

FACTORS CONTROLLING PLANT DISTRIBUTIONS: DROUGHT, COMPETITION, AND FIRE IN MONTANE PINES IN ARIZONA¹

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Abstract. Recent models suggest that a trade-off in plants between tolerance of water limitation vs. tolerance of light limitation results in changes in dominant species over productivity gradients of increasing soil moisture and decreasing forest-floor light. With increasing elevation (1568–2296 m) in the Chiricahua Mountains in southeastern Arizona, soil moisture and plant cover increased and, as a result, mean forest-floor light levels decreased, in accordance with the models. The light–moisture trade-off hypothesis predicts that, over this gradient, (1) shade tolerance and drought resistance should be negatively correlated, (2) decreasing light and lack of shade tolerance (i.e., tolerance of light competition) should control upper elevational limits of species distributions, and (3) low soil moisture availability and lack of drought resistance should control lower elevational limits. With increasing elevation, however, fire frequency and litter depth also increased and soil temperature decreased. I tested the trade-off hypothesis and the role of these three additional factors in controlling upper elevational limits of three pine species distributed along this gradient.

Consistent with the trade-off hypothesis, results suggested that water stress controlled lower elevational limits of all three species. Seeds of each species germinated with the summer rains in experimental plots below their respective lower elevational limits, but all seedlings died by the end of the following May–June drought, apparently from water stress. In contrast, seedlings were still alive in experimental plots within each species' range after 2 yr. Furthermore, with decreasing elevation, seedlings of the three species increasingly occurred in microsites with relatively low light, low soil temperature, and deep litter, all reflecting high soil moisture compared to random microsites. From the middle to the lower portion of each species' range, recruitment, seedling survival, and seedling abundance decreased but height growth increased. Thus, dry season water stress appeared to control lower elevational limits by causing high mortality of young seedlings, rather than by curtailing seed germination or the performance of older seedlings.

Inconsistent with the trade-off hypothesis, upper elevational limits were not controlled uniformly across species by light limitation. In *Pinus leiophylla*, the middle elevation species, low light and deep litter appeared to control the upper elevational limits. In a field experiment, *P. leiophylla* emergence and survival were significantly lower above its upper elevational limit than in plots within its range, removal of litter increased emergence, and removal of canopy increased seedling survival. In a greenhouse experiment, *P. leiophylla* was significantly less shade tolerant than higher elevation pine species. In contrast, in *P. discolor*, the low elevation species, low light, deep litter, and low soil temperature appeared not to influence distribution. Emergence and survival were actually higher at high than middle elevations in the field experiment. Litter removal and canopy removal did not increase *P. discolor* emergence and survival, respectively, even at high elevation. In the highest elevation plots, *P. discolor* seedlings occurred in microsites slightly lower in light, higher in litter depth, and equivalent in soil temperature to random microsites, contrary to expectations if these variables were limiting. Finally, in greenhouse experiments, *P. discolor* was more shade tolerant than higher elevation species, including *P. leiophylla*. Two tests supported the hypothesis that the upper elevational limits of *P. discolor* were controlled by the high fire frequency found at higher elevation. First, *P. discolor* exhibited slow juvenile growth rates, thin bark, and other traits suggesting a lack of fire resistance compared with the two higher elevation pine species. Second, in two wild fires, survival of *P. discolor* stems was significantly lower than that for the other two species. This conclusion is corroborated by the observation that juvenile *P. discolor* occurred commonly at much higher elevations than did adults, into plots with very low light and soil temperature levels and very deep litter, a pattern likely resulting from fire suppression. Results for a third species, *P. engelmannii*, were equivocal, showing weak support for control of upper elevational limits by light.

The lack of a light–soil moisture trade-off in these species may result from *P. discolor*'s strategy of exploiting nurse tree sites at low elevation and the apparent fire-associated regeneration of the other two species. Nevertheless, control of *P. discolor* upper elevational limits by fire may, in part, be a result of constraints imposed by drought resistance on maximum growth rate and height. These results suggest that fire, or other agents of selective mortality correlated with soil resource gradients, can exert strong control over plant distribution and

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community composition, and should be incorporated into the proposed general models relating plant strategies to community structure.

Key words: *Chiricahua Mountains, Arizona; drought resistance; ecological trade-offs; elevational gradients; fire resistance; Madrean vegetation; pine-oak vegetation; pines; plant community composition; plant competition models; plant distributions; resource gradients; shade tolerance.*

INTRODUCTION

A central goal of plant ecology is to understand which factors control the local distribution of plant species and thus the composition of plant communities. A key to this focus is the observation that any given plant species tends to occur at the same relative position along similar environmental gradients within a region (e.g., Daubenmire 1943b, Grime 1979, Tilman 1988). This consistency suggests not only that we can investigate the problem by studying several similar species distributed along complex gradients, but also that similar forces may control plant distributions and community structure over many major environmental gradients. I investigated several hypotheses about the factors controlling distributional limits in three pine species, *Pinus discolor*, *P. leiophylla*, and *P. engelmannii*, which cover the lower half of the elevational gradient, from arid lowlands to productive intermediate elevations, in the Chiricahua Mountains in southeastern Arizona.

In many mountains in the western USA, from lower to upper elevations, soil moisture increases (Shreve 1915, Barton 1991) and, as a result, plant standing crop, cover, and production increase substantially (Whittaker and Niering 1975). Tilman (1988) argued that such increases in plant cover along soil resource gradients should lead to decreasing light available to juvenile plants for photosynthesis. This expectation is supported in the Chiricahua Mountains: over the ranges of the three species studied here, with increasing elevation, soil moisture and plant cover increased and forest-floor light levels decreased (Barton 1991). Several general models of plant population and community structure suggest hypotheses to explain plant distributions along such gradients. Tilman (1988) and Smith and Huston (1989), for example, propose a trade-off in plants between tolerance of water limitation vs. tolerance of light limitation that should result in changes in dominant species along gradients of increasing soil moisture and decreasing light. For the three pine species studied here, the light-moisture trade-off hypothesis predicts that (1) shade tolerance and drought resistance (*sensu* Levitt 1980) should be negatively correlated, (2) decreasing light and lack of shade tolerance (i.e., tolerance of competition for light) should control the upper elevational limits of species distributions, and (3) low soil moisture availability and lack of drought resistance should determine the lower elevational limits.

Variables other than light and soil moisture, however, are also often correlated with elevation and are potentially important in controlling plant distributions

(Daubenmire 1943b, Wright 1966, 1968, Whittaker et al. 1968, Allen and Peet 1990, Barton 1991). Temperature, which generally decreases with elevation, has been cited as a key factor in elevational distributions (Daubenmire 1943b, Lowe 1964). Starting with Merriam (1889), in fact, the common assumption in studies of plants in the southwestern USA has been that upper elevational limits of species are controlled by temperatures too low to meet growing-season heat requirements (see also Shreve 1915, Pearson 1931, Daubenmire 1943b, Lowe 1964). Along many elevational gradients, litter depth increases from near zero at low elevations to depths sufficient to physically inhibit seedling emergence at higher elevations. To the extent that species differ in seed size or other properties related to physical aspects of emergence, this gradient could exert strong control over the elevational positions of plant species. Disturbance gradients often also parallel physiographic and soil resource gradients (Harmon et al. 1983, Keddy 1985). In the Chiricahua Mountains, fire frequency increases from the lowest to the highest elevational position of the three species studied here and then decreases at higher elevations (Barton 1991; see also Allen 1989, Baisan and Swetnam 1990). Accordingly, I tested three alternative mechanisms to the light-moisture trade-off model that may control upper elevational limits: (1) low summer temperatures and differences among species in responses to temperature, (2) the inhibiting action of deep litter on seedling emergence and species differences in tolerance of such physical constraints, and (3) mortality from frequent fires and species differences in fire resistance. The first hypothesis is specific to elevational gradients, whereas the latter two include mechanisms that may operate along many soil resource gradients. Also, for *P. leiophylla*, I tested the hypothesis that deep litter in otherwise favorable microsites sets the lower limit, as an alternative to the control of lower elevational limits by water stress.

I begin the paper by documenting the patterns of distribution and abundance of adults of the three pine species over the elevational gradient. Then, I examine the extent to which abundance, demography, and growth of each species are related to elevation and by implication the environmental variables correlated with elevation, including those discussed above. By comparing within species how elevational changes in environment influence seedling recruitment, survival, growth, and eventual density, I also attempt to decipher which life stages are most important in setting elevational limits.

In the rest of the paper, I test the hypotheses de-

scribed above with a combination of correlation approaches, experimental manipulations, and species comparisons. If, as predicted by the light-moisture trade-off hypothesis, upper elevational limits are controlled by light limitation, then the light-increasing effects of disturbances such as fire should be especially important in controlling regeneration at the higher elevations of a species' range (Daubenmire 1943b, Smith and Huston 1989). Using age structure data, I test this prediction by examining whether upper elevational populations exhibited more even-aged structure and more discontinuous past establishment than lower elevation populations. Next, I use microsite preference data to test the light-moisture, litter, and temperature hypotheses by predicting that along the elevational gradient studied, microsites occupied by seedlings should change most, relative to available microsites, for variables important in distributional limits. I further test the light-moisture trade-off hypothesis with results from greenhouse experiments on the shade tolerance of two of the species, as well as two other higher elevation pine species from the Chiricahuas. These tolerance ranks and other data on response to shade are then compared to results from a previous study (Barton and Teeri 1993) to test the prediction that shade tolerance and drought resistance are negatively correlated.

I also test the trade-off and litter hypotheses with results from two field experiments in which seeds of each species were planted below, within, and above their respective elevational ranges, and litter and canopy cover were manipulated. For each variable, I predict that performance should be lower in high than middle elevation positions, but that this difference should be mitigated by the experimental diminution of that stress. I also manipulated litter cover in the field to examine the hypothesis that lower elevational limits of *P. leiophylla* are controlled in part by its intolerance of deep litter in otherwise favorable microsites. Finally, I examine the extent to which fire, acting as an agent of selective mortality, controls upper elevational limits by testing the prediction that the three species differ in (1) traits thought to confer fire resistance and (2) actual survival of wildfires.

STUDY AREA

My primary study area was in the Cave Creek drainage in the eastern part of the Chiricahua Mountains, in Coronado National Forest (31°52' N latitude, 109°15' W longitude) in southeastern Arizona (Fig. 1). The Chiricahua Mountains are a prominent part of the Mexican Highland Section of the Basin and Range Geologic Province (Fenneman 1931) and extend southeast to northwest for ≈80 km and rise from basins 1100–1300 m altitude to a maximum of ≈3000 m at Chiricahua Peak. Most soils in these mountains are derived from volcanic rhyolites and monzonites deposited in the early-to-mid-Miocene, although, at lower elevations in several major eastern drainages, pre-

tertiary sedimentary parent rock predominates (Marjaniemi 1969, Drewes and Williams 1973).

The climate of the region is arid to semiarid, with two wet seasons, one between July and September, when >50% of total precipitation falls, and the second between December and March. A pronounced dry season usually occurs between the final winter storms in March or April and the onset of the rains in July (Sellers et al. 1985). At the Southwestern Research Station, mean annual rainfall is 506 mm and mean annual temperature is 12.5°C. During 1987 and 1988, the year in which environment and vegetation were intensively measured, precipitation in the Chiricahua Mountains was consistently above normal (except for the 1987 rainy season, which was near normal). Temperatures were consistently slightly below normal in 1987 and near normal in 1988 (NOAA 1987, 1988).

Precipitation increases and air temperature decreases with increasing elevation in southeastern Arizona. For stations near the Mule Mountains, for example, Wentworth (1981) found an increase in summer precipitation (May–October) of 190 mm and a decrease of 7.3°C in mean July temperature for every 1000 m elevation increase, results similar to those of other studies (Shreve 1915, Pearson 1931, Whittaker and Niering 1975).

Vegetation in southeastern Arizona changes markedly along elevational gradients (Shreve 1915, Whittaker and Niering 1965, Niering and Lowe 1984; A. M. Barton, *unpublished data*). From the lowest (≈1550 m) to the highest elevation (≈2300 m) of my study area in the Chiricahuas, the following sequence of vegetation types occurred: open oak woodland (≈1550–1750 m elevation), pine-oak woodland (≈1750–1850 m), pine-oak forest (≈1850–2200 m), and pine forest (≈2200–2300 m).

Fire is a natural recurrent event in the mountains and surrounding desert grasslands of southeastern Arizona (Marshall 1957, 1963, Niering and Lowe 1984). In the western Chiricahuas, in a wide range of plant communities, mean fire return intervals before AD 1801 ranged from 6.2 to 14.6 yr (Swetnam et al. 1989; see also Bahre 1985, Baisan and Swetnam 1990). Since the late 1800s fires have been largely suppressed (United States Department of Agriculture Forest Service 1986). Details on the physical setting, vegetation, and natural and human disturbances on the study area can be found in Barton (1991).

STUDY SPECIES

Nine pine species occur in southern Arizona (Critchfield and Little 1966, Bailey and Hawksworth 1983). Six of these are common and one rare in the Chiricahua Mountains (Kearney and Peebles 1962). The six common species occupy distinct and consistent relative elevational positions in the region (Shreve 1915, Martin and Fletcher 1943, Wallmo 1955, Whittaker and Niering 1964, 1968). Botanical nomenclature follows

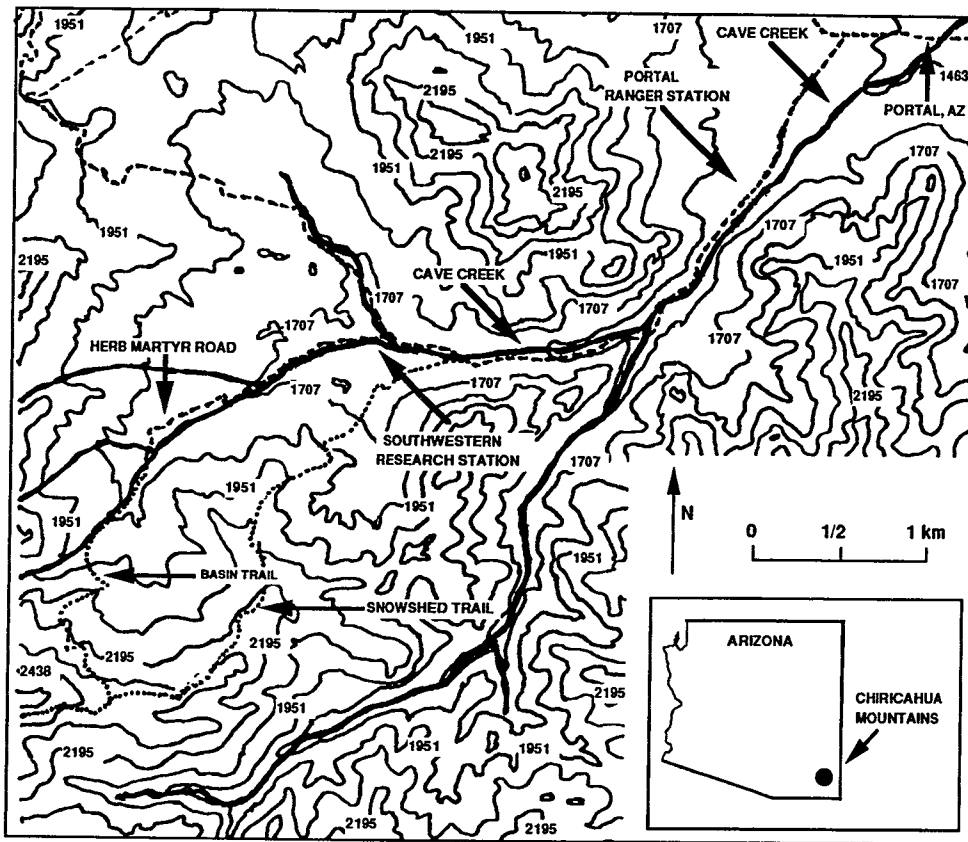


FIG. 1. Map of the study area in the eastern part of the Chiricahua Mountains in southeastern Arizona. The tributaries of Cave Creek are shown as thick dark lines, roads as dashed lines, and trails as dotted lines. Contour lines are from a United States Geological Survey topographic map (Portal Quadrangle, Arizona-New Mexico, 15 minute series, 1:62 500) expressed in feet; these are converted to metres in the figure. The map shows the locations of the nearest town, Portal, Arizona, the Portal Ranger Station, the Southwestern Research Station, Herb Martyr Road, the Basin Trail, and the Snowshed Trail.

Bailey and Hawksworth (1983) for Pinaceae and, for all others, Kearney and Peebles (1960) as updated by Lehr (1978).

In the studies reported here, I focused on the three pines occupying the lower half of the elevational gradient in the Chiricahuas: *P. discolor* Bailey and Hawksw. (= *P. cembroides* Zucc.) (1500–2000 m), *P. leiophylla* var. *chihuahuana* (Engelm.) Shaw (1600–2100 m), and *P. engelmannii* Carr (1900–2200 m). I also report on a greenhouse experiment that includes two higher elevation species, *P. ponderosa* var. *scopulorum* Engelm. (2400–3000 m) and *P. strobiformis* Engelm. (2450–3000 m). *P. discolor* and *P. strobiformis* are soft pines in the subgenus *Strobilus* (Haploxylon) and both have large, probably animal-dispersed seeds. The three other species are hard pines in the subgenus *Pinus* (Diploxylon), with small probably wind-dispersed seeds. *P. discolor* is a small tree (up to ≈ 15 m tall) typical of the pinyon pines, whereas the other species are full-sized trees often reaching 25–35 m in height. *P. ponderosa* is a much-studied pine found primarily north of the Chiricahua Mountains, whereas the distributions of the

four other species are primarily in Mexico (especially in the Sierra Madre Mountains), with northern limits in southern or central Arizona (Critchfield and Little 1966, Bailey and Hawksworth 1983). These Madrean pines have been little-studied from an ecological perspective (see McCune 1988).

