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SEEDLING ARCHITECTURE AND LIFE HISTORY EVOLUTION IN PINES

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Much of the work on life history evolution in plants has dealt with allocation of reproductive effort (Abrahamson 1975; Abrahamson and Gadgil 1973; Gaines et al. 1974; McNaughton 1975; Oka 1976; Stearns 1976, 1977, 1980; Newell and Tramer 1978; Primack 1979). The juvenile period, however, occupies a major and critical portion of the life cycle of many species. Allocation of growth among vegetative organs during the juvenile period may place constraints on later development. The work of Marks (1975) and others (Troughton 1960; Monk 1966; Harper 1977; Pitelka 1977; Abrahamson 1979) suggested that species with short life spans make a greater investment in shoot biomass than do long-lived species. Preferential investment in shoot biomass is thought to permit a faster rate of development, but to sacrifice the capacity to withstand competition.

We explored relationships between division of biomass and other aspects of life history: pines investing heavily in foliage as a proportion of total biomass had characteristics associated with *r*-selection, including small size at maturity, small seeds, low tolerance of competition, early reproduction, and short life spans. Species with the opposite constellation of characteristics invest more heavily in structural and conductive organs, roots, and stems. These character associations suggest that allocation of biomass in the juvenile stage is a fundamental aspect of life history diversification in plants.

METHODS

Materials

To compare life histories, it is best to contrast species with similar phylogeny; evolutionary processes most probably would achieve common solutions to adaptation in related species because they share common phylogenetic constraints. We chose to work with the pines (genus *Pinus*). Pines occupy diverse habitats and assume a variety of ecological roles and life histories (Mirov 1967). Twenty species of pines (Appendix A), about one-fifth of the total number of species in the genus, were used to study allocation of growth in the seedling stage. The partition

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of growth among leaves, stem, and roots is relatively inflexible in pines (Ledig et al. 1970), so results of short-term studies are likely to reflect long-term patterns. Fifteen hard pines (subgenus *Pinus*) and five soft pines (subgenus *Strobus*) were represented in the sample.

Seed was stratified, germinated, and then sown in 490-ml containers. The soil was a 1:1:1:1 mixture of clay loam, river sand, redwood soil conditioner, and perlite. Seedlings of 12 species were grown in a greenhouse at the Institute of Forest Genetics, Placerville, California, for 5 mo during spring–autumn of 1979, and the experiment was repeated with an additional 8 species in 1980 (Appendix B). At monthly intervals, an average of 10 seedlings per species were harvested. Leaves, stem, and roots were washed and then oven-dried at 65° C, and weights recorded to 0.1 mg.

Allometry

The biomass ratio of one organ to another changes during ontogeny (Pearsall 1927; Troughton 1955; Ledig and Perry 1966; Ledig et al. 1970). Even under a constant environment, the ratio will vary with stage of development. To analytically cope with ontogenetic changes when studying organ balance, Huxley (1924) suggested that relative growth of organs could be modeled by the allometric equation $Y = aX^b$. The relative growth of organ Y to another organ or to the total body X is characterized by a linear parameter, a, and an exponential parameter, b, called the allometric coefficient. Instead of measuring individuals once, they are measured several times during ontogeny, and the parameters of the allometric equation are used to describe the pattern of change. The allometric equation can be linearized via logarithmic transformation to simplify interpretation of its parameters: $\log Y = \log a + b \log X$. Since the regression rarely extrapolates to the origin, a relates to initial organ ratios (Pearsall 1927) established while the seedling draws on reserves stored in the seed. The subsequent ratio of the relative growth rates of Y and X is measured by b which remains constant for several years during the seedling stage and perhaps much longer in pines (Ledig et al. 1970), despite fluctuations from episodic or asynchronous growth flushes in leaves, stems, and roots (Cannell and Willett 1976; Cannell et al. 1978; Drew and Ledig 1980). Variation in the allometric coefficient among ecotypes and families is difficult to detect (Cannell and Willett 1976; Cannell et al. 1978; Ledig and Strauss, unpubl. data) compared to variation among species.

