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MORPHOLOGICAL VARIATION OF *PINUS FLEXILIS* (PINACEAE), A BIRD-DISPERSED PINE, ACROSS A RANGE OF ELEVATIONS[1]

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Limber pine (*Pinus flexilis* James) grows across a wider range of elevations than any other tree species in the central Rockies, from ~1600 m at Pawnee Buttes to >3300 m at Rollins Pass. In this study we investigated two possible explanations for limber pine's success across a broad range of elevations: (1) the sites on which it is found, although separated by >1000 m elevation, may not be very different with respect to environmental factors that affect tree growth, and (2) limber pine growth is insensitive to environmental factors that change with elevation. We compared site characteristics of 12 limber pine stands at elevations ranging from 1630 to 3328 m as well as the growth and morphology of trees in each of these stands. Mean daily air temperature in July decreased linearly with the elevation of the site from 22.8° to 12.6°C. The growth and morphology of limber pine leaves, shoots, and trees were, in general, not related to the elevation or July mean air temperature of the sites. There was, however, a significant decrease in stomatal density with increasing elevation, which may be an acclimational response to restrict water loss at high elevations. Our data suggest that the fundamental and realized niche of limber pine is broad with respect to air temperature. In light of the high gene flow and only slight genetic differentiation among populations of species with bird-dispersed seeds, such as limber pine, it is especially unusual to see similar growth throughout an environmental gradient. Physiological and anatomical plasticity or wide physiological tolerance ranges may enable limber pine to uncouple its growth from its environment.

Key words: acclimation; adaptation; altitude; fundamental niche; limber pine; phenotypic plasticity; Pinaceae; *Pinus albicaulis*; realized niche; stomatal density.

Limber pine (*Pinus flexilis* James) ranges in latitude from 33°N to 51°N and in elevation from 870 m in North Dakota to ~3400 m in Colorado (Burns and Honkala, 1990). In the northern Rocky Mountains and west, limber pine is generally found at lower elevations with whitebark pine (*Pinus albicaulis* Engelm.) occupying the higher elevations. In the southern Rocky Mountains limber pine grows at high-elevation sites and is displaced at the lower elevations by southwestern white pine (*Pinus strobiformis* Engelm.). In the central Rocky Mountains limber pine grows from below the lower tree line to the upper tree line, from ~1600 m at Pawnee Buttes to >3300 m at Rollins Pass. Limber pine's elevational range is wider than any co-occurring tree species (Table 1). In the central Rocky Mountains, it is associated at low elevations with ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), whereas at high elevations its associates include lodgepole pine (*Pinus contorta* Dougl. ssp. *latifolia* Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), bristlecone pine (*Pinus aristata* Bailey), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.). Why is limber pine able to exist in such a variety of locations, alongside species that are much more restricted in their elevational distribution?

Limber pine differs from most of it associated species in an obvious way: its seeds are dispersed by birds, and possibly rodents, rather than by the wind. The Clark's nutcracker (*Nucifraga columbiana* Wilson) extracts the seeds from pine cones, carries up to 125 seeds at a time in its sublingual pouch, and caches these seeds up to 22 km away from the parent tree (Vander Wall and Balda, 1977). It prefers to cache seeds on wind-exposed sites that accumulate little snow (Vander Wall and Balda, 1977) and uses geometric relationships between landmarks to facilitate cache retrieval during the winter and spring (Kamil and Jones, 1997). A single nutcracker may cache up to 30 000 seeds per hectare in one season (Lanner and Vander Wall, 1980) but retrieves and consumes only 80% of them leaving the rest to be eaten by rodents or to germinate.

The caching patterns of nutcrackers not only affect where seeds are deposited but also influence the growth form of limber pine. Bird-dispersed trees grow as single-stemmed trees or in clumps or clusters (following the terminology of Tomback, Hoffman, and Sund, 1990). If one seed from a cache germinates, an individual tree becomes established at the tree site. A clump of stems can be the product of a single germinant that has lost apical dominance, resulting in a multiple-stemmed growth form or a cluster of individual germinants from one cache. Genetic analysis is required to determine whether a clump of stems is one genet with multiple stems or a cluster of genets. Approximately half of all clumps are individuals with multiple stems (Carsey and Tomback, 1994) revealing that loss of apical dominance at a young age is common for limber pine.

Another consequence of being bird-dispersed is the genetic structure of populations, which is often less differentiated among populations than that of wind-dispersed species (Bruederle et al., 1998). Estimates of gene flow from the lowest to the highest elevation stands of limber pine in the central Rocky Mountains using molecular genetic analyses are inconsistent

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TABLE 1. Elevation ranges of tree species associated with limber pine in the Central Rocky Mountains. Data are from Peet (1981) and Baker (1992).

Scientific name	Abbreviation	Common name	Elevation range (m)
Pinus flexilis James	PIFL	Limber pine	1600–3400
Juniperus scopulorum Sarg.	JUSC	Rocky Mountain juniper	1600–2800
Pinus ponderosa Dougl. ex Laws.	PIPO	Ponderosa pine	1700–2800
Pseudotsuga menziesii (Mirb.) Franco	PSME	Douglas-fir	1700–3000
Populus tremuloides Michx.	POTR	Quaking aspen	2000–3400
Pinus contorta Dougl. ssp. *latifolia* Bailey	PICO	Lodgepole pine	2300–3300
Picea engelmannii Perry ex Engelm.	PIEN	Engelmann spruce	2400–3500
Pinus aristata Bailey	PIAR	Bristlecone pine	2750–3670
Abies lasiocarpa (Hook.) Nutt.	ABLA	Subalpine fir	2500–3500

and depend on the technique applied (Schuster, Alles, and Mitton, 1989; Mitton, 1995; Latta and Mitton, 1997). The necessary reciprocal transplant studies to examine the genetic-by-environment interaction on the phenotype of limber pine along an elevation gradient have not been done. In general, however, pines that are dispersed by nutcrackers tend to lack the family structure found in pines with wind-dispersed seeds (Furnier et al., 1987; Bruederle et al., 1998).