METHODS

Study elevational transect

Because the lower elevations of the Cave Creek drainage are interrupted by roads, campgrounds, and private land, I worked at four sites along the elevational gradient that were separated by as much as 4 km and did not occur in a straight physical line (Fig. 1): (1) the Ranger Station site, above the Portal Ranger Station between elevations 1550 and 1650 m, (2) the SWRS site, on the property of the Southwestern Research Station between 1675 and 1700 m, (3) the Greenhouse site, along the Herb Martyr Road between 1700 and 1800 m near the beginning of the Greenhouse Road, and (4) the Basin Trail site, along the Basin Trail be-

tween Herb Martyr Campground and Snowshed Trail from ≈ 1800 to 2300 m.

I carried out all investigations, except the greenhouse experiment and the examination of pine survival after fire, within or adjacent to 48 20×50 m plots laid out in a stratified random design in 1987 and 1988 in the four sites along the elevational transect (Fig. 1). Recruitment, survival, growth, seedling microsites, and environment were sampled in a central 20×20 m or 50×4 m area of each plot ("interior plots"). Abundance was sampled in the 20×50 m plot area. For age structure, plots were extended to a larger area, which varied among plots depending on density of target species. See Barton (1991) for details on the elevational transect and plot selection.

*Environmental variables over
the elevational gradient*

In each of the 48 plots, Barton (1991) measured physiographic variables (elevation, aspect, slope, and position on slope), resource variables (soil moisture and forest-floor light levels), and condition variables (soil temperature, fire regime, litter depth, soil organic matter, soil pH, and soil texture) during late May and June 1987. This period is the height of the dry season, a time when some of these variables (e.g., soil moisture) are probably at their most limiting levels. Fire regime was quantified in two ways: (1) a fire history index, in which plots were ranked according to the degree of evidence of past fire and (2) estimates of ignition frequency for each plot, based on the relationship of ignition frequency and elevation calculated from fire records of the United States Department of Agriculture Forest Service.

All environmental variables, except for soil texture, were significantly correlated with elevation, plot aspect, or both variables (Table 1). For all variables, except percentage organic carbon, the best fits over the elevational axis were with second-order polynomial rather than linear relationships (Barton 1991). From low to high elevation plots, there were increases in soil water potential, litter depth, fire ignition frequency, fire history index, and percentage soil carbon, and decreases in soil temperature, percentage full light, openness of the canopy, percentage bare ground, and soil pH (Table 1). Aspect was significantly related to soil water potential, soil temperature, percentage light, percentage open canopy, litter depth, percentage bare ground, and organic matter (Table 1). As expected, change in these significant variables along the continuum from south-southwest to north-northeast aspects paralleled changes from low to high elevations. In accordance with Tilman (1988) and Smith and Huston (1989) (see *Introduction*), forest-floor light levels decreased from low to high soil moisture sites (Fig. 2), although this relationship varied from linear in 1986 to curvilinear

TABLE 1. Simple correlations of environmental variables with elevation and aspect.[†]

Environmental variables [‡]	Elevation	Aspect
1986 soil H ₂ O	.69***	.81***
1987 soil H ₂ O	.67***	.25*
Soil temp	-.80***	-.51***
% light	-.66***	-.29*
% open canopy	-.48***	-.32*
Litter depth	.69***	.29*
% bare soil	-.48***	-.28*
Fire index	.78***	.25
Ignition freq.	.79**	NA [§]
Soil organic C	.57***	.24*
Soil pH	-.35*	-.20
% (silt plus clay)	.03	-.03

* $P < .05$, ** $P < .01$, *** $P < .001$, otherwise $P < .05$.

[†] Data were collected from 48 plots for each variable, with two exceptions: (1) 1986 soil moisture is for 16 plots and (2) the relationship between ignition frequency and elevation was assessed independently with United States Department of Agriculture Forest Service fire records using nine different 100-m elevational increments between 1500 and 2300 m (see Barton 1991).

[‡] Environmental variables: 1986 soil H₂O = 1986 dry season soil water potential between 2 and 12 cm depth; 1987 soil H₂O = 1987 dry season soil water potential between 2 and 12 cm depth; soil temp = dry season soil temperature at 12 cm depth; % light = percentage of unobstructed photosynthetically active radiation at 10 cm above the ground; % open canopy = percentage of canopy not obstructed by vegetation between 10 cm above the ground and canopy level; litter depth = depth in centimetres of duff and litter above mineral soil level; % bare soil = percentage of forest floor with exposed mineral soil; fire index = index from 1 to 3 of increasing extent of evidence of past fire; ignition frequency = number of lightning-caused ignitions per 10 000 m² per 100 yr; soil organic C = percentage organic carbon in soil between 2 and 12 cm depth; soil pH = pH of soil between 2 and 12 cm depth; % (silt plus clay) = combined percentage of silt and clay in soil between 2 and 12 cm depth. See Barton (1991) for details.

[§] NA = not applicable. Because aspect was expressed as one of four cardinal directions in United States Department of Agriculture Forest Service records, correlation between ignition frequency and aspect could not be calculated. Other analyses of ignition frequency and aspect are reported in Barton (1991).

in 1987. Fire incidence was also strongly related to soil moisture: with increasing moisture availability in both 1986 and 1987, the degree of evidence of past fire increased. For details on environmental changes over the elevational gradient, see Barton (1991).

*Abundance, survival, and growth
over the elevational gradient*

Data collection.—I collected data for the three study species on the abundance of all size classes and survival and annual height growth of 1st-yr recruits and older seedlings to examine correlations between these dependent variables and the elevation gradient. In all 48 plots, I measured the diameter at 1.4 m (dbh) of all pine individuals ≥ 2 m in height (called adults) and the

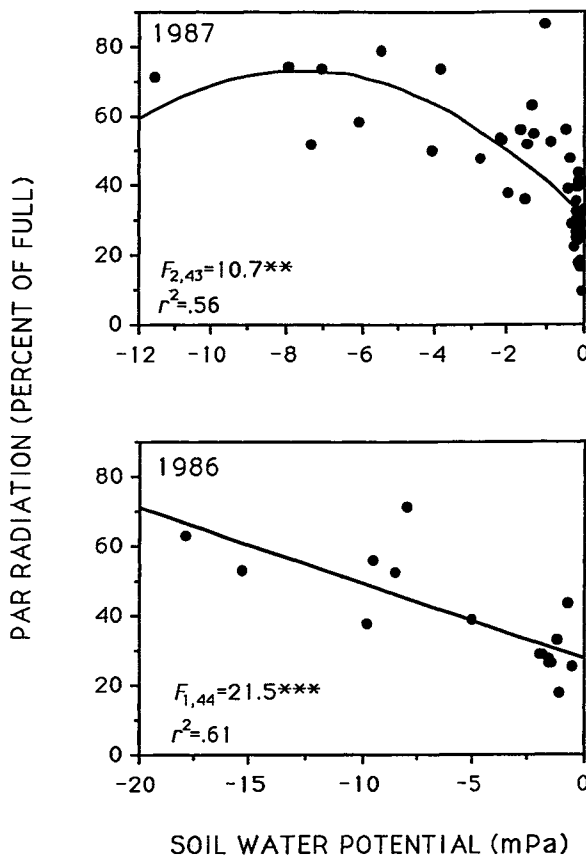


FIG. 2. Photosynthetically active radiation (percentage of unobstructed levels) at 10 cm above the ground, plotted against soil water potential for 1987 and 1986. F values and degrees of freedom are given for a second-order polynomial (1987) and simple linear (1986) regression (** $P < .01$, *** $P < .001$, otherwise $P > .05$).

height of all individuals 0.10–1.99 m tall (called seedlings). In all 48 interior plots, all pine seedlings were tagged or mapped and measured once each April–May and once each July–August between 1986 and 1988. On each visit, I documented survival, height (length of stem), and annual seedling height growth. The number of recruits (1st-yr recruits counted in the following spring, e.g., 1986 recruitment counted in spring 1987) was also counted for 1986 and 1987.

I supplemented the sample sizes for growth for some plots by using randomly chosen plants outside of interior plots but within the full-sized plots. Annual seedling height growth was also estimated back to 1984 by measuring the length of past annual shoots. This method was not used for very small plants that had not yet formed clear annual shoots. For details on this method, see Barton (1991).

In 1987, for all 48 plots and 3 species, I counted 786 adults (≥ 2 m tall), 1534 seedlings (< 2 m tall, > 1 yr old), and 525 1st-yr recruits and followed the survival

of 964 older seedlings and 525 1st-yr recruits and the growth of 1187 seedlings.

Statistical analyses.—Because nearly all of the environmental variables were strongly intercorrelated along the elevational gradient (Barton 1991), regressions of the plant variables on all or subsets of these independent variables produced misleading or uninterpretable results. I avoided this problem by regressing plant variables on the independent variables elevation and aspect. Elevation and aspect were significantly correlated with, although usually curvilinearly (Barton 1991), nearly all of the environmental variables measured in the sample plots (Table 1). Analyses using principal components, derived from the variables in Table 1, as independent variables produced results similar to those using simply elevation and aspect (Barton 1991). I chose to use physiography here because this approach is more straightforward. Aspect was essentially used as a covariate; where it was not significant, elevation alone was used as the independent variable.

The responses of many of the dependent plant variables were curvilinear over elevational and aspect gradients. Although Gaussian models might fit some of these distributions (see Gauch 1982), I chose to use second-order polynomial models because my sampling on the tails of distributions appeared to be insufficient to distinguish between the two models, because polynomial models gave satisfactory fits to most of the data, and because the polynomial models were easy to use for statistical hypothesis testing. I began with a full model of second-order polynomials for elevation and aspect, and dropped polynomial terms that were not significant. For all of the multiple-regression models using height growth as the dependent variable, I included initial height (sometimes as a second-order polynomial) as a covariate. Also for the height growth and all other regression analyses with more than one Y value for each X value, I followed the protocol outlined by Sokal and Rohlf (1981: 483 and Box 10.2) for determining the appropriate error mean square.

To examine how the three pine species physically sorted out along the elevational gradient, I compared their mean elevational locations. I gave each plant the elevation value for the plot in which it resided and then calculated mean elevations for each size class for each species. I first examined whether differences in location among species and among size classes interacted by using a two-way ANOVA of species and size class with interaction term. Where the interaction term was significant, I compared species (for each size class) or compared size classes (for each species) with ANOVAs.

In these and all other analyses reported in this paper, I tested the adherence of data sets to the model assumptions and, where the assumptions were not met, used more appropriate methods (transformed data or nonparametric tests). Significance values for all mul-

multiple comparisons were calculated using the Bonferroni method (Day and Quinn 1989). Analyses were carried out using the SYSTAT (version 3.2, Wilkinson 1988) or Statview 512+ (version 1.1) statistical packages.

*Comparison of age structure at
low and high elevations*

I used age structure data to test the prediction of the light-moisture trade-off hypothesis that upper elevational populations of each species should exhibit more discontinuous establishment than lower elevation populations. I sampled age structure of each species at a low and at a high elevational position relative to the median of its adult distribution along the elevational transect. The two elevational locations were, respectively, 1568–1579 and 1763–1779 m for *P. discolor*, 1768–1779 and 1871–1913 m for *P. leiophylla*, and 1820–1843 and 2096–2187 m for *P. engelmannii*. I sampled all individuals ≥ 10 cm tall for a given species either in all full-sized plots (extended to even larger size where stem density was low) between these elevations or, where seedling stems were cut, in belt transects starting at the corners and running in a direction away from the plots. Plots adjacent elevationally were generally within 100 m physical distance of each other. In *P. discolor*, many seedlings occurred above the elevational range of adults. To assess whether these individuals were young plants or simply slow-growing older plants, I also sampled 10 of the largest individuals found between 1871 and 1974 m. In total, I aged 147 *P. discolor* in 10 000 m² at low elevation and 257 in 3000 m² at high elevation, 111 *P. leiophylla* in 2000 m² at low elevation and 319 in 10 000 m² at high elevation, and 333 *P. engelmannii* in 3000 m² at low elevation and 90 in 4000 m² at high elevation.

I extracted increment cores at 30 cm height, at trunk locations perpendicular to the surrounding slope, and measured diameter at core height and breast height (1.4 m) for all stems ≥ 2 m tall. I estimated ages of these trees by counting the number of rings in sanded, polished, unstained cores at 10–40 \times magnification under a dissecting scope. By using the relationship between plant height and the average annual height growth rate of seedlings (< 2 m tall) from 1986 to 1987, the years for which sample sizes were the largest, I estimated the expected age of stems at the 30 cm core height separately for each species at each of its two age structure sampling locations (Barton 1991). Estimated age at 30 cm was then added to the direct count of rings for each stem.

Stems between 1 and 2 m tall were cut at ground level in the upper elevation *P. discolor* and lower elevation *P. leiophylla* and *P. engelmannii* sites and the rings counted directly. For all other stems between 0.10 and 1.99 m, I measured height in the field and estimated age to the height of the stem using the same

estimation method described above for correcting for increment core height.

*Changes in seedling microsites over
the elevational gradient*

Microsites occupied by pine seedlings were compared with random microsites over the elevational gradient. In a subsample of interior plots chosen to cover the entire range of the study pine species and environments, I simultaneously measured the microsites of previously censused (and thus tagged or mapped) seedlings and random microsites between the times 1030 and 1330 during the cloudless period 1–22 June 1988. This period is the height of the dry season, a time when the microsite variables measured were probably at their most limiting levels. The number of plots sampled was 23 for *P. discolor*, 11 for *P. leiophylla*, and 11 for *P. engelmannii*. In each plot, I used all pine seedlings up to a maximum of 20 per species, in which case 20 individuals were chosen by a random numbers table before sampling. Random microsites, which equalled the total number of seedling microsites per plot, were selected by initially choosing a random direction and distance (up to 3 m) from the center of the plot and subsequently from the previous microsite.

At each microsite, I measured light (photosynthetically active radiation, PAR), litter depth, soil temperature, and canopy openness. Cumulative radiation was measured over 2 min with an integrating LI-COR meter with PAR sensor mounted on a metal stake used to orient the sensor perpendicularly to the horizon at ≈ 10 cm above the ground. For plant microsites, the focal plant was bent away so as not to block light from the sensor. I converted each light datum to percentage of unobstructed radiation, which was measured in the open at the time of the microsite sampling. Soil temperature at 7 cm depth (the approximate rooting depth of typical 2-yr-old pine seedlings) was also measured over a 2-min equilibration period, with Taylor digital pocket thermometers (Model Number 9860). To estimate canopy openness, I imposed an imaginary vertical cylinder 5 m in diameter from each plant toward the zenith and recorded the degree of obstruction by vegetation as closed ($> 2/3$ obstruction), open ($< 1/3$ obstruction), and intermediate ($1/3$ – $2/3$ obstruction). I investigated the relationship of soil moisture to canopy cover and litter depth with data used to characterize the elevational gradient independently of this microsite data set (Barton 1991).

I tested the light-moisture trade-off, litter, and temperature hypotheses by comparing the microsites occupied by pine seedlings to those available (i.e., random) in relation to the location of the plot along the elevational gradient. For example, if light limitation controls the upper elevational limits of species, then from low to high elevation plots, plants should increasingly occupy microsites with high light compared to

random microsites (see Neilson and Wullstein 1983 for a similar method). Because the curves for plant and random microsites over elevation often differed in their shape (e.g., linear vs. second-order polynomial) and thus could not be compared directly, I analyzed the data with a regression for each microsite variable using as the dependent variable each plant microsite value minus the mean random value for the given plot and using elevation as the independent variable. Second-order polynomials were tested first, and the second-order term was dropped from the model if it was insignificant.

Greenhouse experiment: comparisons of species in shade tolerance

Barton and Teeri (1993) examined differences in drought resistance among five pine species in the Chiricahuas with greenhouse experiments. To test the light-moisture trade-off hypothesis prediction that drought resistance rankings from this study are negatively correlated with shade tolerance, I investigated the relative shade tolerance of *P. discolor* and *P. leiophylla*, as well as *P. ponderosa* and *P. strobiformis*, two higher elevation species, in a greenhouse at the University of Michigan Matthaei Botanical Gardens. I collected seeds from October 1986 to April 1987 from at least 20 individuals of each species scattered over the elevational gradient. Details on germination and seedling care can be found in Barton and Teeri (1993). Unfortunately, I did not have sufficient seed to include *P. engelmannii*.

I began the experiment 1 mo after germination by transferring surviving plants to benches under mercury vapor lights supplemented by natural greenhouse light (total photosynthetic photon flux density of 450–850 $\text{mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ depending on plant position, $\approx 25\%$ of full light conditions in June in the study area). From 23 October 1987 to 7 March 1988, plants were grown with ample soil moisture and nutrients in one of two treatment groups: (1) radiation reduced to 5% of ambient by shade cloth or (2) full radiation. Trays were rotated twice per week to avoid bench position effects. I monitored survival weekly and at the end of the experiment harvested, dried (at 95°C), and weighed all aboveground and belowground parts of each plant.

Field experiments: elevational position, litter depth, and light

P. leiophylla, litter experiment.—Along the elevational transect studied, *P. leiophylla*'s lower elevational limit occurs in pine-oak woodland, which supports a partial canopy and a nearly continuous litter layer (mainly pine needles). Below this elevation occurs open oak woodland, islands of vegetation separated by large open spaces. Open areas tend to have very sparse litter cover, whereas vegetation clumps usually support com-

pact, sometimes deep litter (mainly oak leaves and juniper needles). *P. discolor* seedlings occur abundantly under these vegetation clumps and very rarely in the open. I suspected that these protected microsites support high levels of soil moisture and low temperatures, but that the relatively small seeds of *P. leiophylla* are incapable of establishing through the obstructing litter.

