

THE SIGNIFICANCE OF POPULATION SUCCESSIONAL STATUS TO THE
EVOLUTION OF SEEDLING MORPHOLOGY IN *PINUS CONTORTA* VAR.
LATIFOLIA (PINACEAE)

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ABSTRACT

The objective of this research was to test the hypothesis that the successional role of a plant population, because of its implications for the nature of the selective regime experienced by regeneration cohorts, determines, in part, the course of autecological evolution in a lineage of populations. A provenance study, which involved the raising of seedlings of lodgepole pine (*Pinus contorta* Loudon var. *latifolia*) from seed under uniform conditions in a greenhouse, provided a test of this hypothesis. The seeds came from seral, climax, and persistent lodgepole pine populations indigenous to the Blue Mountains region of northeastern Oregon and southeastern Washington. Data about shoot and root system features, collected at the end of the first season of growth, proved useful in evaluating competitive competence, the relative ability of a plant, or group thereof, to compete successfully for essential resources such as light, water, and mineral nutrients. Analyses of variance and discriminant function analysis facilitated the search for correlations between population successional status and seedling morphology. The total leaf area, photosynthetic potential, degree of subdivision of the root system, and total root length of a typical seedling derived from a seral population are smaller than such quantities for the other population types. In climax populations, seedlings tend to exhibit the largest total leaf areas and total photosynthetic potentials among lodgepole pine seedlings. They are equipped with more elaborate and larger root systems. Despite their exceptional heights, seedlings belonging to persistent populations not only have slightly lower total photosynthetic potentials than those from climax populations, they also possess reduced lateral root densities and total root lengths. Greater competitive competences, with reference to life in the subcanopy, characterize seedlings from climax lodgepole pine populations compared to seedlings from seral or persistent populations. The results of this study support the hypothesis that successional status influences the evolution of autecological attributes in a population lineage.

Forest succession is the undisputed exemplar of vegetation change through time. The formation of a canopy as the crowns of adjacent trees expand in size represents the most consequential structural change occurring during forest succession. In coniferous forests, canopy closure may not occur for over a century after stand establishment (Peet 1981). The appearance of a canopy results in the elimination of an open site and the creation of a subcanopy. Gradual alterations in stand structure and abiotic environmental conditions occur as an open site gives way to a canopied stand.

An open site, though it is an area characterized by physical extremes, is a place where a plant, due to the absence or paucity of other plants with similar requirements, participates in little, if any, competition for essential resources such as light, water, and mineral nutrients. In contrast, the canopy insulates tree seedlings and other inhabitants of the subcanopy from the severe abiotic environmental conditions that prevail on an open site. Nevertheless, because resources are highly accessible to, and vigorously exploited by, the fully developed trees composing the canopy, at least one resource ordinarily limits the survival of subcanopy plants. Con-

sequently, a plant almost invariably must participate in intense intra- and interspecific competition when a resident of the subcanopy. Any new autecological trait appearing through mutation or gene flow that improves the "competitive competence" of a subcanopy plant will increase its fitness, i.e., the likelihood that it will become a part of the canopy and contribute to the genetic constitutions of future generations.

Competitive competence is a relative expression of the ability of a plant, or group thereof, given the features that characterize it (including many aspects of genetics, physiology, anatomy, morphology, and breeding behavior), to compete successfully for those resources that limit maintenance and growth activities. It is an heuristic tool that provides a means of comparing plants according to their abilities to survive, grow, and reproduce under a competitive regime. Competitive competence recalls the general version of the concept of tolerance embraced by most silviculturists during the first half of the twentieth century (e.g., Bühler 1918; Baker 1937, 1950; Toumey and Korstian 1937). Competitive competence permits the comparison of plants growing in naturally complex settings, not under simplified garden, greenhouse, or laboratory conditions; it avoids the artificiality of the tendency to

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rank individuals, populations, or species by single-factor tolerances.

To ensure the continued existence of its population lineage (a temporal sequence of conspecific populations related as ancestors and descendants), the members of a population must beget juveniles that are able to compete successfully for resources within the subcanopy, or they must produce propagules that disperse and give rise to individuals capable of surviving, growing, and reproducing in a different location (seed dormancy and cone serotiny may permit the continuity of a population lineage in the absence of emigration). The autecology of a population represents the product of evolutionary history, acting as a phyletic constraint that limits the types of successional role that a population can assume in a given environment. In view of its consequences for regeneration dynamics, successional status certainly contributes significantly to the selective milieu experienced by the members of a population. Consequently, succession potentially influences the course of autecological evolution within a population lineage. Populations of lodgepole pine indigenous to the Blue Mountains region of the Pacific Northwest, which occupy an immense habitat island, represent consummate candidates for studying the relationship between successional status and the evolution of competitive competence.

The successional roles of Blue Mountain lodgepole pine populations. The range of *Pinus contorta* var. *latifolia* (hereafter referred to by its vernacular name "lodgepole pine") encompasses the Rocky Mountains, the Washington Cascades, the area between the Rockies and Coast Range in Canada, and the Blue Mountains. Due to its rapid early growth rate and its tolerance of exposed conditions and poorly developed substrates, lodgepole pine establishes a foothold on many open sites throughout its range (Pfister and Daubenmire 1973; Volland 1985). Hence, lodgepole pine often is a colonizer. In most cases, because of a dearth of nearby seed sources, it becomes only a minor constituent of the stands on these sites. Lodgepole pine adopts a seral role in such situations: It does not regenerate successfully beneath the canopy; species having greater shade tolerances, viz., grand fir (*Abies grandis* (Douglas) Lindley) or subalpine fir (*A. lasiocarpa* (Hook.) Nutt.), replace it in 50–200 years. On some sites, lodgepole pine populations achieve dominance and assume unique successional positions. Pfister and Daubenmire (1973) identified three general successional roles for populations of lodgepole pine in stands that it dominates: (dominant) seral, climax, and persistent. These three population types do not represent different temporal components of a common sere. Rather, each is a particular element of a unique sere. F. C. Hall (USDA Forest Service, unpublished) classified lodgepole pine populations according to successional role in communities that they dominate in the Blue Mountains. Franklin and

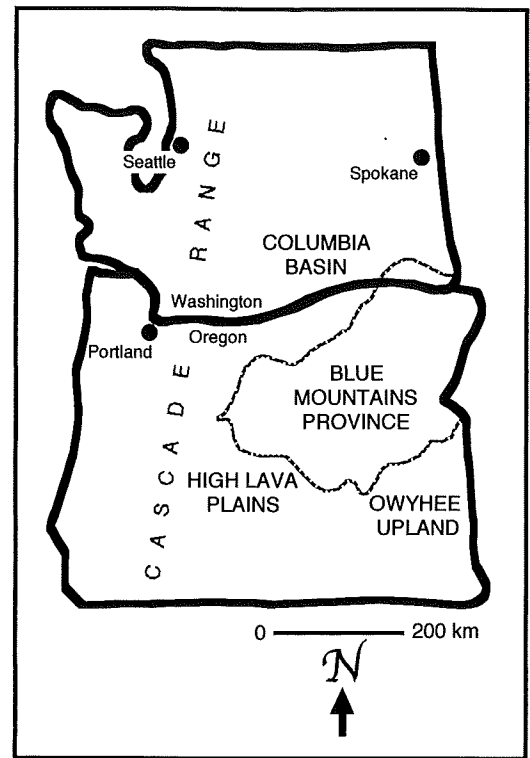


FIG. 1. The Blue Mountains Province, located in north-eastern Oregon and southeastern Washington. Modified from Franklin and Dyrness (1988:6).