If limber pine lacks elevational races, we hypothesize that the effects of elevation on growth and resultant morphology of limber pine would be more obvious than for species that have undergone adaptations to local environments. A complex array of physical factors that affect plant growth vary with elevation: air temperature and atmospheric pressure decrease and precipitation and wind increase (see Friend and Woodward, 1990). While there are numerous provenance studies with conifer species over a range of elevations (see Mitton, 1995), there are surprisingly few studies that have quantified growth of mature trees at different elevations (see Tranquillini, 1979). Native populations of erect trees of *Picea engelmanni* (Hansen-Bristow, 1986), *Pinus sylvestris* L. (Grace and Norton, 1990; James, Grace, and Hoad, 1994), *Pinus contorta* (Schoettle, 1990), *Pinus pumila* Regel. (Kajimoto, 1993), *Abies lasiocarpa* (Hansen-Bristow, 1986), and *Abies koreana* (Kang et al., 1990) have shown reduced leaf length, shoot growth, and leaf production per year with increasing elevation. Similar effects of elevation on growth have been observed in native populations of a tree species in the tropics as well (Cordell et al., 1998). High-elevation populations of *Betula* have reduced sexual reproduction compared to populations growing at lower elevations (Holm, 1994), yet differences in shoot and leaf growth were not evident across an elevation range of 560 m (Kudo, 1995). Herb, shrub, and broad-leaf tree species at high elevations have decreased specific leaf area, increased stomatal density, and different ratios of ^{13}C to ^{12}C compared to those at low elevations (Körner, Farquhar, and Roksandic, 1988; Körner et al., 1989; see Friend and Woodward, 1990, and references therein; Vitousek, Field, and Matson, 1990). The decrease in growth with increasing elevation is interpreted to be a symptom of increasing environmental stress.

In Colorado, limber pine tends to dominate stands only in dry locations (Peet, 1981; Rebertus, Burns, and Veblen, 1991), so it is unlikely that the usual increase in soil moisture with elevation is obvious at these sites. It is possible that through variation of site exposure with elevation, the expected variation in air temperature with elevation could be minimized. In this study we tested two possible hypotheses for limber pine's success across a broad range of elevations: (1) the sites on which it is found, although separated by >1000 m elevation, do not differ much with respect to environmental characteristics that affect tree growth, and (2) the growth and morphology of limber pine are not affected by the differences in environment with elevation.

TABLE 2. Summary of physical characteristics of 12 limber pine (PIFL) stands along an elevation gradient in northern Colorado and southern Wyoming. T_{air} is the mean daily air temperature during the month of July 1997.

Site	Elevation (m)	UTM coordinates		T_{air} (°C)	Slope (deg)	Aspect
		North (m)	East (m)			
Dave's Draw	1630	4520100	582100	22.8	22	N
Red Feather	2450	4519150	451350	18.2	19	WNW
Woods Landing (Wyo)	2609	4548700	409300	16.6	22	WNW
Jelm View (Wyo)	2646	4545200	408250	15.9	5	SW
Lake John	2652	4517000	373250	16.1	5	E
Pond View	2963	4418000	448450	15.7	22	SE
Meeker Drainage	3048	4455100	451550	15.6	22	SE
Wild Basin	3072	4452350	452250	15.5	32	SSW
Lawn Lake	3084	4475350	446350	14.3	28	WSW
Crown Point	3133	4500400	444750	14.0	9	NW
Mid-Rollins Pass	3170	4419150	445650	12.9	22	NNW
Jenny Lake	3328	4420500	443750	12.6	14	SE

MATERIALS AND METHODS

Site characterization—Twelve study areas, which ranged from 1630 to >3300 m in elevation, were selected (Table 2). Sites were located east of the Continental Divide in northern Colorado and southern Wyoming (Fig. 1). At each site, limber pine was the dominant tree species, accounting for at least 50% of the basal area. All of the stands are natural and unmanipulated to the best of our knowledge from historical records. Clark's nutcracker are thought to be involved in the origin of each of these stands although nutcrackers were never sighted in the lowest elevation stand, Dave's Draw. At 1630 m elevation, this site is on a north–south running escarpment in the short-grass steppe. The region between the site at 2450 and 1630 m is primarily a nonforested grassland. While it is not known why this area is devoid of trees yet trees grow on the escarpment, a plausible explanation is low water availability and the escarpment, being a different substrate, may provide greater water availability for tree survival. At the highest elevation site, Jenny Lake, the trees were erect and just downslope from a krummholz zone of limber pine and subalpine fir; we did not sample across the forest-alpine ecotone. Site characterizations were conducted in June and early July 1997.

Slope and aspect were measured using a clinometer and compass. Elevation, latitude, and longitude were read from USGS 7.5 min topographic maps. Air temperatures were measured (Optic Stowaway Temp data loggers; Onset Computer Corp., Pocasset, Massachusetts, USA) within the northern side of a limber pine crown, 2–3 m above the ground, at 30-sec intervals, and hourly averages were recorded for the month of July at all sites. The 24-h average