In 1986, I tested this hypothesis by setting up one 2.3×2.3 m block under each of two large vegetation islands below *P. leiophylla*'s lower elevational limit and two blocks in pine-oak woodland where it is common, both sites located in the Greenhouse study area. Each block contained four 0.75×0.75 m plots separated from each other and the edge of the block by 0.20-m buffer strips. Two randomly chosen plots were manually cleared of litter, exposing mineral soil; the other two were not manipulated. Seeds were collected from 35 trees in the experimental area in April 1986. Thirty-six seeds were planted to a soil depth of ≈ 1 cm in each subplot on 29 June 1986 after rain had fallen on three consecutive days. Seeds of *P. leiophylla*, as well as *P. discolor* and *P. engelmannii*, typically germinate with the summer rains (Jones 1974; A. M. Barton, *personal observation*). I measured percentage soil moisture (gravimetrically between 2 and 12 cm depth) from two randomly chosen microsites in each subplot on 23 June before the treatments were imposed (after >2 mo of no rain) and again on 14 July (after 14 consecutive days of no rain). Emergents were monitored at least twice a week until 25 August and then again on 5 and 30 September. I also checked for survival monthly during the periods March–August 1987 and April–June of 1988 and 1989.

1987 field experiments: elevational position, litter depth, and light.—I performed two field experiments in 1987, one on “xeric limits” and one on “mesic limits,” using all three species. The xeric limits experiment indirectly tested the prediction of the light-moisture trade-off hypothesis that lower elevational limits are controlled by water stress by comparing seedling emergence and subsequent success above and below lower elevational limits. The experiment also tested whether lower limits are enforced by a lack of seed germination or by a lack of subsequent seedling establishment. I set up for each species a separate split-plot design with two factors, litter (two control and two removal plots within a block) and position (near the mean elevation of adult abundance [middle] vs. just below the lower elevational limit of the given species' distribution [lower]). Because of variability in availability of seeds, the number of blocks differed among species and position (lower/middle position) as follows: 6/7 for *P. discolor*, 3/4 for *P. leiophylla*, and 3/3 for *P. engelmannii*. Each of the four plots within a block provided 24×36 cm of space for 30 seeds for a single species and was separated by 18 cm from adjacent plots.

In the mesic limits experiment, I addressed the light-

moisture trade-off and litter hypotheses by testing the prediction that performance should be lower in high than middle elevation positions, but that this difference should be mitigated by the removal of stressful levels of light and/or litter. I set up blocks at middle and at high elevational positions (just above the upper elevational limit) for each species. Blocks contained only one litter removal and one control plot and thus were half the size of the xeric experimental blocks. To investigate the role of light, I paired each control block with a treatment block, identical except that the canopy was opened by wiring trees and branches away or, where this was impractical, cutting overhanging branches. Three pairs (canopy removal vs. control) of blocks were used at each of the two elevational positions for each species.

On 3 and 4 July 1987, just before the usual onset of the summer rains, 30 seeds of each species were planted in each plot for both experiments at a soil depth of ≈ 1 cm. Emergents were tallied at least twice per week until 15 August and then once per week until 13 September. Survival and epicotyl growth were then observed on 7 December 1987, 12 April 1988, 26 June 1988, 5 April 1989, and 20 June 1989.

Because the rains did not arrive fully until several weeks after planting, many seeds were removed by predators before they could germinate (Barton 1991). Perhaps as a result of this predation, the number of emergents and eventual established plants was very low, and I had to abandon the original statistical design. Xeric and mesic experimental data were combined where possible, and only some of the analyses planned prior to the experiment could be performed. Using Mann-Whitney *U* tests, I compared seedling emergence for each species (1) between middle vs. low and middle vs. high elevational positions for control plots and (2) between litter removal and control plots at each of the three elevational positions. Using *G* tests, I compared survival for each species (1) between middle vs. low elevation and middle vs. high elevation and (2) among levels in an analysis of both elevational position (middle vs. high) and canopy removal (control vs. treatment). Because of small sample sizes, I could analyze height growth data for *P. discolor* only and had to conduct these tests (ANOVAs for each measurement date) separately on the effects of elevational position, litter removal, and canopy removal, ignoring interactions among the three factors.

Comparisons of species in fire resistance

I tested the fire resistance hypothesis by comparing the three species in (1) traits thought to be crucial in fire resistance (ability to survive fire) and (2) survival through two wildfires.

Comparisons of species in traits related to fire resistance.—I quantitatively compared the three pine species in terms of three often-cited adaptations for sur-

living fire: fast height growth in seedlings, fast diameter growth, and thick bark (Spalt and Reifsnyder 1962, Daubenmire 1972, Wright and Bailey 1982, McCune 1988). I qualitatively examined other traits thought to play an important role in fire tolerance.

Above, I described methods for comparing annual seedling height growth rates of the species between 1984 and 1987. To illustrate the consequences of the differing rates for the time needed to attain heights sufficient to tolerate mild ground fires, I used 1986–1987 data, the years for which sample sizes were largest, to project the height growth of typical individuals of each species over years. In this projection, I used the least squares solution of this relationship as well as 95% confidence intervals around curves.

Differences among species in adult growth rate were estimated by using the relationship between diameter and age: faster growing individuals should reach larger size at a given age. I used only the age range held in common by the six populations (three species, two populations per species) in regression models, with diameter as the dependent variable and age, populations, and the interaction term (differences in slope) as independent variables. These population (species) comparisons may be confounded by differences in early growth conditions experienced by each population (e.g., establishment immediately after stand replacement vs. in intact stands).

I measured bark thickness of stems ≥ 2 m in height using the increment cores described above. Stems were bored at 30 cm height, avoiding interstices between bark plates where actual bark thickness would have been underestimated. I measured bark thickness directly for 1–2 m tall individuals cut for ring analysis. I analyzed bark data separately in relation to tree diameter and age with regression models including an interaction term for slope differences. I used only the ranges of size and age common to the six populations.

Comparisons of species in survival through fire.—I compared fire resistance of the three species by documenting survival of stems through a 0.38-km² fire in 1985 in Pine Canyon in the Chiricahuas and a >100 -km² fire in 1989 on Animas Peak (within 50 km of the Chiricahuas) on the Nature Conservancy's Gray Ranch near Animas, New Mexico. Prior to fire, the Pine Canyon area contained a mixture of all three pines, as well as *Quercus arizonica*, *Q. emoryi*, *Q. hypoleucoides*, and *Juniperus deppeana*, whereas the Animas fire area contained mainly *P. leiophylla*, *Q. hypoleucoides*, *Juniperus deppeana*, and *P. discolor*. In both fires, the survival of all stems ≥ 1.4 m in height was tallied along transects 5–10 m wide and of variable length in areas where fire killed some but not all aboveground stems. I measured the diameter at breast height (dbh) of all stems and identified them to species based on distinguishing traits not modified by fire (e.g., needle appearance, persistent vs. nonpersistent cones, persistent

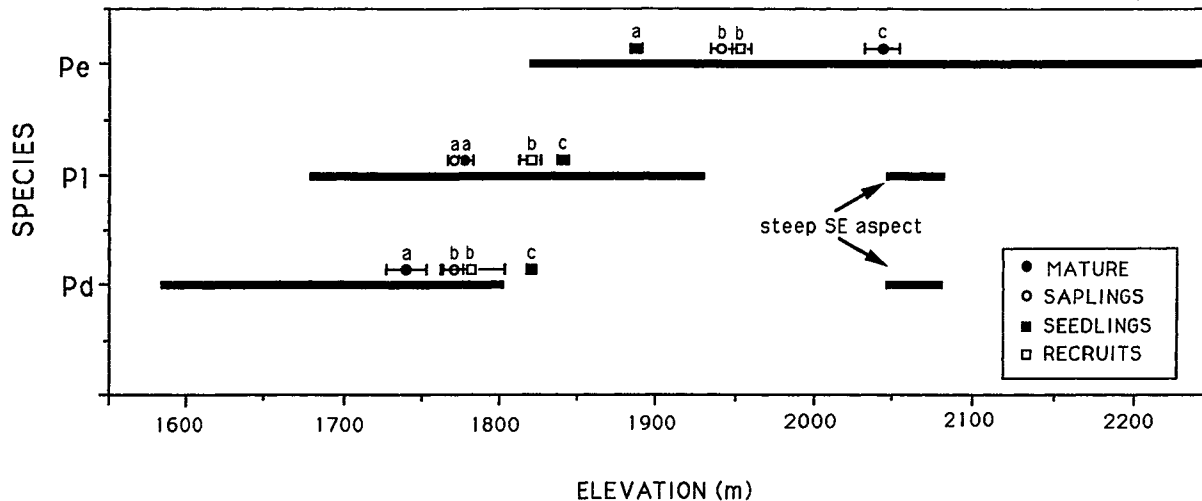


FIG. 3. Elevational distributions (solid line) and mean elevation (± 1 SE) for four size classes of *P. discolor* (Pd), *P. leiophylla* (Pl), and *P. engelmannii* (Pe) from 48 plots located along the study transect. A given plot was included in a species' distribution if its basal area there exceeded 2% of the maximum found for that species. Mature trees were ≥ 15 cm dbh for *P. leiophylla* and *P. engelmannii* and ≥ 10 cm dbh for *P. discolor*, saplings were smaller than canopy trees and ≥ 2 m tall, seedlings were < 2 m in height but > 1 yr old, and 1st-yr recruits were plants that emerged in summer 1987 and survived to spring 1988. Within each species, size classes bearing different letters are significantly different from each other ($P < .05$, Bonferroni multiple-comparison t tests). For each size class, all multiple comparisons of the three species were significant ($P < .05$, Bonferroni multiple-comparison t tests), except for the sapling locations of *P. discolor* vs. *P. leiophylla*.

vs. deciduous bundle sheaths). Differences among species in percentage survival were assessed with G tests.

It is important to recognize one source of bias in such post hoc sampling of survival through fire. Some stems, especially small ones, were burned to the extent that identification was impossible and other small stems may have been completely consumed by fire and also not counted. Thus, survival estimates for small size classes may be inflated. If species differ in their combustibility or in the portion of stems in small size classes, estimated differences in fire resistance could be erroneous.

RESULTS

Distributions and positions of the three pine species over the elevational gradient

The distributions of the three species along the elevational gradient differed as expected, with *Pinus discolor* at lower elevations, *P. leiophylla* at intermediate elevations, and *P. engelmannii* at higher elevations (Fig. 3). The sequence of lower and upper elevation distributional limits of species corresponded closely to these ranks, although upper limits were complicated by variation in aspect. Excluding the short southeast-facing portion of the transect, between 2046 and 2081 m, upper elevational limits were ≈ 1800 m for *P. discolor*, 1913 m for *P. leiophylla*, and 2187 m for *P. engelmannii*. The mean locations of the three species along the elevational axis also corresponded closely with the distributions shown in Fig. 3, and differences among species were strongly significant for all size classes, except saplings (Fig. 3).

Mean locations along the elevational gradient also differed significantly among size classes within each species (Fig. 3): seedlings of *P. discolor* and *P. leiophylla* were higher than mature stems and *P. engelmannii* seedlings were lower than mature stems. Sapling locations were intermediate to those of seedlings and mature stems and 1st-yr recruits tended to occur near seedlings. The most extreme shifts between mature trees and seedlings occurred in *P. discolor*, in which juveniles were found commonly at much higher elevations than mature stems (Fig. 3). As a result of the size class differences, elevational means of the three species were more separated for adults than for any of the other three size classes (species \times stage interaction: $F_{6, 2835} = 37.64$, $P < .0001$).

Abundance, survival, and growth over the elevational gradient

Regressions of abundance, survival, and growth over elevation.—Many of the regressions of abundance, survival, and height growth with elevation were significant, suggesting that some combination of the correlated environmental variables control the elevational distributions of the pine species.

The three species' adult abundance curves were skewed over the elevational gradient (Fig. 4), especially if the outlying southeast-facing plots are excluded. Adult basal area and density of *P. discolor* decreased significantly with increasing elevation, as did *P. leiophylla* adult density. *P. leiophylla* basal area and both abundance variables in *P. engelmannii* were not significantly related to elevation or aspect (Fig. 4). Although the spacing of plots probably resulted in my missing

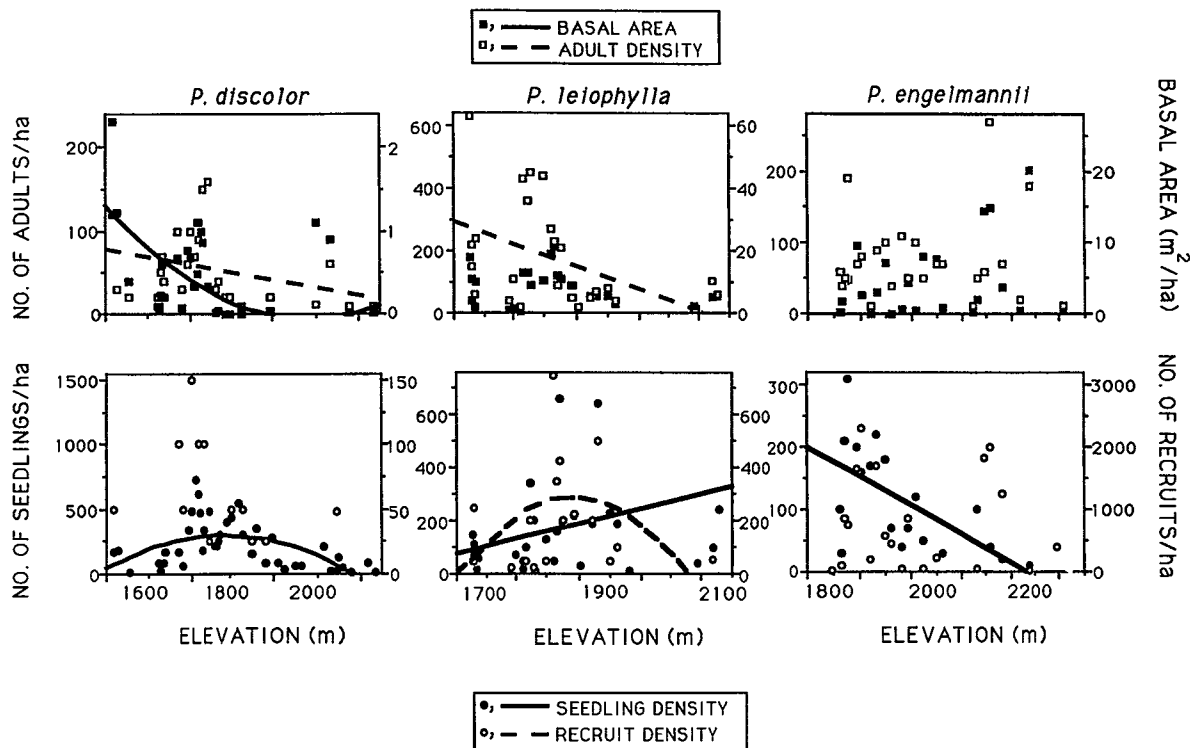


FIG. 4. Basal area and density of adult stems (≥ 2 m tall) and density of seedlings (< 2 m tall but > 1 yr old) and 1st-yr recruits (seedlings germinating in summer 1987 and surviving to spring 1988) plotted against elevation for plots within the range of three pine species. Elevational position of species increases from left to right. Curves are given for relationships with elevation for which $P < .05$, except for seedling density of *P. leiophylla* for which $.05 < P < .10$ (from F tests in which aspect was held constant). Initial models included both linear and second-order polynomial terms of elevation and aspect as independent variables. Insignificant second-order polynomials were subsequently dropped from the analysis. Note that the scales of the x and y axes differ among species.

the lower elevation "tail" of *P. discolor* and *P. leiophylla*, observations at other sites suggested that their lower limits along the study transect were abrupt.

Seedling density was related to elevation for all three species (Fig. 4). *P. discolor* showed a significant second-order polynomial association with elevation; *P. leiophylla* seedling density increased from low to high elevation ($.05 < P < .10$); in *P. engelmannii*, seedling density decreased from low to high elevation (Fig. 4). For *P. discolor* and *P. engelmannii*, recruit densities paralleled seedling densities, but the relationships with elevation were not significant (Fig. 4). *P. leiophylla* recruit density was significantly related to elevation, with the maximum at intermediate elevations.

Survival was so high in all plots for seedlings of all species between 1 and 2 m tall (overall mean = 97%) that I did not analyze its relationship to environment. The survival of 1st-yr recruits and seedlings (< 1 m tall) of *P. discolor* was not significantly associated with elevation (Fig. 5). Given that most plots exhibited 100% survival for both life stages, this lack of pattern may be due to restricted variation among plots. *P. leiophylla* survival increased significantly with increasing elevation for seedlings but not for recruits. For *P. engelmannii*, 1st-yr recruit survival was positively related

to elevation ($.05 < P < .10$), but no clear relationship occurred for survival of older seedlings (Fig. 5).

Annual height growth rates of seedlings from 1984 to 1987 for each species decreased from low to high elevations (only 1986 and 1987 are shown in Fig. 6). This result was significant for all 4 yr for *P. discolor* and *P. leiophylla*, but was significant in 1986 only for *P. engelmannii*. For all of these regressions, initial height was significantly related to height growth either linearly (1985 growth of *P. leiophylla*) or curvilinearly (all others).