Dyrness (1988) defined the Blue Mountains Province as the 2.5 million hectare region of mountain ranges and intervening valleys that extends from central Oregon, east of the Cascades, to southeastern Washington (Fig. 1).

Seral populations. Given the availability of a nearby seed source, a lodgepole pine population assumes a seral role in an essentially unidirectional successional sequence upon colonizing an open site characterized by more-or-less moderate abiotic environmental conditions. Lodgepole pine becomes the dominant canopy element because of its rapid early growth rate. In the subcanopy, lodgepole pine seedlings, which represent the offspring of canopy dominants, participate in a futile fight for essential resources with individuals of species that exhibit superior competitive competences (grand fir or subalpine fir). In the absence of stand disturbance, the lodgepole pine population is unable to replace itself in situ. Its adversaries attain dominance in 100–200 years. Perpetuation of the population lineage to which the lodgepole pines belong depends upon local disturbance or the abilities of the seeds of mature individuals to reach, and give rise to viable seedlings on, other (open) sites. As they produce highly vagile propagules and seedlings capable of tolerating the harsh abiotic environmental condi-

tions of open sites, these seral lodgepole pines are exceedingly fit despite their inferior competitive competences.

Climax populations. Because of the exceptional frost resistances and shallow root systems of its seedlings, lodgepole pine is capable of becoming established in a topographic depression where cold air accumulates and the water table often approaches the soil surface. A lodgepole pine population assumes a climax role in a unidirectional, but truncated, sere in such a harsh location. Individuals of other tree species appear on such bitterly cold, and in some cases, periodically inundated, sites only on occasion and in insignificant numbers (though, *Picea engelmannii*, Engelm. is quite abundant on some sites). Even if potentially competing seedlings of other species are present, the superior initial growth rate of lodgepole pine ensures its rapid domination of the canopy. In the subcanopy, the offspring of canopy lodgepole pines generally remain free of competition for essential resources from species having greater competitive competences (grand fir and subalpine fir). Although intraspecific competition is fierce, lodgepole pine regeneration is possible and, in fact, common. Personal observations indicate that climax populations usually contain a mixture of size classes. Seedlings and saplings crowd many light gaps. Stuart et al. (1989) demonstrated that water/mineral nutrient gaps are necessary for seedling establishment in climax populations of *Pinus contorta* Loudon var. *murrayana* (Grev & Balf.) Cricht. in south-central Oregon. Recruitment and the ascendancy of suppressed lodgepole pines into the canopy in the Blue Mountains may require gap formation. Unlike a seral population lineage, a climax population lineage can persist through regeneration in situ, provided that it takes place with sufficient frequency (at intervals no greater than the longevity of lodgepole pine, about 250 years, according to Franklin and Dyrness [1988]), and in adequate quantities. In view of the intense intraspecific competition below a climax lodgepole pine canopy, selection will confer elevated fitnesses on individuals that produce seedlings with greater competitive competences.

Persistent populations. Ten to twenty years after a crown fire destroys a portion of a mature grand fir stand, lodgepole pine seeds originating elsewhere effect colonization of the resulting open site. The lodgepole pine population takes on a persistent role in a cyclic sere on such a site. Due to intense competition with grasses and shrubs (and sometimes grand fir seedlings), the growing lodgepole pines are widely spaced on the site. Nevertheless, because of their rapid early growth rates, they soon form and dominate a canopy. Before long, the subcanopy becomes filled with lodgepole pine seedlings (the progeny of canopy dominants) as well as seedlings having greater competitive competences, i.e., the offspring of grand fir trees that surround

the site. In 60–80 years, the dominant lodgepole pine trees reach maturity (dbh > 14.5 cm) and become susceptible to attack by mountain pine beetles (*Dendroctonus ponderosae*). The deaths of these trees produce a high fuel load within the stand, which inevitably leads to a hot fire 5–10 years later. The fire consumes all live and dead woody material on the site, including canopy members and potential regeneration in the subcanopy. In 10–20 years, the disturbed site becomes suitable for the establishment of lodgepole pine seedlings. Following dispersal from some external seed source, the sequence begins anew. Succession proceeds until a beetle kill and fire again destroy the stand. As a persistent population cannot replace itself in situ, the appearance of lodgepole pine after each fire depends upon seed dispersal from another site. The temporal continuity of a persistent population lineage depends upon the success with which the seedlings of its constituent populations can colonize open sites. Hall's view of the successional role of a persistent Blue Mountain lodgepole pine population is controversial. The details of his proposed successional scenario will likely change once stand development studies are complete. I assume, provisionally, that seed vagility and seedling tolerance of harsh abiotic environmental conditions, not seedling competitive competence, contribute most significantly to the fitness of a persistent lodgepole pine tree.

MATERIALS AND METHODS

Cone collection. A lodgepole pine population represented a dominant canopy element in 61 stands inspected by F. C. Hall (USFS unpublished data) as part of a plant association analysis of the Blue Mountains region. Twenty of these populations proved appropriate for inclusion in this study: In August 1994, each had at least one dominant, codominant, or intermediate lodgepole pine tree that was cone-bearing, accessible, and apparently free of insect damage (Table 1). Using the tripartite scheme introduced above, Hall identified six of these populations as seral (species with superior competitive competences present with height growth rates that exceed those of lodgepole pine trees), seven as climax (topographic depressions; species with superior competitive competences absent), and seven as persistent (species with superior competitive competences present, but lodgepole pine trees exhibit greater height growth rates). Within each successional type, the populations are widely distributed throughout the Blue Mountains with respect to latitude, longitude, and elevation. To reduce the chances that gene flow, not common site-specific selective pressures, might produce a correlation between successional status and competitive competence, I admitted no contiguous populations possessing identical successional roles into this study.

TABLE 1. BLUE MOUNTAIN LODGEPOLE PINE POPULATIONS SAMPLED. The number of participating families indicates those submitted to analyses of variance and discriminant function analysis.

