not differentiate between light treatments in survival. Leaf water potentials were, as expected, higher in seedlings grown in this treatment, and survival was highest with 8 weeks of water in most species, particularly in the sun. The intermediate water treatment (4 weeks) apparently had the effect of artificially maintaining high soil moisture availability into the height of the dry season and then leaving the seedlings to adjust, if possible, to extreme drought without time to acclimate and develop drought avoidance or tolerance mechanisms such as increased root mass or osmotic regulation. The outcome was higher mortality in the sun treatments in the 4 week water treatment in *A. magnifica* var. *shastensis*, *P. ponderosa*, and *S. giganteum*. These species apparently were not able to adjust quickly enough to counter the drought effects of high irradiance in the sun treatments.

CONCLUSIONS

The seven conifer species responded differently to the multiple stresses of light and drought. In this experiment it was the high light environment that proved to be more stressful to the seedlings, leading to lower predawn leaf water potentials in most species, which led to lower growth and survival.

Overall, light was a more important factor in leaf water potential, growth, and survival than was the length of the growing season during which adequate soil moisture is available, but the interaction of these two factors was important in some species. Leaf water potential values were lower in the sun than in the shade in all species, especially in the summer of 1994, which followed a winter of lower precipitation than did the 1993 growing season. It seems that the seedlings grown in high light adapted by osmotic regulation or some other process that allowed them to maintain photosynthetic activity under drought conditions.

The timing and severity of drought appeared to be important in controlling root:shoot biomass allocation in *A. concolor*, *C. decurrens*, *P. lambertiana*, and *P. ponderosa*. These species are all components of the lower elevation Sierra Nevada mixed conifer forest and appear to have developed adaptations that enable them to adjust to drought stress in high light better than *A. magnifica* var. *shastensis*, which typically grows at higher elevations.

The water treatments, per se, were not a significant factor in the ultimate survival of any species. Because these treatments had the effect of reducing water stress, I expected growth and survival to increase with each successively longer growing season treatment. This did occur in most species, although the differences in survival among water treatments were not significant. Survival was significantly lower in the sun in the 4 week water treatment in *A. magnifica* var. *shastensis*, *P. ponderosa*, and *S. giganteum*. This may be due to the inability to quickly adapt to drought.

Taken together, the results from this experiment suggest that *A. concolor*, *C. decurrens*, *P. jeffreyi*, *P. ponderosa* and *S. giganteum* will have higher seedling survivorship than *A. magnigica* var. *shastensis* and *P. lambertiana* as the climate gradually warms. *A. concolor*, *C. decurrens*, *P. lambertiana*, and *P. ponderosa*, additionally, are more likely to successfully avoid drought stress by increasing root:shoot biomass allocation in response to seedling drought stress, as long as the drought stress occurs gradually and not due to dramatic changes in seasonality such as a 4-week growing season extension.

The range of responses found in this experiment indicate the complexity of seedling responses to light and drought stress in the Sierra Nevada mixed conifer forest. Climatic change will affect these species differentially, potentially creating a forest of significantly different character in the future. Understanding seedling responses to multiple stresses is critical to the management of the current and future forest.

CHAPTER 4

CONCLUSIONS

The Sierra Nevada mixed conifer forest tree community is made up of species with varied strategies for dealing with, and abilities to adapt to, the multiple stresses experienced during the seedling stage. These variations in early life-history tolerance to shade and drought, in particular, create complex seedling dynamics.

The goal of this dissertation research was to compare the seedling growth and survival of seven species of conifers that make up the mid-elevation Sierra Nevada mixed conifer forest -- *Abies concolor*, *Abies magnifica* var. *shastensis*, *Calocedrus decurrens*, *Pinus jeffreyi*, *Pinus lambertiana*, *Pinus ponderosa*, *Sequoiadendron giganteum*.