Comparisons of abundance, survival, and growth among species.—Whereas *P. leiophylla* and *P. engelmannii* often dominated sites visually, *P. discolor* was at most a codominant with several other species. Mean basal area per plot was highest for *P. leiophylla*, intermediate for *P. engelmannii*, and by far the lowest for *P. discolor* (Table 2). In contrast, seedling density of *P. discolor* was higher than that of the other two species, but this was significant only in comparison to *P. engelmannii* (Table 2). The density ranks were exactly reversed in regard to the number of 1st-yr recruits in 1986 and 1987 (Table 2), with *P. engelmannii* having very high and *P. discolor* very low recruit density. Although survival was very high and did not differ among

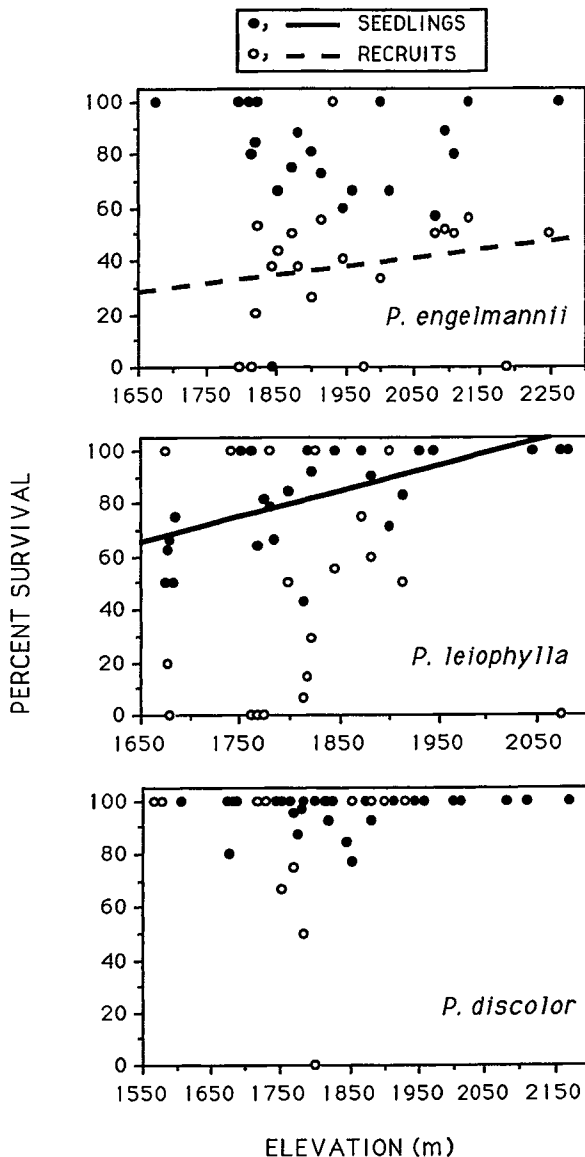


FIG. 5. Percentage survival of 1st-yr recruits (from April 1988 to July 1988) and older seedlings (<1 m tall; from April 1987 to July 1988) plotted against elevation for three pine species. Curves are given for relationships for which $P < .05$. Initial models included both linear and second-order polynomial terms of elevation and aspect as independent variables. Insignificant second-order polynomials were subsequently dropped from the analysis. Note that the scale of the x axis differs among species. Results were as follows: *P. engelmannii*: seedlings, $F_{1,11} = 0.06$, $P > .10$ and recruits, $F_{1,13} = 4.2$, $P = .06$, $r^2 = 0.24$; *P. leiophylla*: seedlings, $F_{1,16} = 13.0$, $P < .01$, $r^2 = 0.47$ and recruits, $F_{1,7} = 2.9$, $P > .10$; *P. discolor*: seedlings, $F_{1,26} = 0.9$, $P > .10$ and recruits, $F_{1,6} = 0.1$, $P > .10$.

species for plants 1–2 m tall, survival of both 1st-yr recruits and seedlings 0–1 m tall was significantly higher in *P. discolor* than for each of the other two species. *P. leiophylla* survival was significantly higher than that of *P. engelmannii* for older seedlings but did not differ for 1st-yr recruits (Table 2). In contrast to survivorship patterns, seedlings of *P. leiophylla* grew the fastest in height, *P. engelmannii* were intermediate, and *P. discolor* were relatively slow growing. In summary, then, *P. discolor* was uncommon as an adult, but seedlings were abundant and survived well but grew slowly. The other two species largely exhibited the opposite traits, but, compared to *P. engelmannii*, *P. leiophylla* grew faster as a seedling and was more abundant as an adult.

Comparison of age structure at low and high elevation

Age structure in *P. discolor* did not support the prediction of the light-moisture trade-off hypothesis that within each species the upper elevation population should exhibit discontinuous, even-aged recruitment relative to the lower elevation population. Although the timing of recruitment pulses differed somewhat (Fig. 7), the two populations of *P. discolor* exhibited similarity in recruitment patterns (Fig. 7), with stand initiation between 1898 and 1908 (i.e., years 80–90 in Fig. 7), a period of recruitment after that lasting 30–40 yr, and abundant recent establishment.

As described previously, many apparent juveniles of *P. discolor* occupy elevations substantially above that of the upper limit of adults. Ring counts of 10 of the larger of these individuals confirmed that they were substantially younger than adults at lower elevations, with a range in age between 20 and 47 yr. By far the bulk of higher elevation juveniles were smaller and thus likely younger than these plants.

For *P. leiophylla*, age structure of the high elevation population suggests pulses of recruitment between 170 and 180 yr ago and 70 and 100 yr ago and abundant recent establishment (Fig. 7). In contrast, the low elevation population was initiated much more recently and experienced abundant recruitment in the first 50 yr but relatively little recent establishment. The two age structure distributions differ significantly, with the high elevation population exhibiting a much higher ratio of juvenile to mature individuals (Fig. 7). However, one could also argue that, over most of the record (all but the most recent two decades), age distribution in the two populations is very similar, both exhibiting marked pulses in recruitment. Both interpretations contradict the prediction of the light-moisture trade-off hypothesis.

The shapes of *P. engelmannii* age structure differed significantly between the high and low populations in a way consistent with the trade-off prediction (Fig. 7). In the low elevation population, the past 70 yr are characterized by continuous recruitment. Before that,

recruitment appeared to occur more consistently between 140 and 240 yr ago than between 70 and 140 yr ago, although this is based on a small number of trees. In contrast, the high elevation population shows strong discontinuity in recruitment, with many stems from ≈ 60 and 90 to 100 yr and a scattering of few stems from 130 to 310 yr. Relatively few seedlings have established recently.

Only the high elevation *P. discolor* and the low elevation *P. leiophylla* populations were sampled on the same site (Greenhouse area). *P. leiophylla* colonized this site at least a decade earlier than *P. discolor* (Fig. 7), despite the high likelihood that both species had seed trees near the site (A. M. Barton, *personal observation*). After 30–40 yr of abundant recruitment, both populations apparently produced few plants over a several decade period. *P. discolor* resumed abundant recruitment 40 yr ago but *P. leiophylla* did not. The resulting age distributions differ significantly in shape (Kolmogorov–Smirnov test, maximum difference = 0.44, $P < .01$). Recent success of *P. discolor* under intact canopy has increased its total stem density to above that of *P. leiophylla*, although *P. leiophylla* still far outstrips *P. discolor* in adult density and basal area.

Changes in seedling microsites over the elevational gradient

Correlations among variables.—The four microsite variables, canopy openness, forest-floor light, soil temperature, and litter depth, were strongly correlated with each other. When the effect of block (i.e., differences among plots in which measurements were taken) is removed, percentage light increases ($F_{2, 1006} = 187.44$, $P < .0001$), soil temperature increases ($F_{2, 1006} = 184.41$, $P < .0001$), and litter depth decreases ($F_{2, 1006} = 169.15$, $P < .0001$) with increasing canopy openness. The three continuous variables show similar correlations among themselves when among-plot differences are removed: with increasing percentage light, soil temperature increased ($F_{1, 1007} = 178.04$, $P < .0001$) and litter depth decreased ($F_{1, 1007} = 69.84$, $P < .0001$), and with decreasing litter depth, soil temperature increased ($F_{1, 1007} = 377.62$, $P < .0001$). Percentage soil moisture was higher under trees than in adjacent open areas ($F_{1, 44} = 11.74$, $P < .001$, random-blocks ANOVA) at lower elevation and increased with increasing litter depth when the effect of plot was removed ($F_{1, 222} = 25.44$, $P < .0001$). In these same plots, litter depth was substantially higher under vegetation ($\bar{X} \pm 1 \text{ SE} = 1.77 \pm 0.17 \text{ cm}$) than in the open ($0.44 \pm 0.09 \text{ cm}$) ($F_{1, 108} = 52.25$, $P < .0001$).

Seedling microsites of each species.—The microsite results were consistent with some aspects of the light-moisture trade-off hypothesis that light controls upper and water stress controls lower elevational limits, but also supported the importance of litter and temperature. In low elevation plots for each respective species,

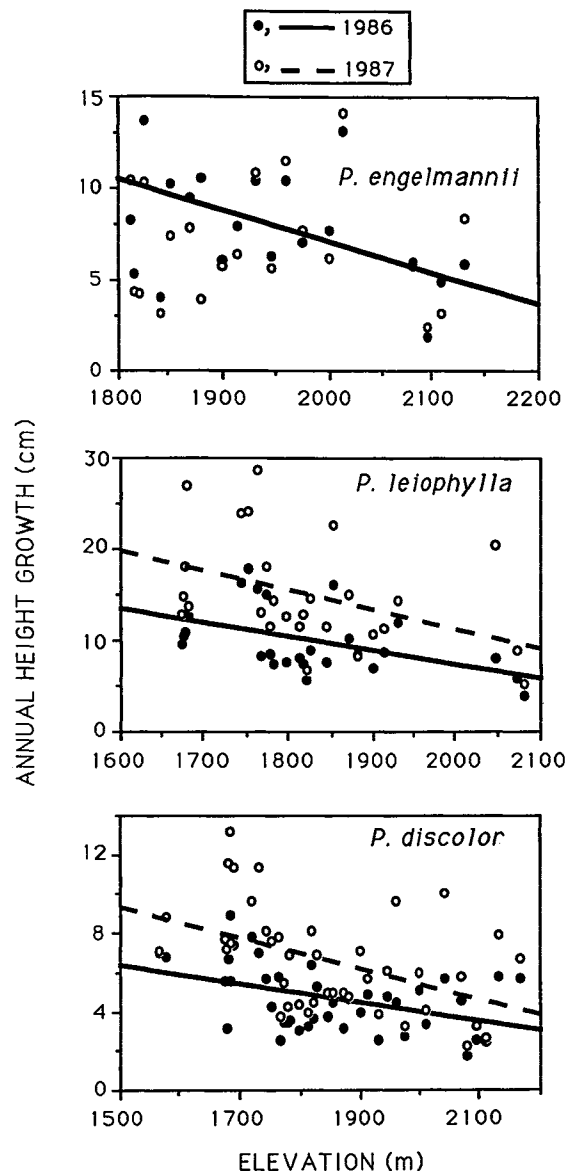


FIG. 6. Annual height growth for 1986 and 1987 of seedlings ($< 2 \text{ m}$ tall but $> 1 \text{ yr}$ old) plotted against elevation for three pine species. Each data point represents the mean of 4–64 seedlings per plot. Curves and r^2 values are given for relationships for which $P < .05$. Initial models included both linear and second-order polynomial terms of elevation and aspect as independent variables. Insignificant second-order polynomials were subsequently dropped from the analysis. Initial height was also included in models as a second-order polynomial term, except for 1985 growth of *P. leiophylla* for which it was included as a linear term. Note that the scales of the x and y axes differ among species. Results were as follows: *P. engelmannii*: 1986, $F_{1, 17} = 5.3$, $P < .05$, $r^2 = .59$ and 1987, $F_{1, 17} = 1.7$, $P > .10$; *P. leiophylla*: 1986, $F_{1, 25} = 17.4$, $P < .001$, $r^2 = 0.52$ and 1987, $F_{1, 25} = 12.8$, $P < .001$, $r^2 = 0.06$; *P. discolor*: 1986, $F_{1, 37} = 57.8$, $P < .001$, $r^2 = 0.56$ and 1987, $F_{1, 37} = 12.7$, $P < .001$, $r^2 = 0.57$.

TABLE 2. Comparisons among three pine species of natural patterns of abundance, survival, and annual height growth rate. Data are means (with 1 SE in parentheses for all but percentage survival, for which sample sizes are given) over plots in which each species occurred. Means bearing different superscript letters are significantly different ($P < .05$) among species, using Bonferroni probabilities after t tests on log-transformed data for basal area, density, and growth, and after pairwise G tests for survival.

Species	Adult basal area* (m ² /ha)	Density of seedlings† (no./ha)	Density of 1st-yr recruits‡ (no./ha)		Percentage survival§			Annual seedling height growth (cm)§			
			1986	1987	1st-yr recruits	0–1 m	1–2 m	1984	1985	1986	1987
<i>P. discolor</i>	0.5 ^c (0.1)	214.1 ^a (28.4)	42.9 ^a (18.4)	21.0 ^c (6.2)	81.8 ^a (22)	96.4 ^a (391)	100.0 ^a (32)	5.1 ^c (0.2)	6.8 ^b (0.3)	4.5 ^c (0.2)	6.3 ^b (0.3)
<i>P. leiophylla</i>	8.0 ^a (1.2)	156.3 ^{ab} (32.1)	50.0 ^a (17.7)	144.0 ^b (37.8)	37.1 ^b (89)	83.0 ^b (253)	95.1 ^a (41)	9.2 ^a (0.6)	13.2 ^a (0.6)	8.7 ^a (0.4)	12.5 ^a (0.6)
<i>P. engelmannii</i>	4.7 ^b (1.1)	112.1 ^b (19.4)	59.1 ^a (21.1)	613.0 ^a (148.4)	42.3 ^b (414)	69.6 ^c (224)	96.9 ^a (23)	7.6 ^b (0.4)	8.0 ^b (0.5)	7.3 ^b (0.5)	6.4 ^b (0.4)

* For stems ≥ 2 m tall, using only plots with nonzero values.

† For stems < 2 m tall, excluding 1st-yr recruits (for definition see Fig. 2), using only plots with nonzero values.

‡ For 1st-yr recruits, using all plots on which stems > 1 yr old occurred.

§ Analyzed for all plots combined.

seedlings tended to occupy microsites lower in light and soil temperature and higher in litter depth than random microsites, whereas in higher elevation plots, seedling microsites exhibited the opposite trend or little

difference from random microsites (Fig. 8). The extent to which seedlings shifted microsites along this gradient, however, depended on both variable and species.

In *P. discolor* microsites, light and temperature were

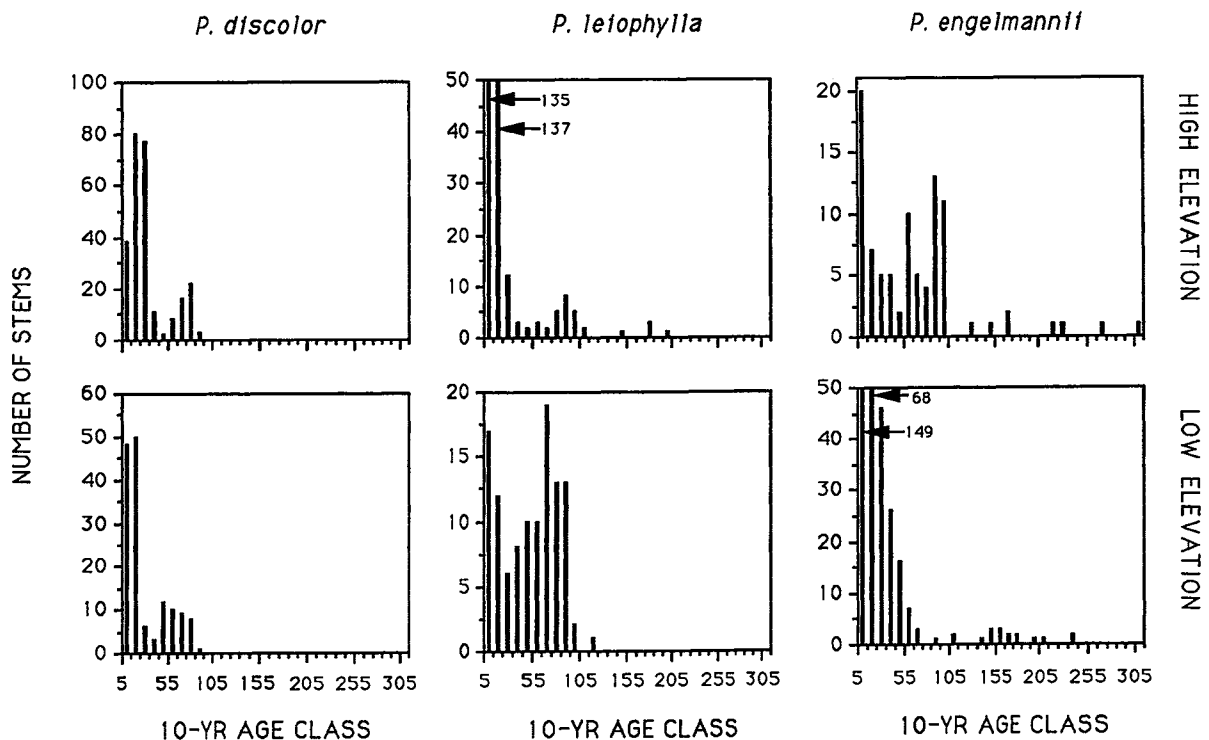


FIG. 7. Age structure in decade classes from ring counts of increment cores and cross sections for three pine species, with increasing elevational position from left to right. A population for each species was sampled in 1988 at a high elevation (top line of frames) and a low elevation site (bottom line of frames) relative to the range of the given species. The cumulative distributions of the two populations were significantly different for each species (Kolmogorov-Smirnov tests, maximum differences = 0.208, 0.591, and 0.483, respectively, $P < .01$ for each). Note that for two frames, number of stems in the youngest two age classes extends far above the y axes shown and the actual values are indicated with numbers and arrows. Two populations (*P. leiophylla*, low elevation and *P. discolor*, high elevation) were sampled in the same site; all other populations were sampled in unique sites.