Population	Participating families	Latitude (N)	Longitude (W)	Elevation (m)
Seral populations				
Mount Pisgah	2	44°28'	120°14'	2,100
Little Kelsay Creek	1	44°54'	118°45'	1,900
North Fork Wolf Creek	2	45°08'	118°08'	1,900
Bingham Spring	1	44°30'	120°30'	1,900
Thompson Spring	2	44°28'	120°15'	2,200
Little Phillips Creek	3	45°42'	118°03'	1,700
Climax populations				
Bingham Prairie	2	44°31'	120°32'	1,900
Jackson Creek	2	44°27'	119°58'	1,800
Crowsfoot Creek Edge	1	43°54'	119°30'	1,800
Summit Prairie Edge	2	44°11'	118°30'	1,800
Wickiup Creek	2	44°11'	119°14'	1,800
Ditch Creek Edge	1	45°07'	119°21'	1,600
Myrtle Creek	2	43°59'	119°05'	1,900
Persistent populations				
Stove Spring	2	44°31'	120°33'	1,800
Summit Prairie Slope	3	44°11'	118°30'	1,900
Camp Creek	2	44°03'	119°07'	1,800
Tribble Creek	1	45°10'	119°02'	1,800
Indian Springs Butte	1	44°15'	118°42'	2,100
Dixie Butte	1	44°33'	118°37'	2,000
Winom Creek	1	45°01'	118°38'	1,700

Several assistants and I collected cones from one or more lodgepole pine trees belonging to each population during August 1994. Since minimum distances of 40–50 m separated the sampled trees, each most likely resides within a distinct genetic neighborhood. We recovered a minimum of 50 cones from each tree. We picked the cones off branches removed from each crown by gunshot or through the use of loppers. To maximize the proportion within each family of progeny derived from crosses between members of the same genetic neighborhood, we generally collected cone-bearing branches from the sides of crowns (the infiltration of pollen grains from afar to branches below the tops of crowns probably is limited, especially for trees belonging to seral and climax lodgepole pine populations where crowns frequently are contiguous or overlapping). We used positional criteria so as to collect only those cones that matured in response to pollination events occurring in the spring of 1992. Although most lodgepole pine trees in the Blue Mountains possess nonserotinous cones (Lottan and Critchfield 1990), we were careful to avoid older closed (serotinous) cones. At the time of collection, most cones were light brown in color, which is indicative of ripeness (Krugman and Jenkinson 1974). Many were beginning to open. We stored the cones in paper bags, loosely packed in cardboard boxes, in the open bed of a truck for the duration of the fieldwork (up to four weeks prior to seed extraction).

Seed extraction. Cone processing took place in September 1994 at the Wind River Nursery Seed Extractory operated by the USFS near Carson, Washington. After transferring the cones from the paper bags to loose-weave nylon sacks, we immersed them in hot water (about 60°C) for 4–5 minutes. We dried the cones in a kiln dryer at 35°C for 24 hours. This treatment effectively opened nearly all of the cones. We shook the seeds out of the open cones by use of a manually-driven tumbler. A Clipper cleaner permitted us to partially de-wing the seeds and remove debris from each seed lot. We used an x-ray machine and Polaroid film to generate images of the contents of 19–200 seeds per cleaned sample.

Seedling production. After soaking 39 seed lots (each representing a single family) in water for 72 hours, I stratified them without media in polyethylene bags at 2°C for 33 days (Bonner et al. 1974; Krugman and Jenkinson 1974; Owens and Molder 1984; J. McGrath, USDA Forest Service, personal communication). We sowed the seeds immediately after completion of the stratification process in containers in a fiberglass, unheated greenhouse at the University of California, Berkeley. We sowed 2–5 seeds in a 1:1 mixture of sphagnum peat moss and vermiculite in each of 50 Ray Leach Pine Cell Cone-tainers per family. The sowing rate, calculated by reference to the x-ray image of a subsample of seeds produced at the time of seed extraction,

varied in direct proportion to the percentage of filled seeds. We subsequently placed each container in a randomly chosen slot in a cluster of rectangular trays in the center of the greenhouse. We raised over 1,000 lodgepole pine seedlings through a single three-stage season (151 days) under uniform conditions in the greenhouse. To encourage seed germination (1–24 days after sowing), we maintained high air temperatures and relative humidities, suspended a 50% shade cloth near the greenhouse roof to reduce photon flux densities, and kept the growing medium in each container constantly wet. As necessary, we thinned each container to a single seedling. During the free growth phase (25–115 days after sowing), we operated an evaporative cooling system for 12 hours per day, illuminated the seedlings with fluorescent lights for 18 hours per day, and injected a Plantex 20:20:20 macro- and micronutrient solution (100 ppm of nitrogen) into the irrigation system during every other watering (about once each week). We created drought stress conditions and terminated the use of daylength extension lights at the beginning of the budset stage (116–151 days after sowing). Throughout this final period of seedling growth, we used an exhaust fan for 24 hours per day to encourage lower temperatures and relative humidities, and we halved the nitrogen content of each fertilizer application (50 ppm of nitrogen).

Collection of data on seedling morphology. Theoretical predictions and empirical evidence suggest that, regardless of sibling relatedness and heritability, an acceptable approximation of a family mean for a given quantitative morphological feature is obtainable by sampling 10–20 progeny (Brady unpublished). Consequently, within three weeks of termination of the growth period (i.e., the end of the bud-set stage), we harvested ten randomly-chosen seedlings per family on which terminal resting buds had developed and acquired information for 12 distinct morphological attributes. A description of each trait appears in Table 2.

Statistical procedures. Following the recommendations of Gould and Johnston (1972) for identifying patterns of geographical variation within and among species, I adopted different approaches, viz., analyses of variance and discriminant function analysis, in my attempt to discover a correlation between lodgepole pine seedling morphology and population successional status. The analysis of variance (ANOVA) furnishes a way to evaluate the observed differences among three or more (statistical) population means (Winer 1971; Tabachnick and Fidell 1983; Lindman 1992; Bogartz 1994). In the context of the present investigation, successional status functions as the sole independent variable with three levels, or groups (seral, climax, and persistent). The morphological features act as dependent variables. Discriminant function analysis includes an array of multivariate techniques that

TABLE 2. DESCRIPTIONS OF 12 ATTRIBUTES PERTAINING TO SHOOT AND ROOT SYSTEM MORPHOLOGY ASSESSED FOR LODGEPOLE PINE SEEDLINGS ON WHICH TERMINAL RESTING BUDS HAD DEVELOPED WITHIN 151 DAYS OF GROWTH IN A GREENHOUSE.