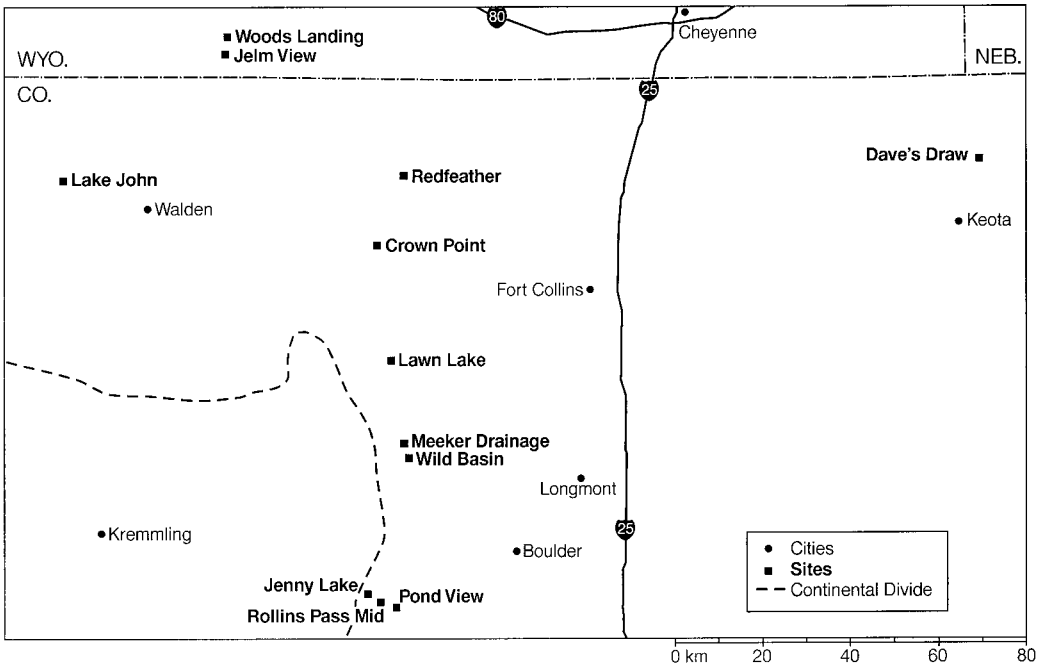

Fig. 1. Map of northern Colorado and southern Wyoming with each of the 12 sample sites shown. The dashed line is the Continental Divide.

air temperature was computed for each day and averaged over the month of July to determine the mean daily (24-h) air temperature for July (T_{air}). Each data logger was shielded from direct radiation by an inverted translucent funnel. Plant species that were common were recorded for each site. These species lists are not exhaustive; they include many but not all of the species at each site. The list of species can be obtained from the authors.

Stand densities, by tree species, were measured using the point-centered quarter method (Mueller-Dombois and Ellenberg, 1974). Tree height (HT, in metres), measured with a height pole and diameter at 1.37 m (DBH, in centimetres) were recorded for the nearest single tree or clump of trees in each quadrant with respect to each of the 10 sample points. A small core was also extracted from the north side of each tree stem at 1.37 m above the ground for quantification of bole growth for each of the previous four years. In addition, for each stem, the presence or absence of male and female cones was noted to determine whether the tree was reproductive.

Soil samples were collected from every other point-centered quarter-sample point for five samples from each site, (except the three sites within Rocky Mountain National Park) and analyzed for texture and nutrients. In the laboratory, the samples for a site were composited and sieved to separate soil (the particles < 2 mm in diameter) from gravel (particles > 2 mm). Visible organic matter was removed from the composited samples. Textures were determined using the hydrometer method of Gee and Bauder (1986) as modified by Stohlgren (T. Stohlgren, personal communication USGS, Fort Collins, Colorado). Percentage nitrogen of the soils was determined using a LECO CHN-1000 element analyzer (LECO Corporation, St. Joseph, Michigan, USA). In addition pH (from paste), percentage organic matter (combustion), and P, K, Zn, Fe, Mn, and Cu (AB-DTPA extract) were quantified.

Tree and shoot morphology measurements—Because we know that tree size (Schoettle, 1994) and growth form (Feldman, Tomback, and Koehler, 1999) can affect growth, we standardized the size of the trees used for among-site comparisons; we selected ten single-stemmed limber pine trees per site that were between 5 and 7 m tall. Tree height, diameter at breast height (DBH), radial annual bole growth (COREGR), and the presence/absence of male and female cones were recorded for each tree. To avoid within-crown variation in shoot characteristics (Schoettle and Smith, 1991), three shoots were collected from the south side of the upper third of the crown of each tree. The shoots were clipped at the base of the oldest annual growth increment with live needles. We determined the length of the foliated portion of the twig (FOL L, in centimetres), age of the oldest leaves (LL, in years), annual shoot extension growth (INCR, in centimetres), needle length (NL, in centimetres) and number of fascicles (FASC#) produced each year, and the dry mass of each annual leaf cohort (LEAFWT, in grams) and twig increment (TWIGWT, in grams) for each shoot (see Schoettle and Smith, 1991, for details). From these data the mass per fascicle (WTFASC, in grams) and fascicle density (FD, number of fascicles per centimetre of twig) were calculated for the leaf cohorts formed in each of the years from 1993 through 1997. Statistical analyses (see below) were conducted on the average of these values from the three shoots per tree for years 1993–1997. In addition, the specific leaf area (SLA, in square centimetres of total leaf surface area per gram dry mass of leaf tissue), a measure of the robustness of the leaf, was quantified for current year (1997) needles. The total leaf surface area was calculated geometrically from measurements of needle length and width (measured at 8× magnification with Optimus v. 6.1 image analysis software). On those same leaves, the number of stomata per leaf surface area (SDEN) and number of stomata per needle volume (STVOL) were quantified (according to Illingworth [1975] using the Optimus v. 6.1 image analysis software). All shoot and leaf samples were collected between 20 August and 24 September 1997.

Data analysis—All of the statistical analyses were performed with SPSS. We applied regression analysis to test for significant relationships between site variables (average daily air temperature in July and soil characteristics) and elevation. The botanical differences among sites were assessed by comparing the species presence data at all sites using Detrended Correspondence Analysis (DCA) (PC-ORD; McCune and Mefford, 1995).

We applied ANOVA to detect whether the tree variables (FOL L, INCR, NL, FASC#, LEAFWT, TWIGWT, LL, FD, WTFASC, SDEN, STVOL, SLA) were affected by the elevation of the sites. An average value for each variable was computed for each tree for a sample number of ten for each site except for the Pond View site where only five trees were sampled. For those variables that were significantly different among sites, we used ANOVA with polynomial contrasts (based on the elevation or T_{air} of the sites) to test whether the relationship was linear, quadratic, or cubic. The assumption of normally distributed residuals and homogeneous variances among sites was tested and confirmed for each variable. All analyses were conducted on the full data set

TABLE 3. Soil characteristics at sites that are dominated by limber pine along an elevation gradient.