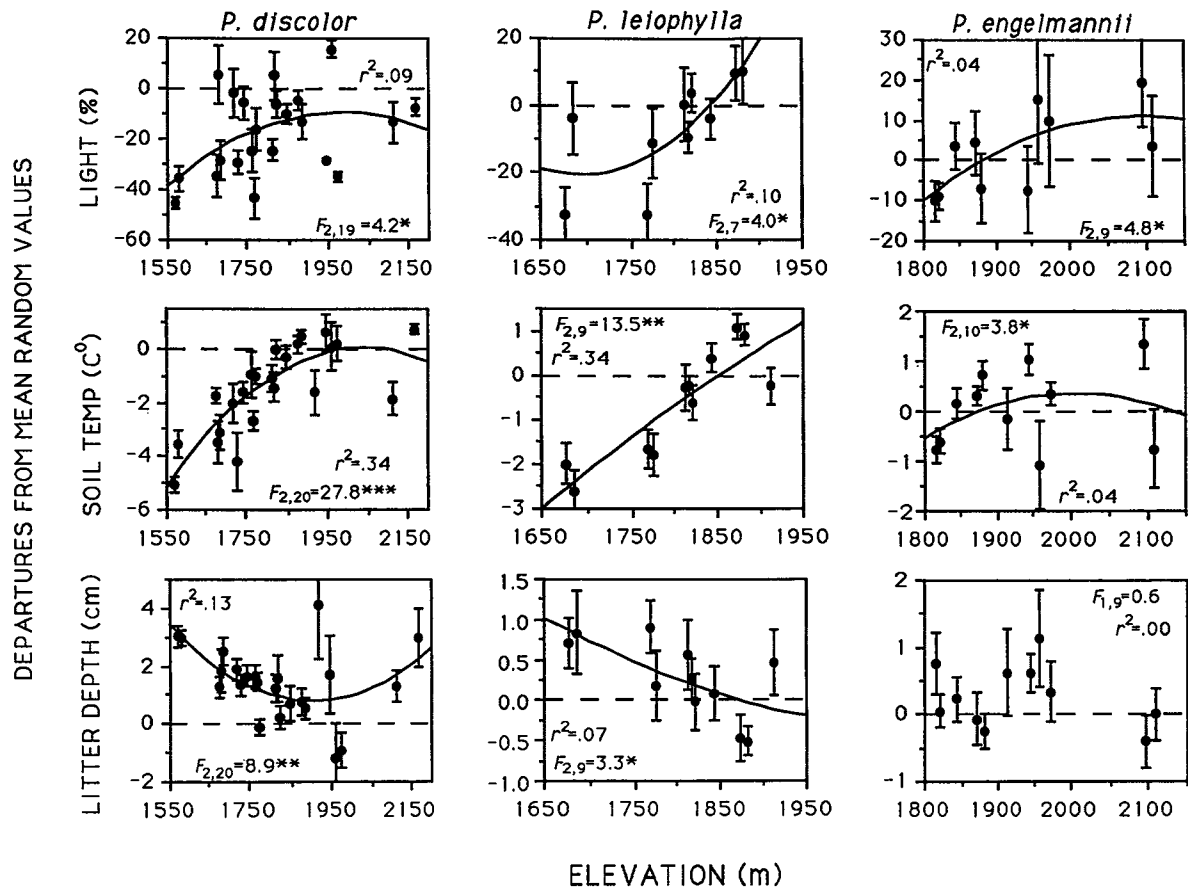


FIG. 8. Changes in percentage full light (at 10 cm height; top line of frames), soil temperature (at 7 cm depth; middle line of frames), and litter depth (bottom line of frames) of microsites occupied by pine seedlings over the elevational gradient. Data are means (± 1 se) for each plot for departures of plant microsites from random microsites (each plant value minus the mean random value for that plot). The dashed line represents no difference between plant and random microsites. Results of linear or second-order polynomial regressions are given in each frame (* $P < .05$, ** $P < .01$, *** $P < .001$, otherwise $P > .10$) and curves are provided for models where $P < .10$.

substantially lower and litter depth much higher than random microsites at low elevation (Fig. 8). With increasing elevation, the difference in soil temperature between plant and random microsites decreased significantly such that plants actually occurred in sites with slightly higher-than-random soil temperature at the highest sites, where ambient temperature was lowest. Light and litter depth showed a similar pattern, but their curves never crossed the zero line (Fig. 8). In other words, *P. discolor* seedlings occurred in microsites with less light and more litter than in random microsites, even where these two variables were likely to be most limiting to growth and seedling emergence. Patterns of canopy openness correspond closely to these results. I analyzed the patterns with G tests of the association among microsite type (plant vs. random), canopy openness (closed, intermediate, and open), and position along the elevational gradient (above vs. below mean of adult density for the given pine species). In *P. discolor*, the three-way association was significant

($G_2 = 9.74$, $P < .008$): plants occurred significantly more often than random in closed microsites ($G_2 = 33.75$, $P < .0001$), but only on the lower half of the elevational gradient. These results agree with the common occurrence of *P. discolor* seedlings under trees and large shrubs (i.e., "nurse trees") and rarely in the open in relatively xeric plots.

As for *P. discolor*, *P. leiophylla* seedlings in low elevation plots were typically in low light, low soil temperature, and deep litter microsites compared to random (Fig. 8). With increasing elevation, this pattern was gradually reversed. In the highest elevation plots, plants occurred in microsites higher in light and temperature and lower in litter depth than random (Fig. 8), although these differences were not significant for any of these plots analyzed separately. The canopy openness data differed somewhat from these results. Seedling microsites were more open than random microsites over the entire gradient ($G_2 = 10.07$, $P < .05$).

The microsites of *P. engelmannii* varied in a similar

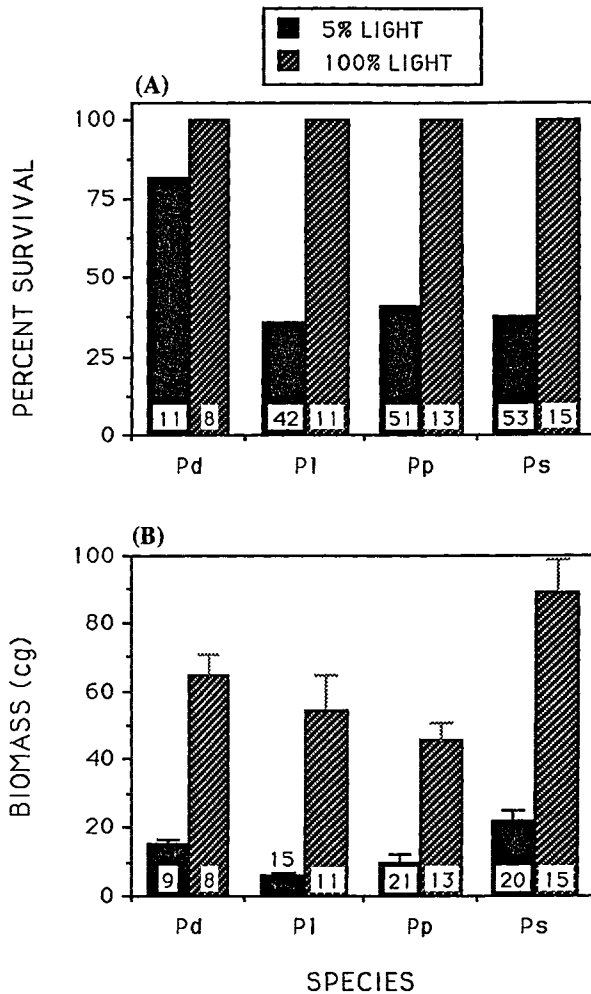


FIG. 9. (A) Percentage survival and (B) mean biomass (plus 1 SE) of seedlings of *P. discolor* (*Pd*), *P. leiophylla* (*Pl*), *P. ponderosa* (*Pp*), and *P. strobiliformis* (*Ps*) grown for 4.5 mo in full light and 5% of full light in a greenhouse in 1987–1988. Sample sizes are given at the bottom of the bars. Full light ranged from 450 to 850 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ supplied by natural light and mercury vapor lamps. At 5% full light, survival was significantly different among species ($G_3 = 9.3$, $P < .05$). For a two-way ANOVA (species and light level) with interaction (inter) on log-transformed biomass data, all three terms were significant [$F_{3,104}$ (species) = 25.2, $P < .001$; $F_{1,104}$ (light) = 331.7, $P < .001$; $F_{3,104}$ (inter) = 2.9, $P < .05$].

way to the other two species, but differences between plant and random microsites were significantly related to elevation only for light and soil temperature (Fig. 8). None of the three-way or two-way tests of association for canopy openness of microsites were significant (G test, $P > .10$).

Comparisons of species microsites.—Using analysis of covariance (elevation as covariate), I found that microsites of the three species differed significantly in percentage light ($F_{2,510} = 5.40$, $P < .001$), soil temperature ($F_{2,510} = 11.43$, $P < .0001$), and litter depth ($F_{2,510} = 15.84$, $P < .0001$). In contrast to expectations from the light-moisture trade-off hypothesis, at any

given elevation, seedlings of the lowest elevation species, *P. discolor*, occurred in microsites lower in light, lower in soil temperature, and higher in litter depth than *P. engelmannii* and *P. leiophylla*. *P. engelmannii* differed similarly from *P. leiophylla*. All nine of the multiple comparisons of means (using Bonferroni-adjusted probabilities) were significant ($P < .001$) except for *P. discolor* vs. *P. engelmannii* for litter depth ($P > .10$).

Greenhouse experiment: comparisons of species in shade tolerance

If light limitation controls upper elevational limits, then higher elevational species should be more shade tolerant than lower species. Furthermore, according to the light-moisture trade-off hypothesis, drought resistance and shade tolerance should be negatively correlated. From greenhouse experiments, Barton and Teeri (1993) found the following species ranking from more to less drought resistant: *P. discolor* > *P. leiophylla* > *P. ponderosa* = *P. strobiliformis*. Accordingly, for survival and biomass response to shading, I compared *P. discolor* to the three species at higher elevations and *P. leiophylla* to the two species at higher elevation. Most of the comparisons did not support the above predictions.

All plants survived in the full light treatment. In 5% of full light, survival was much lower and differed significantly among species (Fig. 9). Contrary to expectation, survival of *P. discolor*, the most drought-resistant species, was significantly higher than the three species at higher elevation combined ($G_1 = 8.14$, $P < .004$, two-tailed test) and *P. leiophylla* survival did not differ from that of the two species at higher elevation ($G_1 = 0.18$, $P > .10$, one-tailed test).

The biomass of plants of each species decreased significantly from full to 5% of full light (Fig. 9B). The extent of this reduction depended on species (i.e., significant interaction), with *P. leiophylla* biomass decreasing to 11.2% of the full light biomass value and the three other species dropping to 22.0–24.4% of the full light biomass value (Fig. 9B). In support of the above predictions, *P. leiophylla* biomass was reduced significantly more than for the two higher elevation species ($F_{1,91} = 4.08$, $P < .05$, one-tailed test). In contrast, the reduction in *P. discolor* biomass was actually slightly but insignificantly less than that for the three species at higher elevation ($F_{1,108} = 0.40$, $P > .10$, two-tailed test).

P. leiophylla litter experiment

Soil moisture, emergence, and survival results support the hypothesis that the lower elevational limit of *P. leiophylla* is controlled, at least in part, by its inability to emerge through deep litter in the relatively mesic microsites under established vegetation. Plots under nurse trees in open oak woodland, where *P. leiophylla* did not naturally occur, contained either similar

TABLE 3. Soil moisture and seedling emergence of *Pinus leiophylla* in summer 1986 for control ("con") and complete litter removal ("rem") treatments in pine-oak woodland and open oak woodland (means with SE in parentheses)†

	Open oak		Pine-oak		F values		
	Con	Rem	Con	Rem	Site	Litter	Interaction
Soil moisture‡							
(A) Before	4.99 (0.60)	5.06 (0.67)	4.36 (0.33)	3.95 (0.17)	2.47	0.17	0.26
(B) After	23.68 (2.66)	20.35 (2.76)	12.68 (1.37)	8.02 (0.68)	36.54***	6.25*	1.15
Seedling emergence	1.00 (0.41)	5.25 (1.49)	5.75 (0.95)	6.75 (1.44)	7.35*	5.19*	1.19

* $P < .05$, *** $P < .001$, otherwise $P > .05$.

† Sampled gravimetrically from 7 to 12 cm depth.

‡ Values for soil moisture are (A) before and (B) after the treatments were imposed. Sampling occurred after >2 mo of no rain for (A) and after about a 2-wk dry period for (B). Values for seedling emergence are the total number of emerged seedlings per plot out of 36 seeds planted. The two sites were in pine-oak woodland (≈ 1775 – 1800 m elevation), where *P. leiophylla* juveniles occur naturally, and under nurse trees in open oak woodland (≈ 1725 – 1750 m elevation), a habitat where *P. leiophylla* does not occur but *P. discolor* does. The experimental design was split-plot with two blocks and two replications per cell and 1, 24 df for each source of variation (i.e., four samples per mean).

soil moisture (before the summer rains; Table 3) or higher soil moisture (after the rains began; Table 3) than did random plots under the partially closed pine-oak woodland, where *P. leiophylla* was naturally abundant. Emergence of *P. leiophylla* seedlings was significantly higher under nurse trees in open oak woodland than in pine-oak woodland, and removal of litter significantly increased emergence despite the lower percentage soil moisture in litter removal subplots (Table 3). The effect of litter appeared to be especially strong in open oak woodland, but the F test interaction term between site and litter was not significant (although it was significant using a G test: $G_1 = 3.99$, $P < .05$). It should be noted, however, that, of the four seedlings emerging in litter control plots under nurse trees, two emerged on microsites where litter was naturally very sparse or nonexistent. Although litter depth is very similar between the two sites (means ≈ 2 cm for each, $F_{1,62} = 0.57$, $P > .10$), litter under nurse trees in the oak woodland is typically fine and dense (derived from juniper needles and small oak leaves), whereas the long needles of *P. leiophylla* in pine-oak sites tend to form a much less compact, dense, and thus less impervious litter.

Survival of emerged seedlings over the first 2 mo was much higher under nurse trees in open oak woodland (52%, $n = 25$) compared to those in the pine-oak site, where none of the 50 seedlings survived (differences between the two sites: $G_1 = 34.5$, $P < .001$). At the end of the study after nearly 3 yr, 36% of the nurse tree seedlings were still alive.

1987 field experiments: elevational position, litter depth, and light

Emergence.—Lack of seed germination did not appear to enforce lower elevational limits in any of the pine species: seeds of all three pine species germinated

below their lower elevational limits in control plots (low elevational position; Fig. 10).

If deep litter controls upper elevational limits, then two predictions should be supported for each species: (1) in control plots, seedling emergence should be higher within a species range than above its range (where litter is relatively deep) and (2) at least above a species range, litter removal should increase emergence. The first prediction is clearly supported for *P. leiophylla* and *P. engelmannii* (Fig. 10). *P. discolor* emergence at middle elevations was higher than at lower elevations, but emergence at high elevation was actually greater than at middle elevation for control plots (Fig. 10).

The results for the second prediction also differed among species. As predicted, *P. leiophylla* emergence was increased by litter removal in high elevation plots (Fig. 10). In contrast, *P. discolor* litter removal decreased emergence at the high elevational position (Fig. 10). *P. engelmannii* emergence was significantly higher in control than litter removal plots at the middle position, but exhibited no differences at high elevation (Fig. 10). Decreased seedling emergence after litter removal probably resulted from seed predation, which tended to be relatively high in litter removal plots (Barton 1991).

For all plots, emergence was higher for *P. discolor* than for *P. leiophylla* and *P. engelmannii*, but this difference was not statistically significant (Kruskal-Wallis test, $H_2 = 0.103$, three species, $n = 76$, 64, and 44 plants, respectively, $P > .10$). If only plots containing pairs of species were used, however, *P. discolor* emergence was significantly higher than *P. leiophylla* (Wilcoxon matched-pairs, $n = 64$, 64 plants, $z = 2.11$, $P < .05$). Sample sizes were insufficient to perform other pairwise comparisons.