<i>SHL</i> (shoot length)	The distance between the cotyledonary node and the base of the terminal resting bud on the main stem as measured with a ruler to the nearest millimeter.
<i>STC</i> (stem caliper)	The maximum diameter of the main stem at its midlength (<i>SHL/2</i>), as measured with a vernier caliper to the nearest 0.025 mm.
<i>NPL</i> (number of needle-like primary leaves)	The number of needle-like primary leaves attached to the main stem, disregarding cotyledons.
<i>NSS</i> (number of axillary short-shoots)	The number of axillary short-shoots attached to the main stem.
<i>NLS</i> (number of axillary long-shoots)	The number of axillary long-shoots attached to the main stem.
<i>BLL</i> (blade length)	Pertaining to the intact and fully developed primary leaf closest to the midlength of the main stem (<i>SHL/2</i>), the distance between the base and tip of the leaf blade along its midrib, as measured with a ruler to the nearest millimeter.
<i>TPC</i> (taproot caliper)	The maximum diameter of the taproot at its midlength (actually, half the distance between the cotyledonary node and the tip of the taproot), as measured with a vernier caliper to the nearest 0.025 mm.
<i>NLR</i> (number of lateral roots)	The number of lateral (secondary) roots attached to the proximal half of the taproot (the region between the cotyledonary node and the midlength of the taproot).
<i>LRL</i> (lateral root length)	The length of the lateral root attached closest to the midlength of the taproot, as measured with a ruler to the nearest millimeter.
<i>NTR</i> (number of tertiary roots)	The number of tertiary (absorbing) roots connected to the lateral root that is attached closest to the midlength of the taproot (we considered a tertiary root and all of its branches, if present, as a single unit).
<i>SHB</i> (shoot biomass)	The weight of the air-dried shoot system (epicotyl), as obtained with an electronic balance to the nearest 0.01 g.
<i>ROB</i> (root biomass)	The weight of the air-dried root system (hypocotyl), as obtained with an electronic balance to the nearest 0.01 g.

make use of a set of independent variables to discover the dimensions along which the differences among groups are greatest, to test the statistical significance of those differences, to predict group

TABLE 3. THE MEAN AND STANDARD DEVIATION OF THE FAMILY MEAN OF EACH OF 12 MORPHOLOGICAL FEATURES OF LODGEPOLE PINE SEEDLINGS BY SUCCESSIONAL CLASS FOR 34 FAMILIES. Units of measurement appear in parentheses. All numbers were rounded to two digits to the right of the decimal point for display purposes.

	<i>SHL</i> (mm)	<i>STC</i> (mm)	<i>NPL</i>	<i>NSS</i>	<i>NLS</i>	<i>BLL</i> (mm)	<i>TPC</i> (mm)	<i>NLR</i>	<i>LRL</i> (mm)	<i>NTR</i>	<i>SHB</i> (g)	<i>ROB</i> (g)
seral (total number of families = 11)												
mean =	58.36	1.87	106.86	4.66	2.02	35.56	0.66	27.20	92.38	26.49	35.56	28.05
sd =	8.17	0.11	10.41	4.10	0.64	2.70	0.11	2.62	5.33	3.79	7.40	4.69
climax (total number of families = 12)												
mean =	61.00	1.95	117.54	1.48	2.26	36.68	0.65	29.66	98.23	29.14	37.13	33.33
sd =	8.00	0.09	16.35	1.91	0.23	1.32	0.12	2.44	7.74	4.01	3.82	2.47
persistent (total number of families = 11)												
mean =	72.26	1.87	115.23	2.60	2.26	37.14	0.69	26.68	95.42	27.69	38.75	32.01
sd =	7.58	0.12	11.86	3.25	0.23	1.87	0.07	3.08	6.90	3.77	3.12	3.87

membership, and to interpret the (biological) meaning of each dimension (Kendall and Stuart 1966; Lachenbruch 1975; Gnanadesikan 1977; Karson 1982; Tabachnick and Fidell 1983; Reymont et al. 1984; Morrison 1990). In this study, successional status is the dependent variable with three groups (seral, climax, and persistent). Morphological attributes act as independent variables. I performed all quantitative analyses for this study on a MacIntosh Quadra 950 using JMP 3.1 application software or programs written by myself and executed with the Microsoft QuickBASIC 1.00B Interpreter.

RESULTS AND DISCUSSION

I calculated the means and standard deviations of family means by successional class (seral, climax, and persistent) on each of 12 morphological traits for a total of 390 lodgepole pine seedlings (39 families). Examination of these statistics as well as histograms depicting the frequency distributions of families for these features (not shown) indicated that five families (one seral, two climax, and two persistent) represent outliers. I made no further use of the data for these five families. Table 3 gives summary statistics on each of the 12 morphological features by successional class for the remaining 34 families. The mean of family means on three of the attributes each exhibits very little variation among successional classes: *NLS* (number of axillary long-shoots), *TPC* (taproot caliper), and *SHB* (shoot biomass). Consequently, I withdrew them from further statistical consideration.

Analyses of variance. The validity of the results of a series of ANOVAs depends upon the assumption that the scores on a particular dependent variable within each group are approximately normally distributed, and upon the assumption that each group possesses a common variance on a given dependent variable. I evaluated the normality assumption separately for the nine morphological traits within each of the three successional classes in two ways: I examined a histogram showing the distri-

bution of family means, which facilitated the visual detection of skewness, and I tested the null hypothesis that this distribution is normal using the Shapiro-Wilk *W*-statistic. An assumption of normality was supported for eight of the attributes in every class ($\alpha = 0.05$). The distribution of one seedling feature, *NSS* (number of axillary short-shoots), exhibited severe positive skewness in the climax and persistent groups. Therefore, I did not probe *NSS* further using ANOVA. I performed four different statistical tests (O'Brien's, Brown-Forsythe, Levene *F*, and Bartlett's tests) to check the homogeneity of variance among the three successional classes for each of eight morphological characteristics. None of the tests detected statistically significant ($\alpha = 0.05$) differences in variance among groups for any of these traits.

Eight ANOVAs revealed that the differences among group means are statistically significant ($\alpha = 0.05$) for three morphological attributes: *SHL* (shoot length), *NLR* (number of lateral roots), and *ROB* (root biomass). In each case, t-tests identified the particular group differences responsible. The results of the significant tests appear in Table 4.

Year-old seedling shoots are, on average, longer in families derived from persistent populations (mean *SHL* = 72.26 mm) than in families belonging to either seral or climax populations (58.36 mm and 61.00 mm, respectively). However, no real difference in seedling shoot length exists between seral and climax groups. The t-tests detected significant differences in the number of lateral roots between seral and climax and between climax and persistent groups. In fact, the largest mean number of lateral roots per seedling (mean *NLR* = 29.66) characterize climax families. However, no evidence exists of a genuine difference in the number of lateral roots between seral and persistent families (27.20 and 26.68, respectively). The biomasses of seedling root systems are significantly smaller in seral families (mean *ROB* = 28.05 g), but the climax and persistent groups are not statistically dis-

TABLE 4. RESULTS OF SIGNIFICANT ($\alpha = 0.05$) ONE-WAY ANALYSES OF VARIANCE AND T-TESTS OF THE DIFFERENCES AMONG SUCCESSIONAL CLASSES IN MEAN VALUES ON EIGHT LODGEPOLE PINE SEEDLING TRAITS. df = degrees of freedom, SS = sum of squares, MS = mean square. I rounded all numbers to two digits to the right of the decimal point for display purposes.