Site	Elevation (m)	Soil texture (% SAND)	pH	Organic matter (%)	Soil N (%)
Dave's Draw	1630	65.7	7.6	1.4	0.043
Red Feather	2450	76.3	6.6	1.7	0.028
Woods Landing	2609	80.6	7.2	1.4	0.029
Jelm View	2646	67.7	6.5	3.1	0.126
Lake John	2652	65.7	6.4	1.9	0.207
Pond View	2963	79.1	6.1	2.3	0.049
Crown Point	3133	69.5	5.2	3.7	0.029
Jenny Lake	3328	78.0	5.1	3.2	0.028
Regression with	*P*	0.270	0.002	0.040	0.869
elevation	r^2	0.198	0.881	0.534	0.005
	Slope		−0.0015	0.0013	
	Intercept		10.4061	−1.0295	

(all 12 sites) as well as on a data set where the lowest elevation site (Dave's Draw) was omitted. Unless otherwise noted, omitting Dave's Draw did not affect the interpretation of results. For those factors where the linear contrast with elevation was significant, a linear regression analysis was performed on the site means ($N = 12$) to generate a regression line ($r^2 = 0.33$ is significant at a $P = 0.05$ level).

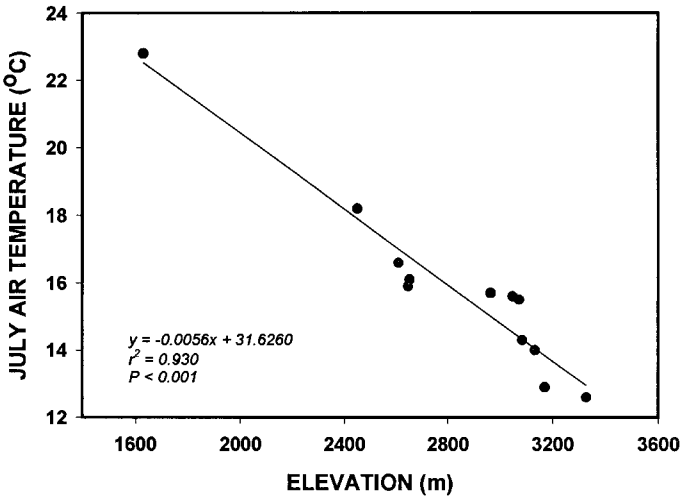

Fig. 2. Relationship between site elevation and average daily air temperature during the month of July 1997. The results of the linear regression analysis of the site means ($N = 12$) is shown on the graph ($y = -0.0056x + 31.6260$; $r^2 = 0.930$; $P < 0.001$).

RESULTS

Some of the physical characteristics of the sites varied with respect to elevation (Tables 2 and 3). All of the sites were sandy and dry. Soil pH declined and percentage soil organic matter increased with increasing elevation; soil nitrogen was not related to the elevation of the site (Table 3). Soil P, K, Zn, Fe, Mn, and Cu were not correlated with elevation (data not shown). Mean daily (24-h) air temperature in July (T_{air}) varied predictably with elevation ($r^2 = 0.93$, $P < 0.001$; Fig. 2). The rate of decrease in T_{air} with increasing elevation (lapse rate) was 5.6°C/km. T_{air} ranged from 22.8°C at the low-elevation site, Dave's Draw, to 12.6°C at the upper tree line site, Jenny Lake (Table 2).

Tree species that co-existed with limber pine at each sites showed the expected progression with elevation from Rocky Mountain juniper to ponderosa to lodgepole pine up to Engelmann spruce, subalpine fir, and bristlecone pine at the higher elevations (Table 4). The distribution of herbs and forbs at each site also varied along the elevation gradient. The Detrended Correspondence Analysis (DCA) of the plant species data revealed that the first axis, which explains the greatest amount of variation in the data (62%), was closely related to elevation (Fig. 3). The second DCA axis was not related in a simple manner to any of the environmental parameters we measured. The variation in other plant species along the gradient within our sites and the air temperature data suggest the growing conditions among the sites differed.

All of the sites had limber pine growing singly and in clumps. There was no apparent relationship between elevation and the proportion of clumped trees or the percentage of stems with male or female cones (Table 4).

The growth characteristics of ten single-stemmed limber pine trees of similar height (5–7 m) at each site varied significantly among sites, although a relationship with elevation or T_{air} was not always clear (Table 5). Bole growth, as measured by mean annual ring width (COREGR), was variable and not simply related to elevation or T_{air} (Table 5). The length of the new twig produced each year (annual shoot growth, INCR) was only weakly related to elevation ($r^2 = 0.137$) or T_{air} (Table 5). Leaf life span increased linearly with increasing elevation (Fig. 4). However, if the lowest elevation site (Dave's Draw) is omitted and the analysis is restricted to the forested elevation range of limber pine (2450–3328 m), the linear relation-

TABLE 4. Biological characteristics of 12 limber pine (PIFL) stands along an elevation gradient in northern Colorado and southern Wyoming. (See Table 1 for key to other species abbreviations.)

Site	Elevation (m)	Density (trees/ha)	% PIFL	PIFL		% of PIFL reproductive		Other tree species
				% singles	% clumps	Female	Male	
Dave's Draw	1630	233	64	39	61	74	45	JUSC
Red Feather	2450	604	68	78	22	69	50	PICO, PIPO, JUSC, PSME
Woods Landing	2609	360	80	56	44	63	70	PICO, POTR
Jelm View	2646	233	88	71	29	78	59	PICO
Lake John	2652	406	93	41	59	68	71	POTR
Pond View	2963	289	50	60	40	60	70	PICO, POTR
Meeker Drainage	3048	856	65	65	35	85	55	PICO, POTR
Wild Basin	3072	634	85	76	24	69	50	PIPO, PICO
Lawn Lake	3084	1220	38	53	47	10	55	PICO, PIEN
Crown Point	3133	866	73	55	45	52	43	ABLA, PIEN, PICO
Mid-Rollins Pass	3170	1329	55	45	55	15	50	ABLA, PIEN
Jenny Lake	3328	404	75	27	73	38	76	ABLA, PIEN, PIAR