Survival.—If low light availability controls upper elevational limits, then two predictions should be sup-

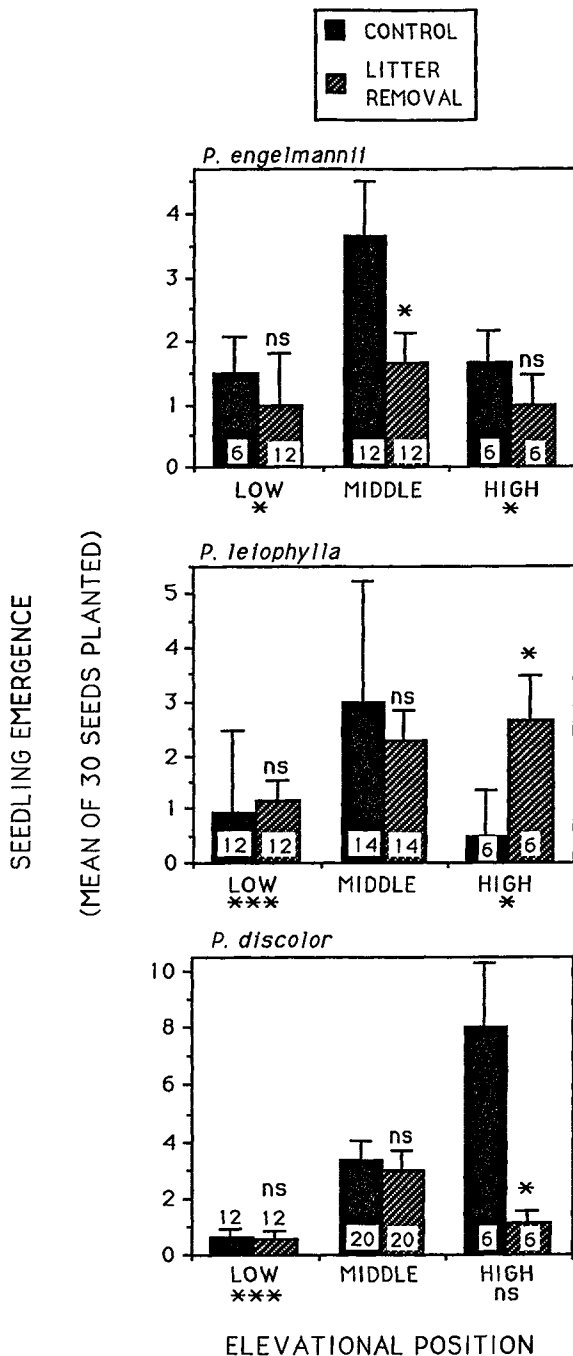


FIG. 10. Experimental effects of elevational position and litter removal on emergence of seedlings of three pine species. For each species, low position was just below the lower elevational limit, middle was in the middle of the species' range, and high was just above the upper limit. Each bar represents mean seedling emergence per plot (out of 30 seeds planted). Sample size (number of plots) is given in the bottom and standard error bars are provided at the tops of the large bars. Differences between middle vs. low and high control plots are given under the high and low label, respectively. Differences between control and removal for each elevational position are given above the standard error bars for removal (* $P < .05$, *** $P < .001$, ns $P > .10$, using Bonferroni probabilities after Mann-Whitney U tests).

ported for each species: (1) in control plots, seedling survival should be higher within a species' range than above its range (where light levels are relatively low), and (2) at least above each species' range, canopy removal should increase survival. As with the seedling emergence results, the first prediction was supported by *P. leiophylla* and *P. engelmannii*. After ≈ 2 mo (middle of July to 13 September 1987), seedling survival for these species was overall highest at middle elevations (Fig. 11). *P. discolor* survived better at middle than at lower elevations, but survival was higher at high than at middle elevations ($G_1 = 3.15$, $P = .09$; Fig. 11). Analyses of survival patterns of *P. discolor* after 5 and 9 mo (not shown) produced very similar results. I could not carry out similar analyses on the other two species because of their low survival. By the end of the following (1988) dry season, all of the seedlings of all three species had died at low elevational positions. In contrast, some seedlings (52% for *P. discolor*, 7% for *P. leiophylla*, and 10% for *P. engelmannii*) of each species at middle and upper elevation plots were still alive after 2 yr.

The results for the second prediction on seedling survival also differed among species in a manner similar to the emergence results. As predicted, canopy removal significantly increased seedling survival of *P. leiophylla* at high elevation (Fig. 12), where light availability was lower and more likely to be limiting. In contrast, canopy removal did not influence survival of *P. engelmannii* and *P. discolor* 2 mo after emergence (Fig. 12) or of *P. discolor* at 5 or 9 mo postemergence (not shown).

Overall survival differed significantly among the three species after 2 mo ($G_2 = 70.27$, $P < .0001$), and was higher in *P. discolor* (81.2%, $n = 197$) than in *P. engelmannii* (44.8%, $n = 105$; $G_1 = 41.39$, $P < .001$) and in *P. leiophylla* (39.7%, $n = 116$; $G_1 = 55.93$, $P < .001$), but did not differ significantly between the latter two species ($G_1 = 0.59$, $P > .10$).

Growth.—Because of the small sample size, I could analyze height growth only for *P. discolor*, and had to analyze separately the influence of elevational position (excluding lower elevation), canopy removal, and litter removal. Seedling height was always greater at middle than at upper elevations, but this difference only approached significance at the end of the experiment (Fig. 13A). For all four dates, height was significantly greater in control plots than in litter removal plots (Fig. 13B). Canopy removal appeared to increase height by June 1988, but this difference disappeared by the end of the experiment (Fig. 13C).

Comparisons of species in fire resistance

Quantitative comparisons of species in traits related to fire resistance.—Consistent with the hypothesis that fire controls its upper elevational limit, *P. discolor* appeared to possess few fire-resistant traits compared to the two higher elevation species. As documented pre-

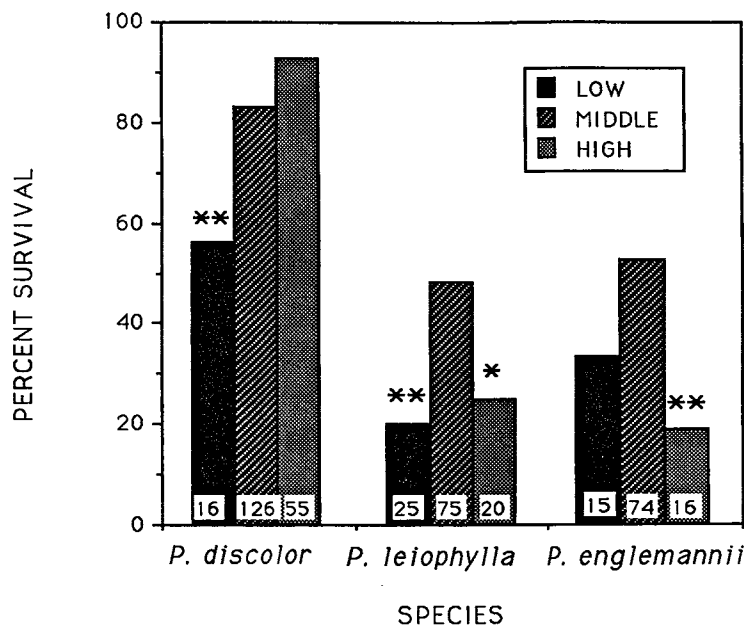


FIG. 11. Effects of elevational position on experimental seedling survival after 2 mo for three pine species. For each species, low position was just below the lower elevational limit, middle was in middle of the range, and high was just above the upper limit. Each bar represents the percentage of seedlings surviving out of the total, which is given at the bottom of each bar. For each species, percentage survival was compared between middle vs. low and middle vs. high elevational position using *G* tests. Significant differences are given at the top of the low and high bars (* $P < .05$, ** $P < .01$).

viously, juvenile height growth rate ranked as follows: *P. leiophylla* > *P. englemannii* > *P. discolor*. Fig. 14 reveals the consequences of these differences in attainment of height over time: a typical newly germinated *P. discolor* requires 27 yr to reach 2 m, whereas *P. englemannii* would require 22 yr, and *P. leiophylla* only 15 yr. The 95% confidence intervals of these species did not overlap. However, the projected height growth of the lowest elevation population of *P. discolor* analyzed separately is very similar to the fast-growing *P. leiophylla* juveniles ($P > .10$; Fig. 14).

Juvenile growth rate patterns appear to be repeated in adults. Fig. 15 shows the relationship between radius (at core height [30 cm aboveground]) and age in a low and high elevation population of each of the three species. Slopes of the curves are indicative of rate of change in size with age and the mean sizes at any given age represent differences in adult sizes. The two populations of *P. discolor* combined have a significantly lower slope than the populations of *P. leiophylla* and *P. englemannii* combined [$F_{1, 316} = 6.79$, $P < .01$ for log (radius)]. However, as with juveniles, the relationship of size to age did not differ for the low elevation population of *P. discolor* vs. *P. leiophylla* and *P. englemannii* combined ($F_{1, 316} = 0.01$, $P > .10$).

The slopes of bark thickness vs. size did not differ among the six populations (for stems 5–16 cm radius at core height: $F_{5, 137} = 0.94$, $P > .10$; Fig. 16A), but the means did (ANCOVA, $F_{1, 142} = 24.02$, $P < .0001$). *P. discolor* bark was significantly thinner than for the

other two species ($F_{1, 142} = 11.64$, $P < .0001$). The latter two species did not differ significantly ($F_{1, 142} = 1.53$, $P > .10$). In one population of each species (*P. discolor* high, *P. leiophylla* low, and *P. englemannii* low), I also collected data on the bark thickness of very small individuals. When these three populations were compared (over the range of 0.3–16 cm radius at core height), the slope of bark thickness vs. size differed significantly among the three species ($F_{2, 305} = 22.87$, $P < .0001$). *P. discolor* bark thickened from small to large individuals at a significantly slower rate than for *P. leiophylla* and *P. englemannii* combined ($F_{1, 305} = 43.32$, $P < .0001$). *P. englemannii*'s slope was higher than that for *P. leiophylla* ($F_{1, 305} = 10.51$, $P < .001$), suggesting very fast bark accumulation with increasing diameter.

Similarly, the slopes for all six populations differed when bark thickness was regressed over age ($F_{5, 302} = 11.32$, $P < .0001$; Fig. 16B). The slopes of the two *P. discolor* populations combined were significantly less than those of the other two species combined ($F_{1, 302} = 28.22$, $P < .0001$), again indicating very slow accumulation of bark with age in *P. discolor*. The slopes of *P. leiophylla* and *P. englemannii* populations did not differ significantly ($F_{1, 302} = 1.52$, $P > .10$).

Qualitative comparisons of species in traits related to fire resistance.—*P. leiophylla* and *P. englemannii* also possess other traits, not exhibited by *P. discolor*, that probably enhance their tolerance of fire (see Wright and Bailey 1982, McCune 1988). As adults, *P. englemannii* and *P. leiophylla* typically are tall trees (15–35

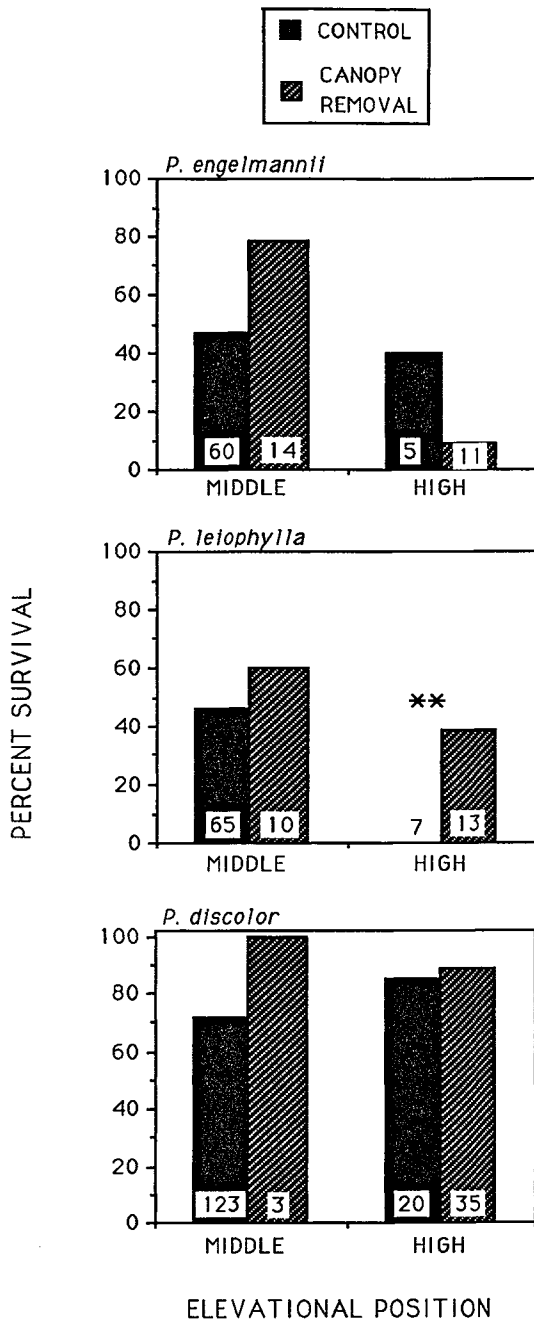


FIG. 12. Experimental effects of canopy removal at two elevational positions on seedling survival to 2 mo for three pine species. For each species, middle position was in the middle of the elevational range and high was just above the upper limit. Each bar represents the percentage of seedlings surviving out of the total, which is given at the bottom of each bar. Data for each species were analyzed with a G test of position \times litter \times survival. For *P. leiophylla*, the three-way interaction was significant ($G = 2.86$, $P < .04$, one-tailed test), survival was significantly higher in canopy removal plots than in controls only at high elevation ($G = 5.17$, $P < .01$, one-tailed test), and survival was significantly higher between middle and higher elevational positions for control plants only ($G = 8.33$, $P < .05$, one-tailed test). Analyses of the other two species were not significant ($P > .10$).

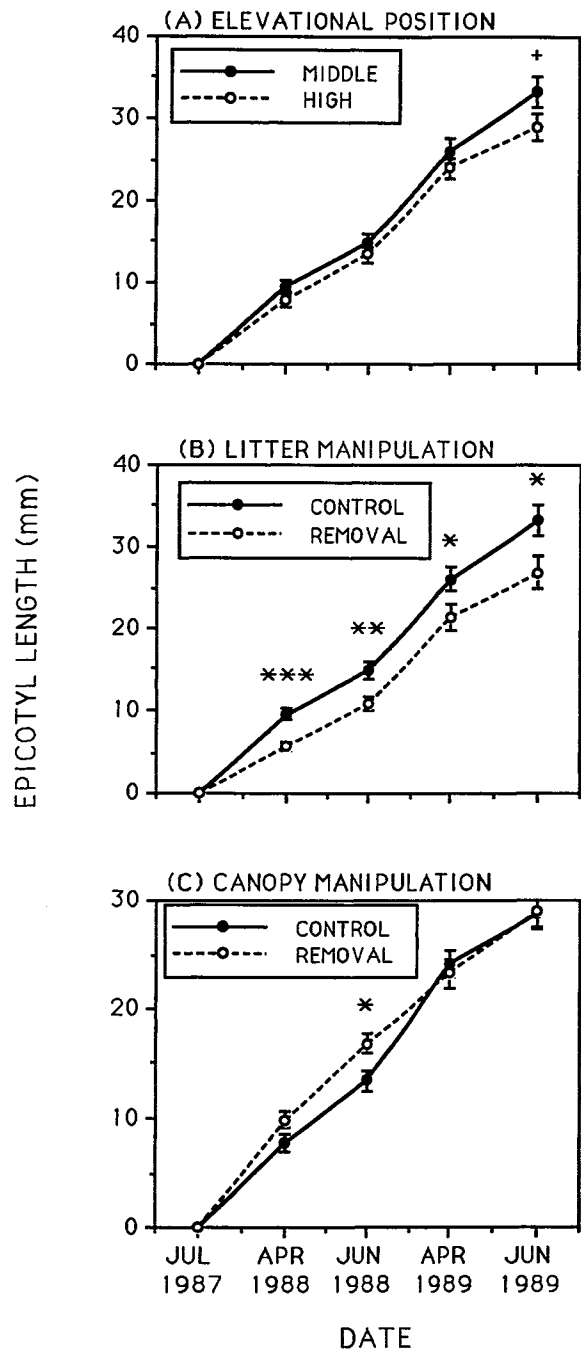


FIG. 13. Growth of seedlings of *P. discolor* as affected by (A) elevational position (see Fig. 12 for definitions), (B) litter removal, and (C) canopy removal. Data are means (± 1 SE) for the cumulative length of epicotyls at four dates between July 1987 and June 1989. Sample sizes at the beginning and end of the time period, respectively, were (top) 32–24 for middle elevation and 13–13 for high elevation, (middle) 32–24 for litter control and 28–23 for litter removal, and (bottom) 13–13 for canopy control and 25–19 for canopy removal. Differences between elevational positions or between control and removal are given above the two means (ANOVA: + $P < .06$, * $P < .05$, ** $P < .01$, *** $P < .001$, otherwise $P > .10$).

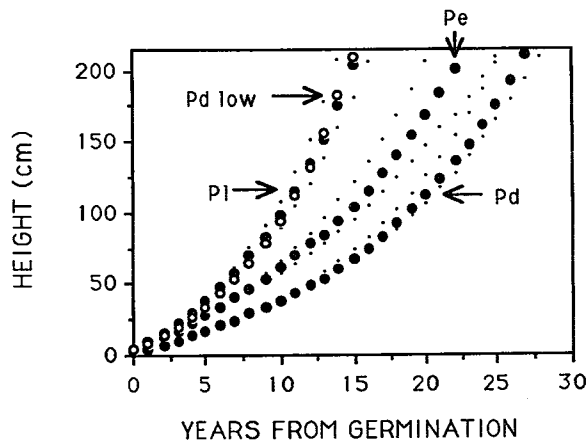


FIG. 14. Projections of height growth over years from germination to 2 m height for *P. discolor* (Pd), *P. leiophylla* (Pl), and *P. engelmannii* (Pe). Large dots represent the growth trajectory based on the least squares relationship between height growth (1986 and 1987 combined) and initial height for all seedlings (<2 m tall) for each of the species (see Fig. 6) and for *P. discolor* seedlings in the two lowest plots ("Pd low"; 1568 and 1579 m elevation). Ninety-five percent confidence intervals of each equation are indicated by small dots around each projection.

and 15–25 m, respectively) with branch-free boles over much of their height, whereas *P. discolor* rarely reaches 15 m tall and exhibits relatively poor self-pruning of branches. As a consequence, the chance of crown fires is probably much higher for adults of *P. discolor* than

for the other two species. Also, unlike *P. discolor*, *P. engelmannii*, and most other pines, *P. leiophylla* is able to resprout vigorously after fire has killed the above-ground stem (Stone and Stone 1954; A. M. Barton, *personal observation*).

P. engelmannii seedlings exhibit several traits that seem especially geared to tolerance of fire. Young seedlings grow little in height, but exceptionally in girth, and form very thick bark (often more than one-half of the total diameter). In juveniles <2 m tall, *P. engelmannii* stems were significantly thicker at a given height than *P. discolor* (Bonferroni contrast after ANCOVA, $F_{1, 180} = 96.68$, $P < .001$) and *P. leiophylla* ($F_{1, 180} = 18.84$, $P < .001$). Also at this stage, terminal buds of *P. engelmannii* appear to be insulated against fire by its very long needles on the most recent annual shoot. Eventually, diameter growth slows and height growth accelerates substantially (A. M. Barton, *unpublished data*), rapidly elevating buds past the zone of highest temperature during ground fires (Wright and Bailey 1982). This growth pattern is similar to that of fire-resistant *P. palustris* in the southeastern USA (Wahlenberg 1946), which has been described as having perhaps the most strongly developed mechanism of fire resistance in pine seedlings (McCune 1988).