<i>SHL</i> (shoot length)					
Source	df	SS	MS	<i>F</i>	<i>P</i>
successional status	2	1208.22	604.11	9.62	0.00
error	31	1946.33	62.79		
'seral:persistent = 4.14	df = 20				<i>P</i> = 0.00
'climax:persistent = -3.46	df = 21				<i>P</i> = 0.00
<i>NLR</i> (number of lateral roots)					
Source	df	SS	MS	<i>F</i>	<i>P</i>
successional status	2	58.82	29.41	3.98	0.03
error	31	228.83	7.38		
'seral:climax = 2.33	df = 21				<i>P</i> < 0.03
'climax:persistent = 2.58	df = 21				<i>P</i> < 0.02
<i>ROB</i> (root biomass)					
Source	df	SS	MS	<i>F</i>	<i>P</i>
successional status	2	171.28	85.64	6.08	0.01
error	31	436.90	14.09		
'seral:climax = 3.43	df = 21				<i>P</i> = 0.00
'seral:persistent = 2.16	df = 20				<i>P</i> < 0.04

tinguishable on the basis of this trait (33.33 g and 32.01 g, respectively).

A series of ANOVAs yields the maximum amount of information about the importance of each attribute to the determination of group affiliation only if none of those traits covary. A matrix of Pearson product-moment correlation coefficients (Table 5) indicates that, in fact, every pair of morphological attributes is, to some degree, correlated. Thus, the claim that differences among successional classes on the mean values of *SHL*, *NLR*, and *ROB* are statistically significant incorrectly implies that successional status affects three independent phenomena. A closer examination of the relationship between seedling morphology and successional status demands a multivariate perspective.

Discriminant function analysis. Justification of a multivariate normality assumption (within each group, the sampling distribution of the mean on each independent variable and all linear combina-

tions of them exhibit normality) is a prerequisite for the use of discriminant function analysis. With small, unequal sample sizes (as in this study), validation of the multivariate normality assumption is largely a matter of judgment. By discarding the attribute *NSS* (number of axillary short-shoots), shown previously to possess a highly skewed distribution within each successional class, the validity of the assumption of multivariate normality is likely.

A discriminant function analysis of 34 lodgepole pine family means on each of eight morphological characteristics, which accounts for about 68.2% of the total variation in seedling morphology, created two discriminant functions (Table 6). The first function effectively ordines all three successional classes by partitioning approximately 66.5% of the variation among successional classes to achieve group separation (Fig. 2). The second discriminant function appropriates about 33.5% of the variation

TABLE 5. CORRELATION MATRIX OBTAINED BY COMPUTING PAIRWISE PEARSON PRODUCT-MOMENT CORRELATION COEFFICIENTS ACROSS ALL THREE SUCCESSIONAL CLASSES FOR EIGHT MORPHOLOGICAL FEATURES.

	<i>SHL</i>	<i>STC</i>	<i>NPL</i>	<i>BLL</i>	<i>NLR</i>	<i>LRL</i>	<i>NTR</i>	<i>ROB</i>
<i>SHL</i>	1.0000							
<i>STC</i>	-0.0049	1.0000						
<i>NPL</i>	0.3757	0.1093	1.0000					
<i>BLL</i>	0.2631	0.0554	0.2300	1.0000				
<i>NLR</i>	-0.3149	0.4287	0.0759	-0.0122	1.0000			
<i>LRL</i>	0.3808	0.2128	0.2941	0.4289	0.0791	1.0000		
<i>NTR</i>	0.1109	-0.0596	0.1189	0.4347	0.3571	0.6601	1.0000	
<i>ROB</i>	0.3650	0.2161	0.3255	0.4426	0.2874	0.4326	0.4246	1.0000

TABLE 6. DISCRIMINANT FUNCTION ANALYSIS OF A DATA SET CONSISTING OF 34 LODGEPOLE PINE FAMILY MEANS ON EIGHT FEATURES PERTAINING TO SEEDLING MORPHOLOGY.

Discriminant function	standardized discriminant function coefficients							
	SHL	STC	NPL	BLL	NLR	LRL	NTR	ROB
1	-1.0138	0.1790	0.2367	-0.2789	0.0476	0.5094	-0.0759	0.2698
2	0.3117	0.1089	0.2082	0.1081	0.2483	0.0600	-0.0327	0.5586

Predicted group membership	Actual group membership		
	Seral	Climax	Persistent
Seral	8	1	0
Climax	1	11	2
Persistent	2	0	9

Discriminant function	Loading matrix							
	SHL	STC	NPL	BLL	NLR	LRL	NTR	ROB
1	-0.7301	0.3860	0.0434	-0.1769	0.5557	0.1818	0.1757	0.0939
2	0.5628	0.3780	0.5765	0.4998	0.3649	0.5492	0.4326	0.8950

among successional classes to distinguish seral from the other groups (Fig. 2).

A jackknife technique failed to expose any unusually large Mahalanobis' distances (the distances in multivariate space from family means to their group centroids); and plots of standardized family scores for the seral, climax, and persistent groups revealed roughly equal dispersions. These findings verify the absence of multivariate outliers and sup-

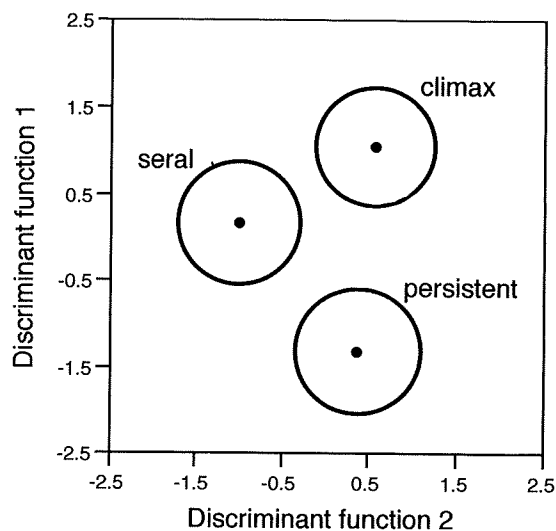


FIG. 2. The location of each of three lodgepole pine successional classes in multivariate space as defined by a discriminant function analysis of eight attributes pertaining to seedling morphology. Each axis consists of standardized scores on the indicated discriminant function. A dot marks each group centroid (mean standardized discriminant function score). The area enclosed by a circle corresponds to the 95% confidence region around a given centroid.

port the assumption of homogeneous variance-covariance matrices, which validate the use of discriminant function analysis in this study. Two results confirm the statistical significance of this multivariate inquiry: Firstly, an approximate F -ratio justified rejection of the null hypothesis that the centroids associated with the three successional classes are equal. Secondly, in a comparison of actual group memberships and those based on posterior probabilities obtained from Mahalanobis' distances, 82% of the 34 family predictions proved correct (Table 6). The large value (0.73) of the associated Kappa statistic, which measures the agreement between predicted and actual group affinity, connotes that the results of the present discriminant function analysis are, indeed, very reliable.

I referred to the loading matrix (Table 6) to explain the differences among seral, climax, and persistent population types on each of the two discriminant functions. Following statistical convention, I deemed only those loadings of at least 0.50, which implies an overlap in variance of about 25% between an independent variable and a discriminant function, as eligible for interpretation.