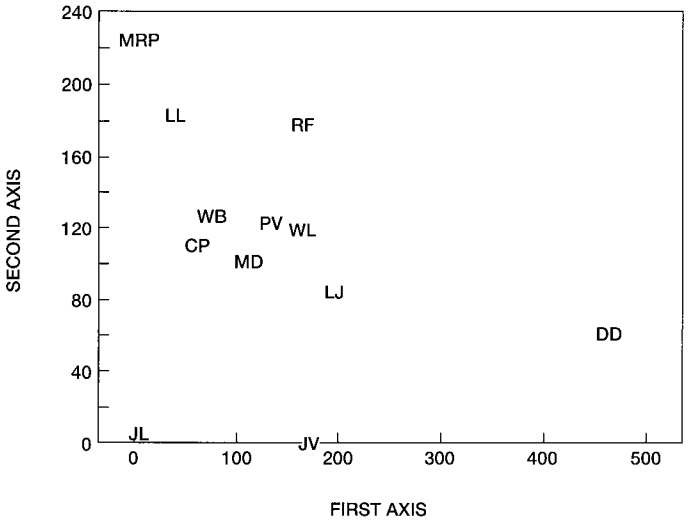

Fig. 3. Site scores for the first two DCA axes based on species presence at the sites. The points are labeled with the site abbreviation (DD, Dave's Draw; RF, Red Feather; WL, Woods Landing; JV, Jelm View; LJ, Lake John; PV, Pond View; MD, Meeker Drainage; WB, Wild Basin; LL, Lawn Lake; CP, Crown Point; MRP, Mid-Rollins Pass; JL, Jenny Lake).

ship between leaf life span and elevation is lost ($P = 0.238$). The length of the shoot that retained foliage (FOL L) varied among sites, yet was only weakly, nonlinearly, related to the elevation or T_{air} of the site (Table 5).

Fascicle and needle characteristics varied among sites for limber pine (Table 6). The number of fascicles produced per year (FASC#) decreased slightly with elevation and T_{air} ($r^2 = 0.20$ and $r^2 = 0.31$, respectively). Specific leaf area (in square centimetres per gram, SLA) of leaves rose sharply near upper tree line. The mass of fascicles tended to decrease with increasing elevation (WTFASC, $r^2 = 0.40$), this may have been a result of a significant decrease in needle length (NL, $r^2 = 0.45$). Fascicle density was weakly related to elevation (FD, $r^2 = 0.04$) (Table 6). Stomatal density (Fig. 5) and number of stomata per needle volume (Fig. 6) declined significantly with increasing elevation.

DISCUSSION

The distribution of a species along an environmental gradient is a function of both the species' tolerances and competitive abilities. Tolerances define its fundamental niche, whereas competitive abilities restrict that species to sites with a narrower suite of conditions—the realized niche. Sites along an elevation gradient often vary with respect to air temperature and moisture. Limber pine occurs over a wide range of elevations along the Front Range of Colorado, but dominates only dry or exposed sites. This pattern of distribution suggests that limber pine's fundamental and realized niches are broad with respect to air temperature, while its realized niche is narrow with respect to moisture. This study was conducted to determine whether the sites dominated by limber pine across a range of elevations in fact vary with respect to air temperature and how the growth and resultant morphology of limber pine trees respond to those conditions.

The 12 limber pine-dominated sites were typical for their elevations with respect to air temperature. The rate of change in mean July air temperature, T_{air}, with increasing elevation was −5.6°C/km, which is similar to the average lapse rate of −6.91°C/km for a 10-yr period calculated from 39 Colorado weather stations across a similar elevation range east of the Continental Divide ($r^2 = 0.93$; data obtained from the Colorado Climate Center). The mean daily temperatures in July for

TABLE 5. General characteristics of single-stemmed limber pine trees and shoots from ten trees per site at 12 sites along an elevation gradient. Samples were only from trees that were between 5 and 7 m tall. $N = 10$ for each site except Pond View where only five trees were sampled.

Site	Elev. (m)	COREGR		INCR		FOL L		LL	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Dave's Draw	1630	81.9	9.2	1.6	0.12	9.3	0.8	4.4	0.27
Red Feather	2450	104.5	14.6	1.3	0.10	13.0	0.8	7.9	0.32
Woods Landing	2609	88.3	8.1	1.5	0.18	20.9	1.3	9.6	0.55
Jelm View	2646	160.6	17.2	1.9	0.13	20.2	1.6	8.4	0.38
Lake John	2652	90.1	16.4	1.2	0.20	13.8	1.8	8.4	0.34
Pond View	2963	175.1	9.3	1.7	0.16	15.9	1.1	8.4	0.97
Meeker Drainage	3048	69.1	4.9	1.0	0.06	7.4	0.6	6.0	0.28
Wild Basin	3072	93.4	8.4	1.7	0.11	17.3	1.3	7.8	0.30
Lawn Lake	3084	38.0	5.3	1.0	0.09	12.1	1.2	9.8	0.72
Crown Point	3133	22.1	3.1	0.6	0.05	7.2	0.6	9.6	0.41
Mid-Rollins Pass	3170	135.5	20.2	1.5	0.16	18.5	1.7	9.4	0.28
Jenny Lake	3328	101.9	6.5	1.2	0.16	12.3	1.3	9.2	0.42
		ANOVA results (P)							
ANOVA - effect of site		<0.001		<0.001		<0.001		<0.001	
ANOVA - contrasts with elevation									
linear		0.655		0.001		0.564		0.001	
quadratic		0.004		0.157		0.001		0.001	
cubic		0.444		0.883		0.257		0.006	
ANOVA - contrasts with T_{air}									
linear		0.996		0.003		0.057		0.001	
quadratic		0.064		0.417		0.001		0.073	
cubic		0.004		0.338		0.041		0.115	

Note: SITE = site location; ELEV = site elevation (m); COREGR = mean annual radial growth (mm/100) (1993–1997); INCR = mean annual shoot extension growth (cm) (1993–1997); FOL L = length of the twig that retained foliage (cm) (all leaf age classes); LL = maximum leaf life span (yr); SE = standard error.