Comparisons of species in survival through fire.—If the higher fire frequency of high elevations controls the upper elevational limits of *P. discolor*, then survival through fire by this species should be lower than for the two pine species that occur at higher elevations. In both wildfires studied, this prediction was supported:

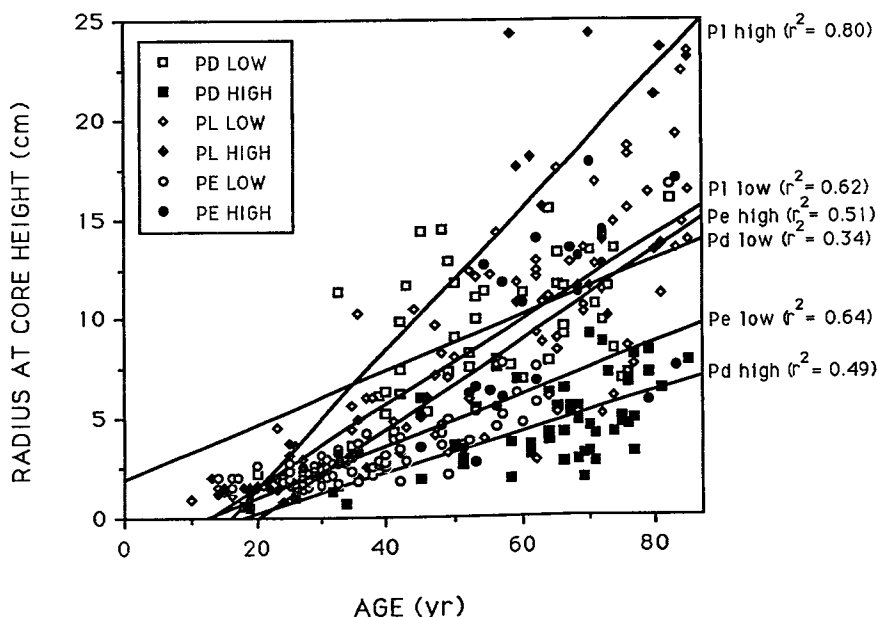


FIG. 15. Relationships between radius (at core height [30 cm aboveground]) and estimated total age in a low ("low") and high ("high") elevation population of each of *P. discolor* (Pd), *P. leiophylla* (Pl), and *P. engelmannii* (Pe). Curves and r^2 s are given for each population. Simple least squares regression was significant for each population ($P < .05$). Results on differences in slopes and means are given in *Results: Comparisons of species in fire resistance: Quantitative comparisons of species. . .*

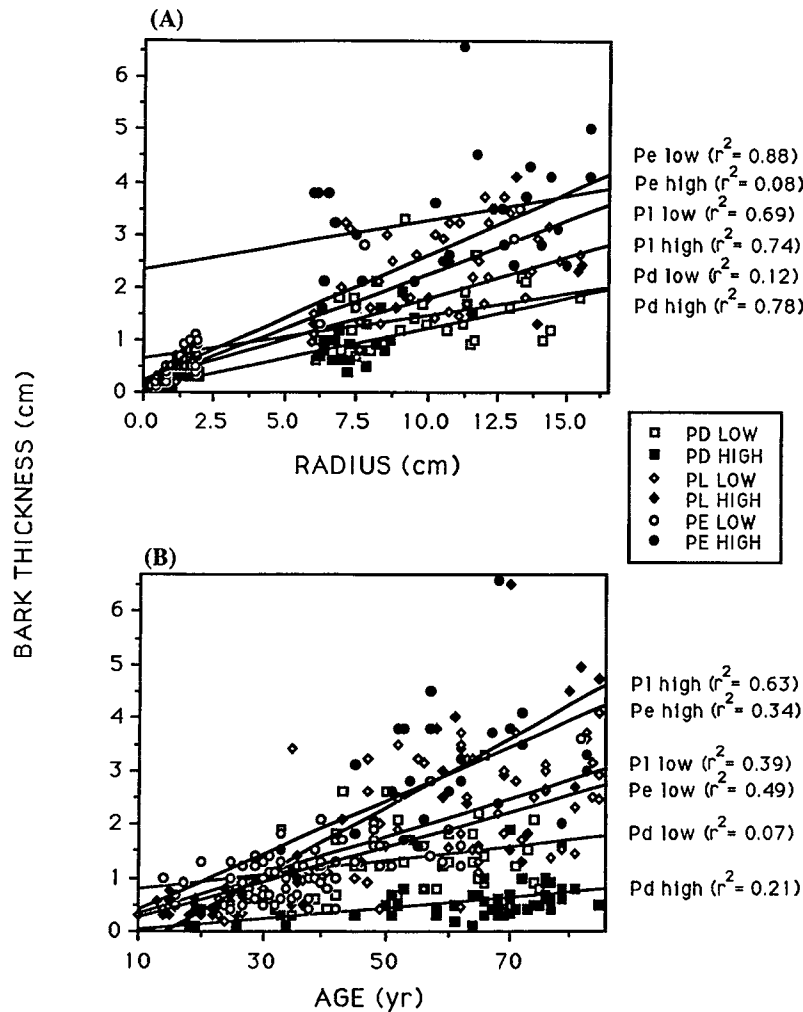


FIG. 16. Relationships between bark thickness and (A) radius at core height and (B) estimated total age in a low ("low") and high ("high") elevation population of each of *P. discolor* (Pd), *P. leiophylla* (Pl), and *P. engelmannii* (Pe). Curves and r^2 s are given for each population. Simple least squares regression was significant for each population ($P < .05$). Results on differences among slopes and means are given in *Results: Comparisons of species in fire resistance: Quantitative comparisons of species*. . . .

survival of aboveground stems of *P. discolor* was significantly lower than for *P. leiophylla* and *P. engelmannii* (Table 4). Because survival tended to increase from small to large size classes and *P. discolor* had most of its individuals in smaller size classes, part of this difference in survival appeared to arise from differences in maximum and typical sizes of these three species. However, when the analysis is confined to stems < 20 cm dbh, survival of *P. discolor* was still significantly lower than that for *P. leiophylla* ($G_1 = 5.3$, $P < .05$ for Pine Canyon and $G_1 = 7.4$, $P < .05$ for Animas) and lower than that for *P. engelmannii* ($G_1 = 4.0$, $P < .05$). For the above analyses, plants for which the aboveground stem was killed but that resprouted after the fire were not included as survivors. Only individuals of *P. leiophylla* exhibited resprouting: 20 of 73 stems resprouted in the Pine Canyon fire and 4 of 32

resprouted in the Animas fire. If these plants were included as survivors in the above analyses, differences between survival of *P. discolor* and *P. leiophylla* would be even more marked.

DISCUSSION

The pattern: elevational positions of the three pine species

The elevational distributions of the three pine species found in this study in the Chiricahua Mountains correspond closely to their distributions in other mountain ranges in the region (Shreve 1915, Martin and Fletcher 1943, Wallmo 1955, Marshall 1957, Whittaker and Niering 1964, 1968). The three species differed in mean elevational position, with *P. discolor* at lower elevations, *P. leiophylla* at intermediate ele-

TABLE 4. Data collected in 1992 on percentage of individuals (≥ 1.4 m tall) of three pine species for which aboveground stems survived in two fires in southeastern Arizona.

Fire location	Size class (cm)								G
	0–10		10–20		> 20		Total		
	%	n	%	n	%	n	%	n	
Pine Canyon (1985, 0.38 km ² ; Chiricahua Mountains, Arizona)									
<i>P. discolor</i>	0.0	7	0.0	13			0.0	20	
<i>P. leiophylla</i> †	11.3	62	28.0	25	100.0	7	22.3	94	8.9**
<i>P. engelmannii</i>	12.5	8	35.3	17	84.5	58	67.5	83	37.1***
Animas Peak (1989, >100 km ² ; Animas Range, New Mexico)									
<i>P. discolor</i>	23.5	17	0.0	7			16.7	24	
<i>P. leiophylla</i> †	40.9	22	60.0	30	82.9	41	65.6	93	18.1***

** $P < .01$, *** $P < .001$ (G test comparisons [$df = 1$] of percentage survival of all sizes combined for *P. discolor* vs. either *P. leiophylla* or *P. engelmannii*).

† For this table, plants that sprouted new stems after the fire (*Pinus leiophylla* only) were not counted as survivors (see Results: Comparison of species in fire resistance: Comparisons of species in survival through fire).

variations, and *P. engelmannii* at higher elevations (Fig. 3). Lower and upper elevational limits of the three species corresponded closely to these differences in mean elevation (Fig. 3).

Lower elevational limits

Factors controlling lower elevational limits.—The results suggest that lower elevational limits of the pines were controlled, in part, by water stress, which correlated strongly with elevation. For all species, seedlings germinated with the summer rains in experimental plots below their respective lower elevational limits, but all died by the end of the following May–June drought. Although some deaths were attributable to herbivory, most seedlings slowly dried out, lost turgor, died, and turned brown, typical symptoms of water stress (Levitt 1980). Seedlings of all three species were still alive at middle and higher elevation positions in the experiment after 2 yr. Furthermore, with decreasing elevation, seedlings of *P. discolor* and *P. leiophylla* increasingly occurred in microsites with relatively low light, low soil temperature, and deep litter (Fig. 8), all reflecting higher soil moisture as well as lower evaporative demand (Gates 1980) compared to surrounding random microsites.

These results agree with greenhouse experiments on these and two other pine species from the Chiricahua Mountains (Barton and Teeri 1993), in which seedlings of lower elevation species were found to be more drought resistance than those of higher elevation species. Together, the studies strongly suggest that lower elevational limits of the pines are controlled by moisture stress and species differences in drought resistance, a conclusion similar to that of other experimental studies in the western USA (Pearson 1931, Daubenmire 1943a, Wright 1968, 1970a, b, Bunce et al. 1979, Barnes and Cunningham 1987, Delucia et al. 1988, Schlesinger et al. 1989). However, because soil temperature also correlated strongly with elevation, the additional or reinforcing effects of high temperature cannot be ex-

cluded (see Nobel 1984). Wright (1968), testing this hypothesis with three pines in the San Bernardino Mountains, California, found that well-watered 5-mo-old potted seedlings did not sustain visible damage from air temperature of 41°C and soil surface temperature of 66°C on the hottest day of 1965. These temperatures are above the maximum temperatures recorded near the lower elevational limit of *P. discolor* in the Chiricahuas (A. M. Barton, *personal observation*), suggesting that high soil temperatures may not be important in the distributions of the species studied here (see also Daubenmire 1943a). Nevertheless, it is important to recognize that high temperature may combine with water stress to impose the physiological conditions leading to mortality over longer periods of time.

P. discolor seedlings occurred in remarkably more mesic microsites than random in low elevation plots (Fig. 8), which was clearly related to their near restriction to microsites beneath nurse trees in these xeric plots, an observation consistent with studies of other pinyon pines in the southwestern USA (e.g., Emerson 1932, Everett et al. 1986). Studies of soil moisture under nurse trees in arid regions have produced conflicting results, some finding higher moisture (Shreve 1931, Neilson and Wullstein 1983) and some lower moisture (Franco and Nobel 1988, 1989) in comparison to bare, open microsites. In this study, soil moisture was clearly higher in protected microsites, for it (1) increased from microsites in the open to under vegetation, (2) increased with increasing litter depth, and (3) decreased with experimental removal of litter. The degree to which nurse trees enhance or reduce soil moisture available to seedlings may depend on whether absorbing roots of established vegetation are near the surface (Franco and Nobel 1989) or at greater depth (Smith 1985), the latter of which probably characterizes the large shrubs and small trees that serve as nurse trees in this study area. These varying results illustrate the importance of considering in theoretical and em-

pirical work both potential positive and negative effects of plants on resource availabilities (Goldberg 1990; see also Mitchell et al. 1993).

P. leiophylla appeared to be excluded from nurse tree microsites just below its lower elevation limit by deep litter. In these microsites, almost no *P. leiophylla* seedlings emerged unless litter was removed, an effect that was less marked in experimental plots within the species' natural range (Table 3). Furthermore, whereas no experimental seedlings survived within *P. leiophylla*'s natural range, survival was relatively high in nurse tree microsites even at the end of the study after nearly 3 yr. *P. leiophylla*'s failure to penetrate through deep litter in nurse tree microsites is likely the result of its very small seed size compared to *P. discolor* (nearly 40 times lower seed mass; United States Department of Agriculture Forest Service 1974). Many studies have cited such differential effects of litter on small-seeded compared to large-seeded species (Salisbury 1942, Baker 1972, Knapp and Smith 1982, Foster and Jansen 1985). Any given site supports a broad range of microenvironments. These results suggest that with decreasing elevation the portion of this range favorable to *P. leiophylla* establishment is constrained by two factors. Because of increasing water stress, this species is increasingly confined to relatively moist microsites. However, those microsites supporting tolerable levels of soil moisture (i.e., under established vegetation) increasingly also harbor litter sufficiently deep to block the emergence of *P. leiophylla*. Below its lower elevational limit, then, these two environmental constraints, water stress and deep litter, appear to exclude *P. leiophylla* entirely.

Crucial life stages in the control of lower elevational limits.—Dry season water stress appears to control lower elevational limits by causing high mortality of young seedlings, rather than by curtailing germination or performance of older seedlings, at least in *P. discolor* and *P. leiophylla*. Seedling densities of these two species declined from the middle of their range toward lower elevations (Fig. 4), as did survival of *P. leiophylla* seedlings (Fig. 5). Similarly, experimental seedlings of each species died below their respective elevational limits but continued to survive within their range. In contrast, juvenile height growth rates of all three species peaked at the lowest elevations (Fig. 6). These results suggest that with decreasing elevation conditions become difficult for seedling establishment, but, once established, seedlings grow very well (see Cui and Smith 1991).

In *P. discolor*, regressions of diameter over age in adults suggested that higher growth at lower elevation continued into maturity: diameter increased much faster with age in a lower elevation population compared to a middle elevation population (Fig. 15). This discrepancy in growth rate probably explains why *P. discolor* adult densities are highest at middle elevations (where establishment is more frequent), but mean adult diameter and even total basal area are greater at lower

elevations (where establishment is infrequent but growth is higher; Fig. 4).

The above scenario on the action of drought is consistent with Barton and Teeri's (1993) conclusion, based on greenhouse experiments, that below each species' elevational limit, water stress kills very young seedlings by causing a collapse in plant water potential rather than by longer term effects on carbon gain (Chabot and Bunce 1979). This suggests that although seeds of each species are capable of germinating below their present elevational limits, they die at a young age because of water loss during especially dry periods. Just above their lower limits, conditions for establishment are also difficult, but some seedlings do survive through the early, vulnerable stages by germinating in protected microsites (see Cui and Smith 1991). Probably because of its large seeds, *P. discolor* is much more effective at this strategy than the other two species, occurring in extremely moderated conditions relative to random microsites and to those in which the other two species occur. Once established with a deep root system, these seedlings are probably much less vulnerable to the effects of water stress and, as a result, grow very well in the relatively warm, long growing seasons characteristic of lower elevations.

Upper elevational limits

Pinus discolor.—The results for *P. discolor* reject the light-soil moisture trade-off hypothesis that light limitation and lack of shade tolerance control upper elevational limits. They also reject a strong role for deep litter and low temperature in these limits. Adult and seedling abundance declined from the middle of *P. discolor*'s range to higher elevation plots, but, surprisingly, the seedling distribution extended to far higher elevations than for adults, into plots with relatively low light and soil temperature and deep litter (Figs. 3 and 4). Tree ring counts revealed that these plants were not simply slow-growing old individuals, but were much younger than the oldest cohorts in populations within the adult range. Several lines of evidence suggest that conditions in these higher elevation plots were not inimical to *P. discolor* seedlings. First, *P. discolor* emergence and survival were actually higher at upper than middle elevations in the field experiment, whereas the other two species performed better at their middle elevation sites (Fig. 11). Second, litter and canopy removal did not increase *P. discolor* emergence and survival, respectively, even at high elevation, but did increase these components of performance in *P. leiophylla* (Figs. 10 and 12). Third, in the highest elevation plots, *P. discolor* seedlings actually occurred in microsites slightly lower in light and higher in litter depth compared to random microsites, contrary to expectations if these variables were limiting (Fig. 8). Finally, in greenhouse experiments, *P. discolor* was much more tolerant of shade than *P. leiophylla* and possibly two other pine species from higher elevations (Fig. 9). Only

the height growth rate of *P. discolor* appeared to be reduced by conditions at higher elevation (Figs. 6 and 13).

The results suggest both that the current adult population of *P. discolor* was not in the past limited in its upward distribution by competition for light, deep litter, or low temperature and that invasion of higher elevations occurred recently. These patterns suggest either that (1) conditions at higher elevations have recently changed in a way favoring establishment of *P. discolor* or that (2) some agent of mortality, acting selectively on *P. discolor*, previously controlled upper elevational limits, but has recently ceased acting. I do not have data to address the former hypothesis. The following evidence, however, suggests that changes in mortality from fire may explain the observed patterns.