A seedling's growth polarity. The first, and most information-laden, discriminant function, or dimension of variation in seedling morphology, reflects a change in the pattern of asset allocation, not the overall amount of growth. In morphometric terms, most of the variation among successional classes, as explained by the first dimension, is attributable to the alteration of seedling "shape", not "size". This finding differs markedly from the results of most multivariate morphometric studies, which hopelessly confound the genetic determination of form and phenotypic plasticity, and where the first axis of variation corresponds to a generalized size dimension (Reyment et al. 1984). All of the inde-

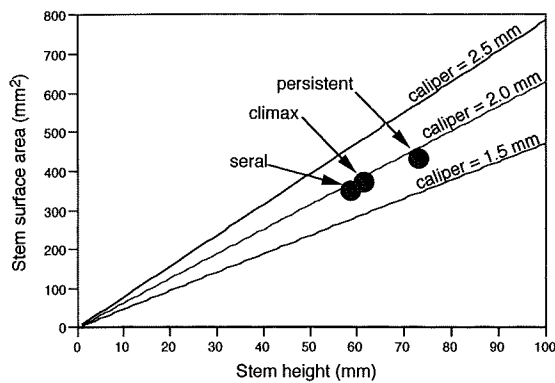


FIG. 3. Surface area of a cylindrical stem as a function of stem caliper and height. The three points indicate the average stem surface areas of lodgepole pine seedlings derived from seral, climax, and persistent populations.

pendent variables that contribute substantially to a size dimension must exhibit discriminant function coefficients, correlations among themselves, and loadings of like sign (Jolicoeur and Mosimann 1960; Reyment et al. 1984). In the present case, the two morphological attributes having the largest absolute loadings on the first discriminant function (*SHL* and *NLR*) possess discriminant function coefficients, correlations, and loadings of opposite sign. The first dimension of variation clearly portrays an anisotropic pattern of change in seedling growth among seral, climax, and persistent lodgepole pine populations.

The trait *SHL* (shoot length) represents a measure of the total amount of seedling height growth during the first season of development, or a height growth rate. Internode elongation, the primary component of height growth, may lead to the production of new leaves in regions of higher photon flux densities, it may move existing leaves into sunlight, and it tends to reduce self-shading by increasing the distances among appendages attached to the stem (e.g., Horn 1971; Hallé et al. 1978; Fisher 1986; Givnish 1986, 1988, 1995; Sakai 1986; Kohyama 1987; Küppers 1989). Since their epicotylar stems remained green during the first season of development, height growth via internode elongation may further contribute to the carbon economies of lodgepole pine seedlings by promoting stem photosynthesis (see Nilsen 1995). The total green stem surface area provides a means of comparing the stem photosynthetic potentials of different groups of seedlings. As the epicotylar stems observed in this study lacked taper, I calculated the surface area of a stem by assuming that it is cylindrical in shape. The surface area of a stem increases with both height and caliper (Fig. 3). Because long-shoots were relatively small and nearly constant in number across all lodgepole pine seedlings (*NLS* in Table 3), the exclusive application of a simple cylindrical model to the main stem furnishes an adequate com-

parative measure of the total stem photosynthetic potential. The three points in Fig. 3 mark the average main stem surface areas for the three lodgepole pine successional classes (based on mean *STC* and mean *SHL* from Table 3). Due to their exceptional heights (mean *SHL* = 72.26 mm), seedlings from persistent families possess the greatest stem photosynthetic potentials. Seedlings from seral and climax populations have comparable stem photosynthetic potentials (mean *SHL* = 58.36 mm and 61.00 mm for seral and climax groups, respectively).

NLR (number of lateral roots) is the second morphological attribute making a large contribution to the differentiation of successional classes along the initial dimension of variation. As it provides an estimate of the degree of branching, or subdivision of the root system, *NLR* relates the thoroughness with which a seedling can extract water and mineral nutrients from a given volume of soil (Fitter 1985, 1991, 1994; Caldwell and Richards 1986). While only its tip functions in uptake, a lateral root provides a "platform" for numerous absorbing tertiary roots. Because the most efficient zone of absorption occurs near the tip of any root, the total number of root tips in a specified volume of soil acts as a measure of the absorptive capacity of a root system (Kramer and Kozłowski 1960; Caldwell and Richards 1986). Imagine a lodgepole pine seedling root system that is completely embedded in a cylindrical mass of soil. The height and vertical centerline of the cylinder correspond to the length and position of the taproot, and its radius equals the length of a lateral root. All lateral roots are identical in length, and each possesses the same number of attached tertiary roots. The following equation gives the total number of root tips characteristic of the root system per mm³ of soil:

$$T = \frac{P + l_{\text{taproot}}d_{\text{laterals}} + l_{\text{taproot}}d_{\text{laterals}}l_{\text{lateral}}d_{\text{tertiary roots}}}{\pi(l_{\text{lateral}})^2l_{\text{taproot}}} \quad (1)$$

where P is the number of taproot tips (usually, $P = 1$); l_{taproot} is taproot length; d_{laterals} is a density, the number of lateral roots produced per unit length of taproot; l_{lateral} is the length of a lateral root; and $d_{\text{tertiary roots}}$ is the density of tertiary roots along a lateral root. The product $l_{\text{taproot}}d_{\text{laterals}}$ gives the total number of lateral root tips. The product $l_{\text{taproot}}d_{\text{laterals}}l_{\text{lateral}}d_{\text{tertiary roots}}$ yields the total number of tertiary root tips. The denominator is the volume of the reference cylinder of soil. Based on estimates of P (1), l_{taproot} (160 mm) and $d_{\text{tertiary roots}}$ (0.29 per millimeter of lateral root length) from this study (all are essentially constant among the seedlings analyzed), Fig. 4 presents T as a function of lateral root density for three different lateral root lengths. The number of root tips composing a root system per unit volume of soil increases in response to both an augmentation in the number of lateral roots attached to

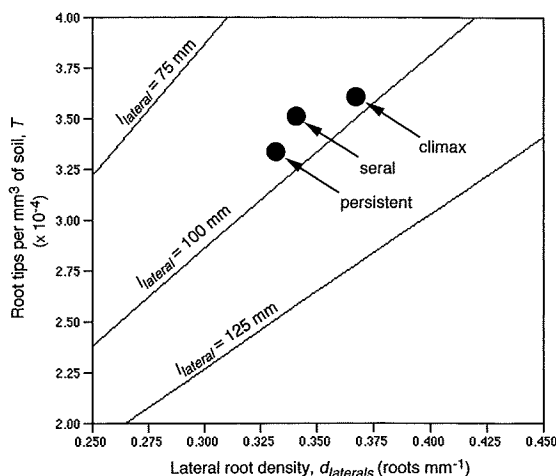


Fig. 4. The number of root tips composing a lodgepole pine seedling root system per mm^3 of soil (T) as a function of lateral root density (d_{lateral}) and lateral root length (l_{lateral}). The three labelled points indicate the average values of T for seedlings belonging to the seral, climax, and persistent groups.

the taproot and a decrease in the lengths of lateral roots (the radius of the cylindrical mass of soil). The three points in Fig. 4 indicate the average values of T for lodgepole pine seedlings belonging to the seral, climax, and persistent groups (d_{lateral} is twice the value of mean NLR from Table 3 divided by a taproot length of 160 mm; l_{lateral} is mean LRL from Table 3). Bearing in mind the simplifying assumptions associated with the calculation of T , the absorptive capacities of seedlings from climax populations only slightly exceed those of seral seedlings, though, given their longer lateral roots, the former may have access to water and mineral nutrients from larger volumes of soil than either seral or persistent seedlings. Seedlings derived from persistent populations possess distinctively lower absorptive capacities, due mainly to the production of fewer lateral roots (mean $NLR = 27.20, 29.66,$ and 26.68 for seral, climax, and persistent families, respectively).