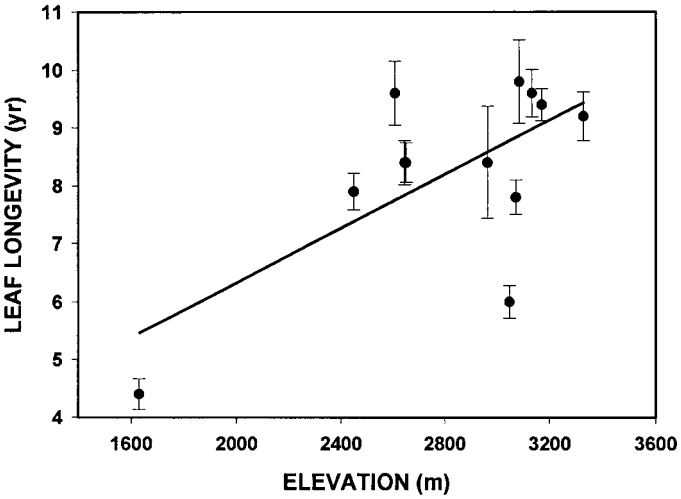

Fig. 4. Relationship between elevation and leaf longevity for limber pine. Only trees that were between 5 and 7 m tall were sampled. Values are the average of three shoots from ten trees per site (± 1 SE). The result of the linear regression analysis of the site means ($N = 12$) is shown on the graph ($y = 0.002x + 1.641$; $r^2 = 0.451$; $P = 0.017$).

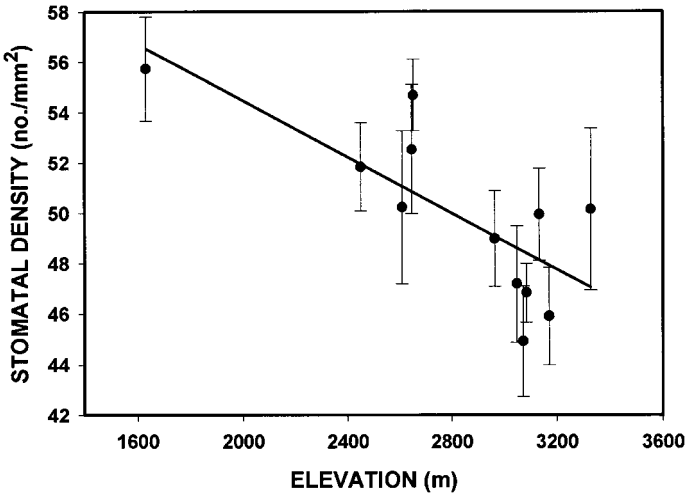

Fig. 5. Relationship between elevation and stomatal density for limber pine. Only trees that were between 5 and 7 m tall were sampled. Values are the average of three current-year fascicles per shoot from ten trees per site (± 1 SE). The result of the linear regression analysis of the site means ($N = 12$) is shown on the graph ($y = -0.006x + 65.627$; $r^2 = 0.578$; $P = 0.004$).

the sites were also not unusual. The Jenny Lake site, at upper tree line, had a July mean temperature of 12.6°C, whereas the mean air temperatures at Red Feather and Woods Landing, near the lower tree line, was 18.2°C and 16.6°C, respectively (Table 2). Around the world, the mean July temperature for the upper tree line is 13°C and for the lower tree line is 17°C (Cogsbill and White, 1991). Therefore the tree line sites that support limber pine are relatively typical with respect to air temperature. In addition, the other plant species (trees, shrubs, and herbs) varied predictably with elevation among the 12 sites, further suggesting that the growing conditions varied among sites.

Every site studied had limber pine growing singly and in clumps. The percentage of locations occupied by limber pine of the multistemmed growth form averaged 45% among our stands. This is similar to the percentage of clumps in limber pine stands in Utah (Lanner, 1980) and Colorado (Carsey and Tomback, 1994), but it is slightly higher than other stands in

TABLE 6. Summary of shoot and needle growth characteristics of ten single-stemmed limber pine trees at each site. Samples were only from trees that were between 5 and 7 m tall. $N = 10$ for each site except Pond View where only five trees were sampled.

		FASC#		SLA		LEAFWT		TWIGWT		WTFASC		NL		FD	
Site	Elevation	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Dave's Draw	1630	18.4	1.5	139.1	3.6	1.1894	0.0997	0.2669	0.0349	0.0644	0.0030	5.0	0.19	11.48	0.87
Red Feather	2450	15.4	1.1	140.2	3.0	0.7904	0.0628	0.1538	0.0150	0.0524	0.0022	4.3	0.11	11.64	0.75
Woods Landing	2609	16.6	1.5	133.6	5.0	0.8229	0.0918	0.2478	0.0374	0.0491	0.0028	3.8	0.14	11.21	0.72
Jelm View	2646	16.6	1.0	138.3	5.6	0.9104	0.0899	0.2468	0.0226	0.0551	0.0024	4.2	0.13	8.96	0.61
Lake John	2652	14.1	1.2	137.9	3.9	0.7424	0.0888	0.1597	0.0273	0.0581	0.0031	3.9	0.20	12.63	1.05
Pond View	2963	13.2	1.9	139.3	5.2	0.7905	0.1226	0.1977	0.0232	0.0573	0.0026	4.4	0.15	8.04	0.87
Meeker Drainage	3048	17.9	1.1	147.3	3.4	0.8189	0.0692	0.1405	0.0141	0.0461	0.0020	3.7	0.12	18.04	0.70
Wild Basin	3072	20.5	1.1	131.2	3.0	1.3110	0.1085	0.3104	0.0291	0.0622	0.0028	4.4	0.08	12.00	0.62
Lawn Lake	3084	13.7	0.9	133.9	1.1	0.6752	0.0580	0.1403	0.0168	0.0470	0.0016	3.8	0.12	13.83	0.85
Crown Point	3133	12.4	0.7	154.3	4.3	0.5175	0.0402	0.0753	0.0081	0.0412	0.0014	3.4	0.05	21.85	1.40
Mid-Rollins Pass	3170	13.4	1.0	159.0	5.5	0.6715	0.0755	0.1782	0.0224	0.9501	0.0035	4.3	0.18	9.15	0.73
Jenny Lake	3328	12.3	1.3	173.4	5.7	0.5512	0.0725	0.1663	0.0265	0.0416	0.0018	3.6	0.09	10.37	0.50
		ANOVA results (P)													
ANOVA-effect of site		<0.001		<0.001		<0.001		<0.001		<0.001		<0.001		<0.001	
ANOVA-contrasts with elevation															
linear		0.002		<0.001		<0.001		<0.001		<0.001		<0.001		0.004	
quadratic		0.653		<0.001		0.698		0.987		0.962		0.147		0.129	
cubic		0.039		<0.001		0.003		0.307		0.002		0.028		0.001	
ANOVA-contrasts with T_{air}															
linear		<0.001		<0.001		<0.001		<0.001		<0.001		<0.001		0.301	
quadratic		0.096		<0.001		0.318		0.737		0.518		0.174		0.709	
cubic		0.155		0.001		0.035		0.446		0.112		0.914		0.076	

Note: SITE = site location; ELEV = site elevation (m); FASC# = mean number of fascicles produced per shoot per year; SLA = specific leaf area of current year leaves (cm^2/g); LEAFWT = mean mass of new fascicles produced per shoot per year (g); TWIGWT = mean mass of twig produced per shoot per year (g); WTFASC = mean mass per fascicle (g); NL = mean needle length (cm); FD = mean number of fascicles produced per length of twig (no./cm); SE = standard error.