The first field experiment, comparing seedling growth and survival in two discrete light levels at each of three elevations, demonstrated the importance of survivorship and the survival-growth relationship in seeding dynamics. The seven conifer species studied respond differently to changes in elevation and light availability. Therefore, expected climate warming will not simply cause an upward elevational shift of the intact forest community, but rather changes in the relative abundances of each species as the seedling survival and growth of each of the co-occurring species change independently.

The changes in relative position with elevation may indicate future changes in community dynamics in response to global warming. As the climate warms, the effect on these species will be analogous to a lowering in elevation and the community structure will likely change along the trajectory seen as elevation changes from high to low in Figures 18 and 19. For example, *A. magnifica* var. *shastensis* survivorship will likely decrease, but those that survive will grow relatively well, especially in high light environments. *S. giganteum* survivorship would also be expected to decrease with climate warming, but its growth capacity is not likely to change. *C. decurrens*, on the other hand will not be affected much in open sunny areas owing to its "weedy" characteristics of high survival and rapid height growth in the sun, but it will be likely to decrease in survivorship in shade areas as the climate warms.

The seven conifer species also responded differently to the multiple stresses of light and drought as measured in the second experiment. In this experiment it was the high light environment that proved to be more stressful to the seedlings, leading to lower predawn leaf water potentials in most species, which led to lower growth and survival.

Overall, light was a more important factor in the parameters measured in the second experiment (leaf water potential, growth, and survival) than was the length of the growing season during which adequate soil moisture is available, but the interaction of these two factors was important in some species. Leaf water potential values were lower in the sun than in the shade in all species, especially in the summer of 1994, which followed a winter of lower precipitation than did the 1993 growing season. It seems that the seedlings grown in high light adapted by osmotic regulation or some other process that allowed them to maintain photosynthetic activity under drought conditions.

The timing and severity of drought appeared to be important in controlling root:shoot biomass allocation in *A. concolor*, *C. decurrens*, *P. lambertiana*, and *P. ponderosa*. These are all components of the lower elevation Sierra Nevada mixed conifer forest and appear to have developed adaptations that enable them to adjust to drought stress in high light better than *A. magnifica.*

The water treatments, per se, were not a significant factor in the ultimate survival of any species. As these treatments had the effect of reducing water stress, I expected growth and survival to increase with each successively longer growing season treatment. This did occur in most species, although the differences in survival among water treatments were not significant. Survival was significantly lower in the sun in the 4 week water treatment in *A. magnifica* var. *shastensis*, *P. ponderosa*, and *S. giganteum* due to the inability to quickly adapt to drought.

The range of responses found in this experiment indicate the complexity of seedling responses to elevation, light and drought stress in the Sierra Nevada mixed conifer forest. Climatic change will affect these species differentially, potentially creating a forest of significantly different character in the future. Quantitative, comparative field studies such as this are necessary for understanding possible impacts of global climate change on plant communities and for successful management of forests in the coming decades.

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BIOGRAPHY

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EDUCATION

Duke University, Durham, North Carolina
Department of Botany, Ph.D. December 1996
Dissertation title: A Comparative Field Study of Growth and Survival of Sierran Conifer Seedlings
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University of Cambridge, England
Botany School
One-year course in plant ecology funded by University of Minnesota Cambridge Scholarship, 1986-1987; Conducted research projects on paleoecology with Dr. Keith Bennett and plant physiological ecology with Dr. Ian Woodward.

University of Minnesota, Minneapolis-St.Paul
College of Biological Sciences
Bachelor of Sciences in Biology, Summa cum laude
Received March 1988
Thesis title: The Effect of Microtopography on Species-Richness in Maritime and Continental Bogs
Advisor: Dr. Eville Gorham

FELLOWSHIPS AND AWARDS

Graduate Fellowship for Global Change, U.S. Department of Energy, 1991-1996
Spatio-Temporal Dynamics Conference, Nat'l Center for Ecol. Analysis & Synthesis, Feb. 1996
NASA Earth Science Summer School "Processes of Global Change", July 1995
Catherine Keever Award, Duke University Department of Botany, 1993 and 1994
Duke University Graduate School Conference Travel Award 1992 , 1994, and 1995
National Science Foundation Graduate Fellowship Honorable Mention, 1990
University of Minnesota Cambridge Scholarship, 1986-1987
College of Biological Sciences Undergraduate Merit Scholarship, 1985
University of Minnesota Undergraduate Research Opportunities Grant, 1985
University of Minnesota President's Student Leadership and Service Award, 1985 & 1986
University of Minnesota Presidential Scholarship, 1982
National Science Foundation Student Scholar in Environmental Biology, 1980