A seedling's resource acquisition potential. Discriminant function analysis identified a second, less explanatory, dimension that highlights the variation in the ability of Blue Mountain lodgepole pine seedlings to obtain essential resources from their surroundings. It utilizes information about overall seedling size and the sizes of individual organs involved in the interception/uptake of light, water, and mineral nutrients to separate the three successional classes in multivariate space. In accord with the interpretation of the second dimension as a size vector, all five morphological attributes with high loadings (≥ 0.50) on the second discriminant function ($SHL, NPL, BLL, LRL,$ and ROB) possess standardized discriminant function coefficients, corre-

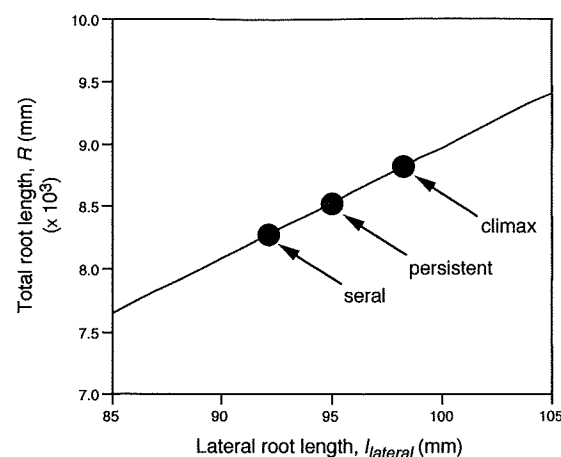


Fig. 5. Total root length (R) as a function of lateral root length (l_{lateral}). The three labelled points mark the average total root lengths for the three lodgepole pine successional classes.

lations among themselves, and loadings of similar sign (Tables 5 and 6).

ROB (root biomass), the morphological characteristic having the greatest loading on the second discriminant function, grades the overall size of the seedling root system. ROB does not convey information about shape, i.e., the pattern of subdivision of the root system. Instead, it incorporates, and inevitably confounds, two aspects of development: total root length (the sum of the lengths of all roots) and average root caliper. Consider a lodgepole pine seedling in which all lateral roots are identical in length, each lateral root possesses the same number of attached tertiary roots, and all tertiary roots are equal in length. Under these conditions, the following equation expresses the total root length in mm:

$$R = l_{\text{taproot}} + n_{\text{lateral}} l_{\text{lateral}} + n_{\text{lateral}} l_{\text{lateral}} d_{\text{tertiary roots}} l_{\text{tertiary root}} \quad (2)$$

where l_{taproot} is taproot length; n_{lateral} is the number of lateral roots attached to the taproot; l_{lateral} is the length of a lateral root; $d_{\text{tertiary roots}}$ is a density, the average number of tertiary roots that arise per unit length of lateral root; and $l_{\text{tertiary root}}$ is the length of a tertiary root. The quantity $n_{\text{lateral}} l_{\text{taproot}}$ is the sum of the lengths of all lateral roots. The product $n_{\text{lateral}} l_{\text{taproot}} d_{\text{tertiary roots}} l_{\text{tertiary root}}$ represents the sum of the lengths of all tertiary roots. The results of this study supplied constant values for l_{taproot} (160 mm), n_{lateral} (55.8, twice the mean of 34 family means on NLR from Table 3), and $d_{\text{tertiary roots}}$ (0.29 mm^{-1}). The approximate median of the range of mature tertiary root lengths of forest trees reported by Sutton and Tinus (1983) provided a reasonable value for $l_{\text{tertiary root}}$ (2.0 mm). Figure 5 shows that the total length of a lodgepole pine seedling root system (R) increases in direct proportion to lateral

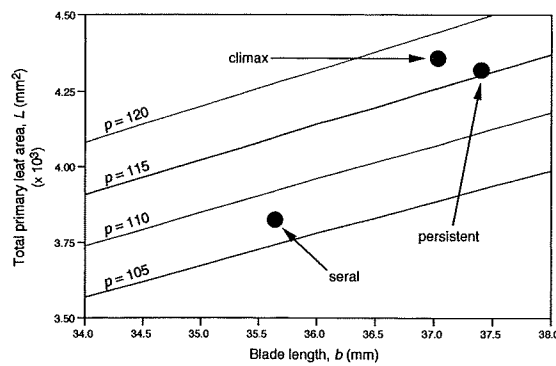


FIG. 6. Graph of total primary leaf area (L) for various values of p (number of primary leaves) and b (blade length). The three labelled points correspond to the total primary leaf areas of average lodgepole pine seedlings belonging to the seral, climax, and persistent groups.

root length ($l_{lateral}$). The three points in Figure 5 denote the values of R for typical seedlings belonging to the seral, climax, and persistent groups (based on mean LRL from Table 3). The typical specific root lengths (calculated from R and mean ROB in Table 3) associated with seral, climax, and persistent seedlings are 296.06, 264.64, and 244.62, respectively. An increase in total root length allows the root system to explore the soil and locate unexploited resources (Fitter 1985, 1991, 1994; Caldwell 1987, 1994). Seral seedlings possess the smallest total root lengths. The total root lengths of seedlings from climax populations surpass those of seedlings from other population types. Hence, superior abilities to find water and mineral nutrients within the soil distinguish climax seedlings.

Three shoot system attributes (SHL , NPL , and BLL) help to isolate the seral group along the second dimension of variation (Table 6). As discussed above, SHL (shoot length) reflects, among other things, the surface area of the green epicotylar stems. Leaf morphology significantly influences the amount of light that a plant can intercept for use in photosynthesis (e.g., Taylor 1975; Givnish 1979, 1988; Givnish and Vermeij 1976). Specifically, NPL (number of needle-like primary leaves) and BLL (blade length) jointly provide information about total primary leaf area, a useful comparative measure of leaf photosynthetic potential among lodgepole pine seedlings. All primary leaves analyzed in this study were dorsiventrally flattened and approximately rectangular in outline. By assuming that the leaves are identical in length and width (1 mm), the following equation gives the total primary leaf area (the sum of the single-sided areas of all primary leaves) in mm^2 of a lodgepole pine seedling:

$$L = pb \quad (3)$$

where p is the number of primary leaves and b is blade length. As shown in Figure 6, L increases

with both blade length and number of leaves. Based on the mean values of NPL and BLL from Table 3, the three points in Figure 6 betoken the total primary leaf areas of average lodgepole pine seedlings belonging to the seral, climax, and persistent groups. Since they produce fewer and shorter primary leaves, seedlings derived from seral populations are distinguished by having substantially smaller total primary leaf areas than seedlings of other successional affinities. The average total primary leaf area of climax seedlings barely exceeds that of persistent seedlings. Despite their long blades, the modest production of primary leaves by persistent seedlings restricts their total primary leaf areas.