Fire incidence increased significantly from lower elevations where *P. discolor* adults and seedlings were common to higher elevations where only seedlings occurred (Table 1; Barton 1991). Fire intensity may also increase from the open lower elevation areas, which support low fuel loads, to the more densely vegetated higher elevation sites along the study transect. Compared to the two species at higher elevation, *P. leiophylla* and *P. engelmannii*, *P. discolor* appeared to be very poorly suited for surviving frequent fire, a conclusion that has been reached for other pinyon pines in the western USA (Leopold 1924, Wright et al. 1979, Everett and Ward 1984, West 1984, Everett et al. 1986). Adults of *P. discolor* had relatively thin bark (Fig. 16), small diameter (Fig. 15), short stature, and poorly developed self-pruning, traits that probably greatly increase vulnerability to the high temperatures generated by fire and promote the spread of fire into the crown (Spalt and Reifsnnyder 1962, Fahnestock and Hare 1964, McCune 1988, Ryan and Reinhardt 1988, Peterson and Arbaugh 1989). Furthermore, juveniles of *P. discolor* grew very slowly compared to the other two species (Fig. 14). In the western Chiricahua Mountains, in a range of vegetation types overlapping those studied here, mean intervals of fires scarring adult trees ranged from 6.2 to 14.6 yr before AD 1801 (Swetnam et al. 1989). Even if intervals were several times greater than this, the large difference in potential height growth between *P. discolor* and the other two species alone could result in the periodic removal of *P. discolor* and the persistence of *P. leiophylla* and *P. engelmannii*. It is notable, however, that both juveniles and adults at the lowest elevation of *P. discolor*'s distribution grew at rates comparable to the two other species (Fig. 15). The substantial reduction in height growth rate from low to high elevation may have been a result of reductions in light availability or decreasing length of growing season (or both). This raises the possibility that complex interactions among growing season, forest-floor light levels, growth rate, and fire resistance control the upper elevational limits of *P. discolor*.

Arguably, *P. discolor* is also poorly adapted for ex-

plotting postfire conditions (fire resilience, sensu McCune 1988) compared to the other two species. *P. discolor*'s slow growth rate may mean that its seedlings are at a competitive disadvantage when growing on bare sites with enhanced light, nutrients, or moisture resulting from fire. *P. discolor* also does not possess the ability to resprout after fire, a trait common to *P. leiophylla*, all oaks, and many other fire-adapted species in the Chiricahuas. Finally, seed dispersal of *P. discolor* may be substantially limited compared to the other two pine species. The large, wingless seeds of *P. discolor* suggest that it is adapted to dispersal primarily by birds (Vander Wall and Balda 1977, Ligon 1978, McCune 1988). Given that their elevational ranges are almost identical in the Chiricahuas, the Mexican Jay (*Apelocoma ultramarina*) is probably the main disperser of *P. discolor* seeds in these mountains. In contrast to corvids dispersing pine seeds in other parts of the western USA (e.g., Clark's Nutcracker, Vander Wall and Balda 1977; Pinyon Jays, Ligon 1978), these jays have very small home ranges and are not migratory (J. L. Brown, *personal communication*) and thus probably are not effective in dispersing *P. discolor* seeds long distances. The smaller, winged seeds of *P. leiophylla* and *P. engelmannii* are probably primarily wind dispersed, with longer dispersal distances than those of *P. discolor*. This purported superiority of *P. leiophylla* over *P. discolor* in fire resilience is supported by age structure data: *P. discolor* apparently lagged at least 10 yr behind *P. leiophylla* in colonizing a site where a stand-replacing disturbance occurred ≈ 105 –110 yr ago (Fig. 7: low elevation *P. leiophylla* vs. high elevation *P. discolor*).

I suggest, then, that *P. discolor*'s lack of fire resistance and perhaps fire resilience coupled with the positive correlation between fire frequency and elevation have in the past controlled its upper elevational limit. For much of the 20th century, fire has been largely suppressed and, as a consequence, *P. discolor* has begun to invade higher, more mesic elevations, slowed perhaps by limitations on its dispersal distance. Recent encroachment of pinyon pines, junipers, and other tree species into areas that were previously desert grassland has also been attributed to fire suppression, suggesting previous control of lower elevational limits by fire (Blackburn and Tueller 1970, Arno and Gruell 1983, West 1988; but see Betancourt 1987).

Whether fire is important in controlling lower or upper elevational limits of tree species probably varies regionally and even within the same mountain range. At higher elevations in the Chiricahuas, for example, the relationship of fire to elevation (and soil moisture) appears to differ strongly from the results reported here. Whereas within the ranges of the three pines studied here these two variables were positively correlated, at higher elevations they appear to be negatively correlated (Barton 1991; see also Allen and Peet 1990). Under these conditions, fire potentially could control the

lower elevational limit of high elevation tree species, such as Douglas-fir (*Pseudotsuga menziesii*). Wright (1968), for example, concluded that, in the San Bernardino Mountains in southern California, fire adaptations of *Pinus attenuata* allowed this species to occur at more fire-prone, lower elevations than *P. coulteri*, which was fire intolerant. A fire-elevation pattern similar to that at high elevations in the Chiricahuas occurs over the entire elevational gradient in the northern Rockies. Fire frequency decreases from low to high elevation and, in general, from low to high soil moisture conditions (Habeck and Mutch 1973, Tande 1979, Arno 1980, Romme and Knight 1981). Throughout these ranges, fire is most likely to control lower not upper elevational limits of tree species.

Pinus leiophylla.—Several lines of evidence suggest that low light (i.e., competition for light) and deep litter control the upper elevational limits of *P. leiophylla*. First, in the 1987 field experiment, *P. leiophylla* emergence and survival were significantly lower above its upper elevational limit compared to plots within its range, removal of litter increased emergence, and removal of canopy increased seedling survival (Figs. 10–12). Second, based on greenhouse experiments, *P. leiophylla* was significantly less shade tolerant than *P. discolor* and two pine species that occur at higher elevations (Fig. 9). Third, approaching its upper elevational limit, *P. leiophylla* seedlings increasingly occurred in microsites with relatively high light and soil temperature and low litter depth compared to random microsites (Fig. 8), suggesting increasing limitation by these variables. Finally, although abundance and survival of natural *P. leiophylla* seedlings was relatively high at upper elevations (Figs. 4, 5, and 7), these seedlings appeared to be performing very poorly. Seedlings in high elevation sites grew very slowly compared to those at lower elevations (Fig. 6). The success of *P. leiophylla* seedlings at higher elevation also was commonly hampered by an unidentified white-colored fungus, which often spread over the entire plant (relationship of fungal attack with elevation: $r^2 = 0.32$, $F_{1,22} = 10.48$, $P < .01$). Several authors have suggested that a primary negative impact of light limitation on plants is to increase the probability of fungal attack (Vaartaja 1952, 1962, Grime 1966). In most cases, plants attacked by this fungus resprouted or sent out new leaders after extreme needle and stem death. In fact, based on my observation of very large root collars in many of the high elevation *P. leiophylla* seedlings, I speculate that stress in such sites results in repeated stem death–resprout episodes in this species.

Here, I argue for a strong role of light limitation in the control of the upper elevational limit of *P. leiophylla*. Later (see *Trade-offs, ecological strategies, and elevational positions*), I conclude that fires are probably crucial to regeneration of *P. leiophylla*, especially at higher elevations, where vegetation is dense and forest-floor light levels are low. These results suggest that light

limitation may be a key causal factor in the decrease in abundance of *P. leiophylla* from middle to higher elevations. However, because *P. leiophylla* can exploit the high light levels available in fire-caused openings at high elevations, some other factor, such as low temperature, may set the absolute upper distributional limit. Such separation between the control of abundance and the control of distributional limits may be a common feature of tree species populations occurring along elevational (or other) gradients over which soil moisture (or other soil resources) and plant cover increase. Most studies of plant distribution focus on absolute distributional limits rather than abundance changes (e.g., Pearson 1931, Bunce et al. 1979, Neilson and Wullstein 1983, Nobel 1984) probably because their focus is on extremes in physiological stress or on biogeographical limits. Because the goal of this study was to understand change in the makeup of plant communities with elevation (see *Introduction*), abundance is the most appropriate focus. This difference in approach may explain the role of low temperature in controlling upper elevational limits cited in previous studies vs. the importance of light cited here for *P. leiophylla*.

Pinus engelmannii.—The results do not allow firm conclusions on the roles of light, litter, and temperature in controlling the upper elevational limit of *P. engelmannii*. The abundance and performance of natural and experimental seedlings overall declined from the middle of this species range to high elevations (Figs. 4–7), despite the fact that adult densities of *P. engelmannii* did not decline over this gradient (Fig. 4). The results reject a major role for deep litter and low soil temperature in this decline: *P. engelmannii* seedlings exhibited little response to these variables in the microsite study (Fig. 8) and emergence was actually higher where litter was not experimentally removed (Fig. 10). The results are equivocal regarding the role of light limitation in *P. engelmannii* seedling performance at higher elevation. In plots near the upper elevational boundary, seedlings of *P. engelmannii* tended to occur in microsites that were higher in light than found in random microsites (Fig. 8). However, canopy removal did not increase survival in middle or upper elevation plots (Fig. 12). Compared to the lower elevation site, age structure at the high elevation site was greatly skewed towards adults and indicated relatively discontinuous establishment over the past 300 yr, suggesting that regeneration occurred only when the canopy was removed and light increased by fire or other disturbances (Fig. 7). It is possible, however, that the different age structures resulted from higher fire frequency at higher elevation (see Tande 1979) rather than from inhibition of regeneration at high elevation due to light limitation.

It is unlikely that the increasing fire incidence with elevation controls the upper elevational limits of *P. engelmannii*. The available evidence suggests that, if

anything, *P. engelmannii* should be more fire resistant than species at higher elevations, including its close relatives *P. arizonica* and *P. ponderosa*. *P. engelmannii* closely resembles these species, but its juveniles exhibit faster height growth (Righter and Duffield 1951), thicker bark (A. M. Barton, *personal observation*), and a growth pattern that probably confers strong fire resistance compared to the other two species (see *Results: Comparison of species in fire resistance: Qualitative comparisons of species in traits related to fire resistance*). Also, unlike *P. discolor*, there is no evidence of juvenile encroachment of *P. engelmannii* into higher elevations (Fig. 4). These observations suggest that other factors not included in this study, such as limited growing seasons (Shreve 1915, Pearson 1931, Smith 1985) or low winter temperatures, may control the upper limits of *P. engelmannii* along this elevational transect.

*Trade-offs, ecological strategies, and
elevational positions*

The results of this study do not support the hypothesis that trade-offs between shade tolerance and drought resistance control the elevational positions of the three pine species. Although water stress dictated lower elevational limits, upper elevational limits were not controlled by competition for light uniformly across species. Furthermore, shade tolerance and drought resistance were not negatively correlated: the most drought-resistant species, *P. discolor*, also appeared to be the most shade tolerant among the tested species.

The success of *P. discolor*'s seedlings in mesic environments may in part result from traits promoting its success in xeric habitats. Its large seeds, probably originally an adaptation for bird dispersal (see Vander Wall and Balda 1977, Ligon 1978), allow *P. discolor* to exploit microsites under vegetative cover where litter is deep and soil moisture and temperature are ameliorated. The relatively low light environments characteristic of these microsites may have selected for a degree of shade tolerance unusual for plants occupying xeric habitats. These traits have probably pre-adapted *P. discolor* to the more mesic conditions at higher elevations. In addition to increasing the chance of emergence through the deep litter, large seed size may also enhance the probability of surviving fungal attack and other depredations acting on young seedlings in these shady environments (Salisbury 1942, Grime 1966, Baker 1972). Under a natural fire regime, however, this pre-adaptation would rarely operate because frequent fires would kill the fire-sensitive seedlings of *P. discolor*, preventing its establishment at higher elevations.

In contrast, *P. leiophylla* has a poorly developed ability to exploit conditions under heavy vegetative cover. Its establishment at lower elevations is constrained by water stress, and, probably because of its small seeds, it has difficulty emerging in more favorable nurse tree microsites with deep litter (Table 3). At higher eleva-

tions, seedling establishment is greatly enhanced, probably as a result of increased soil moisture, but intolerance of conditions there, especially low light, appear to limit the success of these seedlings. Its very low seedling densities at lower elevations where adults are abundant (Fig. 4) and the preference of seedlings for openings over the entire gradient suggest that the negative effects of shade may extend to lower elevation, xeric sites, perhaps acting cumulatively with water stress to limit *P. leiophylla* seedling establishment (Oosting and Kramer 1946, Withers 1979). The strong negative effects of vegetation cover on seedlings and the discontinuities in past stand establishment (Fig. 7) suggest that regeneration in *P. leiophylla* is closely tied to fire, which can increase light and temperature and decrease litter cover (Zobel 1969, Wright and Bailey 1982). Its thick bark, self-pruning, resprouting ability, and fast growth should provide *P. leiophylla* with a strong competitive advantage in postfire environments.

The above descriptions of *P. discolor* and *P. leiophylla* are consistent with their placement in a recent classification of strategies of pines by McCune (1988). *P. discolor* was placed in the stress-tolerant group with species that have animal-dispersed seeds and are able to tolerate conditions in cold or dry sites where fire is infrequent. *P. leiophylla* was grouped with fire-resilient species, which have small, abundant seeds and the ability to exploit postfire conditions. *P. engelmannii* was grouped with its close relative *P. ponderosa* in the fire-resistant group of species with large stature and thick bark, a classification that agrees well with the few conclusive results reported here on *P. engelmannii*. These three very different strategies apparently reflect the phylogeny of the genus *Pinus* rather than convergences between clades (McCune 1988). The phylogenetic entrenchment of these combinations of traits suggests that the rejection of the light-moisture trade-off hypothesis in the pines studied here did not result from idiosyncrasies acquired through recent evolutionary departures in these three pine species from the rest of the genus *Pinus*. Instead, the control of the distributions of these pines appears to result from ecological strategies common to pines (see McCune 1988).

The trade-off between the use of light and soil resources (such as soil moisture) predicted by Tilman's ALLOCATE model (1988) rests on the pattern that decreasing soil resources favors increased allocation to roots and decreased allocation to stems and leaves. Although in the field the two lowest elevation species allocate a higher percentage of biomass to roots compared to *P. engelmannii* (A. M. Barton, *unpublished data*), greenhouse studies show the opposite pattern and suggest that differences in drought resistance among these species arise from differences in the ability to conserve water that are unassociated with biomass allocation (Barton and Teeri 1993). Although it is unclear which specific mechanisms led to differences in water retention, apparently they did not impose shade in-

tolerance on *P. discolor*. A wide array of morphological and physiological traits can confer drought resistance in plants (Levitt 1980, Turner and Kramer 1980, Kramer 1983, Caldwell and Richards 1986). Some of these are likely to impose shade intolerance on plants through their effects on biomass allocation (Tilman 1988) and other traits (Smith and Huston 1989). Others, such as the ability to tolerate internal dehydration, may bear little relation to mechanisms of shade tolerance but may impose trade-offs on tolerance of other stresses or on growth rate. This complexity suggests that plant community and physiological ecologists should seek to understand the extent to which different strategies of drought resistance and shade tolerance are likely to lead to trade-offs between these two or other physiological attributes (see, for example, Woodward 1987). It is likely that such progress will require a much better understanding of the cellular, anatomical, and physiological mechanisms underlying plant tolerance and growth.

Although *P. discolor* appears to avoid trade-offs in light and water use, its drought resistance may impose other limitations that impinge on its distribution. Several studies have suggested that tolerance of water stress is negatively correlated with growth rate among species (Orians and Solbrig 1977, Bunce 1981; see also Chapin 1980 for tolerance of low nutrient availability). Tilman (1988) has also argued that drought resistance imposes limits on the height of plants. These hypotheses suggest that the slow growth rate and short stature of *P. discolor* may result from mechanisms conferring drought resistance in this species. Constraints on growth rate and stature may in turn limit the ability of *P. discolor* to survive periodic fires or exploit postfire conditions where fire is frequent, as discussed previously. Its short stature also raises the question of whether *P. discolor* would ever become an important component of the tree canopy in mesic sites, even under current fire suppression. Despite their high survival and consistent height growth in these sites, these individuals exhibit slower height and branch growth compared to plants at lower elevations (A. M. Barton, *personal observation*). Lack of access to the canopy may limit reproductive capacity and population abundance of this species. In a sense, then, this scenario suggests that *P. discolor*'s drought resistance may impose trade-offs on other traits (i.e., stature) that could lead to its failure to exploit conditions of higher moisture and lower light.

*Resource gradients, fire, and models of
plant populations and communities*

Correlations between fire and soil resource gradients appear to be ubiquitous in nature (e.g., Habeck and Mutch 1973, Heinzelman 1973, Arno 1980, Harmon et al. 1983, Whitney 1986, Clark 1989). Fire can affect plant individuals and populations indirectly by modifying resource availability and other conditions or directly by killing plants outright. Many studies have

documented a dominant role of fire in structuring plant communities and landscapes both through its indirect effects (e.g., Bray and Curtis 1957, Heinzelman 1973, Romme and Knight 1982, Foster and King 1986, Peet 1988) and direct effects (e.g., Habeck and Mutch 1973, Heinzelman 1973, Grimm 1984, Christensen 1985). This study suggests that fire, especially as a direct agent of selective mortality, can exert strong control over species distributions and community composition in the Chiricahua Mountains. Similarly, Habeck and Mutch (1973) and Tewari et al. (1989) found that with increasing probability of fire along elevational gradients, the bark thickness and fire resistance of tree species increased, suggesting that fire acted as an environmental filter determining the elevational distributions of species (see also Knight and Loucks 1969, Heinzelman 1973).

The results of this study suggest that the direct effects of fire and its correlation with soil resources should be incorporated into the models addressed in this paper (Tilman 1988, Smith and Huston 1989). Previously, I argued that drought resistance may constrain maximum growth rate and height, two traits that may be crucial to fire resistance. By connecting population mortality rates with growth rate or maximum height of species, possible strategies and trade-offs related to the differential direct effects of fire among species could be incorporated into Tilman's ALLOCATE model and possibly that of Smith and Huston. In some systems, however, resource use, growth rate, and resistance to fire or other agents of selective mortality may relate differently, even oppositely, to that suggested above (e.g., Coley et al. 1985, Wilson and Keddy 1986, Loehle 1988), as discussed previously for fire. These divergent results suggest that models connecting plant traits, species distributions, and community structure may need to be sufficiently flexible to incorporate a variety of possible trade-offs.

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