TEACHING AND RELATED PROFESSIONAL EXPERIENCE

Graduate Teaching Assistant in General Biology, Duke University, Department of Botany, Durham, North Carolina, 1990-1991

National Science Foundation sponsored workshop "Preparing the Next Generation of Biology Instructors", August 1994

Represented the Botany Department and Duke University during the 1995-96 academic year in "Preparing Future Faculty", a national pilot program designed to prepare graduate students for the multiple roles expected of faculty members at academic institutions

Environmental Resource Manager, Ulster County Environmental Management Council, Kingston, New York, March 1988-July 1990. Principal staff member for a county-wide environmental management agency. Coordinated budgeting, planning and implementation (including public education)for a wide variety of environmental resource management and protection programs. Major issues included wetlands protection, natural resource inventory mapping, household recycling, waste motor oil collection and recycling, household hazardous waste collection and disposal.

Naturalist, Education Programs Specialist, Office and Bookshop staff, J.F. Bell Museum of Natural History, Minneapolis, Minnesota, April 1984-August 1986. Led tours and working in experiential learning area of natural history museum. Developed museum education programs and outreach programs for area children's hospitals. Also worked in bookshop and museum offices.

Field Assistant for ecological studies of Carex exilis, University of Minnesota, Department of Ecology and Behavioral Biology, 1984 and 1985. Assisted in plant ecology experiments in bogs and fens of Nova Scotia and Newfoundland, Canada and northern Minnesota.

Resident Assistant, Bailey and Comstock Halls, University of Minnesota, September 1984 - June 1986.

PUBLICATIONS

Kern, R.A. & W.H. Schlesinger. 1992. Carbon stores in vegetation. Nature 357:447-448

Kern, R.A., V.H. Dale, and J.J. Beauchamp. The effect of elevation, light and water availability on the growth and survival of Sierran conifer seedlings. (in prep)

Kern, R.A., D.L. Urban, and N.L. Christensen. Spatial patterns of seedling establishment, growth, and survival in Sierra Nevada mixed conifer forests. (in prep)

Kern, R.A. Seed rain and seed germination patterns in Sierra Nevada mixed conifer forests. (in prep)

PAPERS PRESENTED AT PROFESSIONAL MEETINGS

Kern, R.A, R. Zimmermann, & R. Oren. 1996. Canopy transpiration in a Giant Sequoia - mixed confier forest, Sequoia National Park, California, USA. Abstract in Bulletine of the Ecological Society of America 77(3):231.

Kern, R.A. 1995. The effect of light and water availability on the leaf water potential, growth, and survival of Sierran conifer seedlings. Abstract in Bulletin of the Ecological Society of America 76(2):85.

Kern, R.A., V.H. Dale & J.J. Beauchamp. 1994. The effect of elevation, light and water availability on the growth of Sierran conifer seedlings. Abstract in Bulletin of the Ecological Society of America 75(2):109.

Kern, R.A.. 1992. An estimate of the change in carbon storage in the American southwest from the Last Glacial Maximum to the present. Abstract in Bulletin of the Ecological Society of America 73(2):229.

INVITED SEMINARS

Department of Botany, Duke University, November 1996 and February 1995
Environmental Sciences Division, Oak Ridge National Laboratory, March 1994
Sequoia National Park, Interpretive series, July 1994
Sequoia National Park, Interpretive staff training, June 1994 and June 1993

MEMBERSHIPS

Ecological Society of America
American Institute of Biological Sciences
American Association for the Advancement of Science
Association for Women in Science
Phi Beta Kappa Honor Society