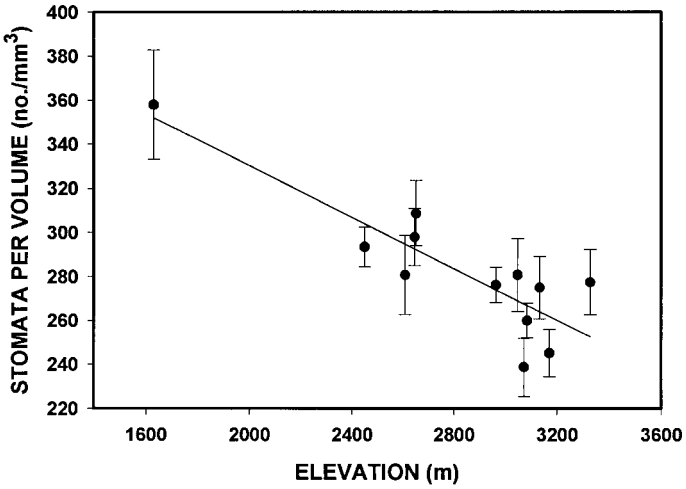

Fig. 6. Relationship between elevation and the number of stomata per leaf volume for limber pine. Only trees that were between 5 and 7 m tall were sampled. Values are the average of three current-year fascicles per shoot from ten trees per site (± 1 SE). The result of the linear regression analysis of the site means ($N = 12$) is shown on the graph ($y = -0.059x + 447.423$; $r^2 = 0.749$; $P < 0.001$).

Colorado observed by Tomback and Linhart (1990) and Schuster and Mitton (1991). Growth form did not vary predictably with elevation, therefore it is unlikely that the distribution of limber pine growing singly vs. in clumps contributes to the species' broad elevational range.

The environmental stress of increasing elevation that is apparent in the growth patterns of other tree species was less obvious for limber pine. Most of the growth characteristics of ten single-stemmed limber pine trees per site (tree heights of 5–7 m) were not strongly related to the elevation or air temperature of the site. The length of the new twig produced each year (annual shoot growth) was only weakly related to site elevation or T_{air} for limber pine in this study, in contrast to annual shoot growth, which decreased dramatically with increasing elevation for Engelmann spruce and subalpine fir (Hansen-Bristow, 1986) and lodgepole pine (Schoettle, 1990) in the central Rocky Mountains and to a lesser degree for whitebark pine in the Northern Rocky Mountains (Schoettle, unpublished data) (Table 7), and other species found elsewhere (see Tranquillini, 1979). Shoot growth probably indexes the carbon gain of the shoot (Schoettle and Smith, 1991) or the branch (Sprugel, Hinckley, and Schaap, 1991; Stoll and Schmid, 1998) during the current and prior year to its growth. The weak relationship between shoot growth and elevation suggests that carbon gain for limber pine may not be affected by elevation.

An increase in leaf life span is hypothesized to be a phenotypic response to increased environmental stress (Schoettle, 1990; Schoettle and Fahey, 1994; Reich et al., 1996). Thus increased leaf life span with elevation has been suggested to be an acclimational response to stress, compensating for reduced shoot growth and foliage production per year and enabling trees with different growth capabilities to retain similar crown architectures and photosynthetic surface areas (Schoettle, 1990; Schoettle and Fahey, 1994). For most *Pinus* species, including limber pine (this study), leaf life span increases with increasing elevation (Ewers and Schmid, 1981; Schoettle, 1990). However, if the exceptionally low elevation site (Dave's Draw) is omitted and the analysis is restricted to the forested elevation range (2459–3328 m), the linear relationship between leaf life span and elevation is lost for limber pine. Limber pine also did not exhibit the same relationships with elevation and shoot morphological characteristics (decreased annual shoot growth and similar foliage retention per shoot) as other pine species (Weidman, 1939; Schoettle, 1990). This also suggests that limber pine is less stressed than other species by the elevation and T_{air} gradient.

Two fascicle and needle characteristics of limber pine varied with elevation in a different manner than has been observed in other species, implying either less stress or broader tolerances than other species. First, we saw an increase in specific leaf area of current-year leaves at the highest elevations for limber pine. In contrast, in natural populations of herb, shrub, and broad-leaved tree species, the specific leaf area of leaves decreases (Körner et al., 1989; Vitousek, Field, and Matson, 1990; Körner, Farquhar, and Wong, 1991) or remains constant (Kudo, 1995; Sveinbjörnsson, Nordell, and Kauhanen, 1992) with increasing elevation. Similarly, in common gardens, specific leaf area of conifers decrease or remain unchanged from populations originating from high to low elevations (Zhang, Marshall, and Jaquish, 1993; Zhang and Marshall, 1995; Oleksyn et al., 1998). Second, needle length decreased with elevation for limber pine to a lesser degree than observed for other conifers (Hansen-Bristow, 1986; Steele, Coutts, and Yeoman, 1989; Kang et al., 1990; James, Grace, and Hoad, 1994) (Table 7). Needle length has been shown to vary along other environmental gradients including growing-season length (Armstrong et al., 1988), availability of water during the growing season (Fritts, Smith, and Stokes, 1965; Isik 1990; Raison, Myers, and Benson, 1992), and growing-season temperature (Mikola, 1962; Junttila and Heide, 1981; Armstrong et al., 1988). It appears that needle length is sensitive to the most limiting factor in any given environment but does not provide insight to help to identify that factor.