The competitive competences of Blue Mountain lodgepole pine seedlings. In a comparative sense, seedlings from seral lodgepole pine populations in the Blue Mountains are unremarkable in exhibiting no conspicuous preference for either shoot or root system growth (Fig. 2; Tables 3 and 6). However, they are notably smaller than seedlings belonging to climax and persistent populations in overall and individual organ size (Fig. 2; Tables 3 and 6). Due to restricted height growth and the production of few and small primary leaves, relatively low photosynthetic potentials characterize seral seedlings (Figs. 3 and 6). Although seedlings derived from seral populations manufacture modest numbers of root tips per unit volume of soil (Fig. 4), root extension growth is anemic. Their small total root lengths (Fig. 5) imply that seral seedlings can explore only limited regions of the soil for water and mineral nutrients. Compared to the juvenile members of climax populations, seedlings taken from seral populations possess morphological traits that would place them at distinct competitive disadvantages wherever light or soil resources are scarce, i.e., within the subcanopy (even in a light or water/mineral nutrient gap). With reference to life in the subcanopy, seedlings from seral lodgepole pine populations exhibit relatively low competitive competences.

Allocation patterns in climax seedlings favor root system elaboration over shoot growth (Fig. 2; Tables 3 and 6). In addition, in terms of both general size and the sizes of organs involved in light interception and water/mineral nutrient uptake, climax populations have the largest seedlings of all successional groups (Fig. 2; Tables 3 and 6). Climax seedlings exhibit unimpressive stem photosynthetic potentials (Fig. 3). However, compared to seedlings from seral and persistent populations, climax seedlings exhibit superior primary leaf photosynthetic potentials, principally as the result of the fabrication of greater numbers of leaves (Fig. 6). Seedlings from climax populations produce relatively large numbers of root tips per unit volume of soil (Fig. 4) as well as long roots (Fig. 5). Climax seedlings have morphological traits, especially those reflect-

ing their abilities to find and absorb extremely scarce soil water and mineral nutrients, that would give them clear advantages over other lodgepole pine seedlings within the subcanopy. Seedlings from climax populations possess greater competitive competences, as regards subcanopy life, than those from seral or persistent populations.

Development in seedlings from persistent lodgepole pine populations is aimed at expansion of the shoot system to the detriment of root growth (Fig. 2; Tables 3 and 6). Persistent seedlings are roughly comparable in size to those belonging to climax populations, but considerably larger than seedlings from seral populations (Fig. 2; Tables 3 and 6). Because of their incredible heights, the stem photosynthetic potentials of persistent seedlings far exceed those of seedlings from other population types (Fig. 3). However, since they produce fewer leaves, the primary leaf photosynthetic potentials of persistent seedlings are slightly lower than those of seedlings from climax populations (Fig. 6). Although moderate root lengths characterize seedlings from persistent lodgepole pine populations (Fig. 5), they bear relatively few root tips per unit volume of soil (Fig. 4). Persistent seedlings have "stunted" root systems that impair their abilities to locate and extract water and mineral nutrients from the soil. Hence, they probably could not survive competition with climax seedlings in a canopied stand, except, perhaps, in a water/mineral nutrient gap. Seedlings derived from persistent lodgepole pine populations display intermediate competitive competences, as concerns life in the forest subcanopy.

Possible sources of unexplained variation in seedling morphology. Error variation accounts for 31.8% of the total variation among 34 Blue Mountain lodgepole pine family means on eight attributes pertaining to seedling morphology considered by discriminant function analysis. Here, error variation is equivalent to the variation among families within successional classes. Discriminant function analysis cannot identify specific sources of error variation. However, several factors, including both experimental inadequacies and evolutionary forces, represent plausible causes. While failings in the experimental procedure undermine the assumption that all observed morphological variation reflects underlying genetic variation, selection, gene flow, and drift may yield error variation with a genetic basis.

A lack of spatial uniformity in the environmental conditions within the greenhouse could account for some proportion of error variation. During development, the seedlings were randomly distributed within the cluster of trays on the greenhouse benches. They were not blocked by family or successional class. Unless it produced skewed distributions of counts or measurements, this factor would benignly promote within-family variability, not variation among family means within a successional

group. No visible spatial pattern of variation in above-ground growth performance had emerged by the time of harvest. Therefore, any unintended systematic variation in photon flux density, watering, fertilizer application, temperature, or relative humidity probably played a relatively minor role in the generation of morphological variation among families.

In forested settings, lodgepole pine seedlings usually form ectomycorrhizae with various basidiomycetes and ascomycetes following the development of tertiary roots (Castellano and Molina 1989). Because we sowed the seeds in artificial growing medium, the seedlings used in this study could become naturally ectomycorrhizal only through wind dispersal of spores from fruiting bodies on infected trees near the greenhouse. As ectomycorrhizae influence the growth of lodgepole pine by enhancing the uptake of water and mineral nutrients (Cline and Reid 1982; Ekwebelam and Reid 1983), the differential infection of seedlings could generate error variation. In fact, careful, but non-microscopic, examinations failed to provide evidence (fungal mantles or trailing hyphae) of a single infected seedling.

Diagnostic mistakes also could produce error variation. Since the order in which we diagnosed the seedlings was random, inaccuracies in counting and measuring would tend to increase within-family variability rather than error variation (unless they rendered skewed data). To minimize systematic diagnostic inconsistencies, the same individual assessed a given morphological attribute for all seedlings.

Selective pressures induced by environmental variables unrelated to successional status (e.g., climate, soil parent material composition, topographic position, and elevation) doubtless are partly responsible for the creation of error variation. Although they probably are not independent of population successional status, such symbiotic relationships as herbivory, parasitism, and mutualism may influence the evolution of seedling morphology in ways not directly affecting the outcome of competition for resources (e.g., Coley 1983). In the most general sense, the observed pattern of genetic variation in lodgepole pine seedling morphology represents a compromise among phyletic constraints, concurrent, but often conflicting, selective pressures imposed by numerous environmental factors, gene flow, and drift.

Conclusions. The purpose of this research was to carry out a test of the hypothesis that the successional role of a plant population, because of its implications for the nature of the selective regime experienced by regeneration cohorts, determines, in part, the course of autecological evolution within a lineage of populations. The results demonstrate that, in accordance with predictions deduced from the hypothesis, a rather strong and statistically sig-

nificant correlation exists between a heritable pattern of variation in competitive competence, as revealed by seedling morphology, and the successional status (seral, climax, or persistent) of a lodgepole pine population in the Blue Mountains region of northeastern Oregon and southeastern Washington.

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