How can limber pine uncouple its growth from temperature changes from the upper to below the lower tree line, i.e., from mean daily air temperatures in July under 13°C to over 22°C? The rates of most physiological and biochemical processes are

TABLE 7. Regression relationships between elevation and annual shoot growth and needle length for limber pine and associated conifer species. Cells where the information was not available are denoted by ''NA''.

Species	Elevation range (m)	No. of sites	No. of trees per site	*Annual shoot length*		*Needle length*		Data source
				Slope (cm/km)	r^2	Slope (cm/km)	r^2	
Pinus flexilis	1630–3328	12	10	−0.30	0.137	−0.68	0.454	this study
Picea engelmanni	3018–3465	4	NA	−31.76	0.944	−1.83	0.901	Hansen-Bristow, 1986
Abies lasiocarpa	3018–3465	4	NA	−28.18	0.962	−2.66	0.831	Hansen-Bristow, 1986
Pinus contorta	2800–3200	6	4	−1.75	0.931	NA	NA	Schoettle, unpublished data
Pinus albicaulis	2174–2693	4	6	−0.49	0.925	−1.89	0.727	Schoettle, unpublished data

a function of temperature. Therefore, for growth to be insensitive to variation in air temperature, there must be (1) an adjustment of the morphology or physiology of the plant such that the temperature of the plant is not that of its surroundings, (2) an adjustment of the temperature optima for biochemical processes or the biochemical capacity directly, and/or (3) unusually broad temperature optima.

Leaf clustering reduces the wind speed around needles, increasing the boundary layer resistance, which enables the temperature of the leaves to be well above air temperatures during the day (Hadley and Smith, 1987). Foliar density, a measure of the clustering of needles or fascicles on a shoot, increases near the upper tree line for Engelmann spruce and subalpine fir (Hadley and Smith, 1987), Japanese stone pine (*Pinus pumila*; Kajimoto, 1993), and others species (see Tranquillini, 1979). But fascicle density did not increase along the elevation gradient for limber pine. This suggests that the lapse rate for the temperature of limber pine leaves is likely to be similar to that of ambient air temperature, as suggested by McNaughton (1984).

Whereas a close coupling of limber pine leaf temperatures to air temperatures throughout the elevation gradient may not overcome the temperature limitations of biochemical processes, it may avoid the increase in the leaf-to-air vapor pressure deficit with elevation predicted by Gale (1973) and Smith and Geller (1979). Even so, the potential for greater water stress at high elevations, especially on dry sites, remains since the diffusivity of water vapor in air increases with elevation due to reduced atmospheric pressure. Stomatal density is correlated with stomatal conductance to water vapor (Nobel, 1983) and can vary between individuals growing on dry vs. moist sites (*Pinus ponderosa*; Monson and Grant, 1989). The decrease with elevation in stomatal density and number of stomata per leaf volume in limber pine is consistent with an acclimational response to reduce water loss at high elevations.

Stomatal density is inversely correlated with the concentration of carbon dioxide in the atmosphere for many species, including limber pine (Van de Water, Leavitt, and Betancourt, 1994; Beerling and Kelly, 1997, and references therein). Carbon dioxide concentration (mass per volume) decreases with increasing elevation, however carbon dioxide availability may decline only slightly with elevation due to the counteracting effects of decreased atmospheric pressure and temperature on gaseous diffusivity (Gale, 1972; Smith and Donahue, 1991; Terashima et al., 1995). Studies of non-water-stressed species along elevation gradients have reported that stomatal densities among species increase (Woodward, 1986) or remain unchanged (Körner et al., 1989) with increasing elevation. Stomatal densities among broad-leaved woody species decrease with increasing elevation (Körner, Allison, and Hilscher, 1983). The few studies that have examined variation in stomatal density of a tree species growing at different elevations have shown both unchanged and decreased stomatal densities with increasing elevation (Zelawski and Niwinski, 1966, as cited by Tranquillini, 1979; Illingworth, 1975; Hultine and Marshall, 1998). Stomatal densities also decrease with elevation in limber pine. The decrease in stomatal density with elevation for limber pine suggests that conserving water may be more advantageous than facilitating carbon dioxide uptake for this species on dry, high-elevation sites.

Limber pine differs from most of its associated species in that its seeds are more widely dispersed due to birds. Species with bird-dispersed seed are less genetically differentiated across environmental gradients than those species whose seeds are dispersed only by wind (Bruederle et al., 1998). Consequently, we might have expected limber pine growth to be affected to a greater extent by the factors that change with elevation than associated wind-dispersed species that are adapted (genetically differentiated) to local conditions along the elevation gradient (Grant and Mitton, 1977; Rehfeldt, 1983, 1994a). However, this was not the case, and the variation in growth of limber pine with elevation resembled that of whitebark pine, another bird-dispersed pine, to a greater degree than the other species. Limber pine may be an example of a genetic generalist, as described by Rehfeldt (1994b), characterized by wide tolerance ranges. A high capacity for physiological plasticity or broad physiological tolerances could be adaptive for a species with long-distance seed dispersal across elevations and low genetic differentiation. Alternatively, high physiological plasticity may mask or prevent the development of genetic differences among populations (Sultan, 1992) and be responsible for a stabilized growth pattern and morphological phenotype along environmental gradients. Previous studies have suggested that limber pine has an especially wide range of physiological plasticity within and among individuals and sites (Mooney, Wright, and Strain, 1964; Mooney, Brayton, and West, 1968; Lepper, 1974, 1980; Barrick and Schoettle, 1996; Schoettle and Rochelle, in press). Without long-term transplant studies to specifically address the genetic-by-environment interaction, we cannot determine conclusively the relative role of physiological plasticity vs. genetic differentiation. The variation in the physiology of natural populations of limber pine trees across the elevation gradient will be addressed in a companion paper (Schoettle, unpublished data), and the establishment of a reciprocal transplant study along the elevation gradient is in progress.

In summary, the fundamental and realized niche for limber pine is broad with respect to air temperature. Not only can the species persist on sites experiencing a wide range of air temperatures, limber pine growth and resultant morphology were not related to the elevation or seasonal air temperature at the sites. These data suggest that limber pine has a high degree of physiological plasticity.

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