Allometric parameters were estimated by nonlinear regression (Glass 1967). On the average, allometric regression explained 84% of the covariation between leaf weight and total plant weight in 1979 and 91% in 1980. Estimates of the coefficients are given in Appendix B.

Life History Traits

Correlation analysis was used to relate the allometric coefficients, or b-values, to the species' life history characteristics. Allometric coefficients were adjusted for variation among years by analysis of covariance before use in correlations.

Correlations were calculated within subgenera, in which phylogenetic distance is minimal, as well as for the genus as a whole. The life history characteristics were seed weight, age at first reproduction, tolerance of competition, average adult tree height, mean longevity, and several measures of the size of the largest tree known for the species (Appendix A). These statistics were obtained from the literature since their normal expression takes decades to centuries in forest trees. Our estimates of life history parameters, therefore, contain environmental variance (since species occupy different habitats), and this probably introduces additional error into the analysis. "Size score" was created by the American Forestry Association; it combines measures of trunk circumference at 1.4 m, height, and crown spread. Tolerance index was adapted from Baker (1950); it indicates the ability of a species to tolerate shade and other stresses resulting from inter- and intraspecific competition. Reciprocal seed weight was used to measure allocation of maternal resources between seed number and seed size. Unless indicated otherwise, all statements of statistical significance in the text refer to two-tailed probabilities at or below the 5% level.

RESULTS

Many of the life history characteristics were significantly correlated (table 1). Larger seeds were associated with later age at first reproduction for species in the hard pine subgenus (n = 13–15), as well as in the genus (n = 18–20), and with larger maximum height in the hard pine subgenus. Delayed reproduction was associated with greater maximum trunk circumference in the genus and with greater maximum height and maximum size score in the hard pines. Longevity was correlated with age at first reproduction in the genus, a relationship previously noted for other taxa (Harper and White 1974; Caswell 1982). Longevity was correlated with mature tree size in both the genus and the hard pine subgenus. Intolerant tree species tended to be smaller in size in the genus and in the soft pine subgenus (n = 5). The various measures of size were positively correlated. Several correlations which approached statistical significance reinforced the positive associations of seed weight, age at first reproduction, and tolerance with the measures of ultimate size. Thus, characteristics usually associated with species of late seral stages, such as large seeds, late reproductive maturity, tolerance of competition, large size, and longevity, tend to occur together among the pines. This pattern is in accord with several theories of life history evolution, such as r- and K-selection, selection under seasonally fluctuating environments, and selection in expanding or declining populations (Pianka 1970; Gadgil and Solbrig 1972; Stearns 1977; Boyce 1979; Caswell 1982).

Allometric coefficients were significantly correlated with all life history characteristics (table 1, fig. 1). Analysis of the subset of hard pines showed correlations which agreed in sign, but were significant only for reciprocal seed weight and maximum height; correlations with longevity and maximum size score were significant at the 10% level.

The correlations among allometric growth and life history characteristics were summarized by principal-components analysis. The first principal component

TABLE 1

Correlation Matrix for Life History Variables and the Allometric Coefficient Describing Foliage to Total Plant Dry Weight in a Sample of the Pine Genus (above diagonal) and the Hard Pine Subgenus (below diagonal)

Variable	1	2	3	4	5	6	7	8	9	10
1. Allometric coefficient		.40**	−.34**	.58***	−.61***	−.63***	−.52***	−.37**	−.48***	−.66***
2. Reciprocal seed weight	.45**		−.46**	−.12	−.08	−.30	−.22	−.35	−.31	−.08
3. Age at first reproduction	−.12	−.56**		.08	.13	.50**	.03	−.11	.37	.51**
4. Tolerance index	.07	−.08	.40		−.64***	.41	−.47**	−.39	−.47*	−.21
5. Average tree height	−.31	−.22	.42	−.12		.58***	.82***	.54**	.77***	.70***
6. Maximum trunk circumference	−.30	−.22	.46	−.18	.70***		.48**	.29	.92***	.71***
7. Maximum height	−.44**	−.56**	.71***	.17	.72***	.75***		.55**	.78***	.46*
8. Maximum crown diameter	−.25	−.55*	.29	.18	.43	.48*	.40		.46*	.16
9. Maximum size score	−.38*	−.39	.59**	−.06	.76***	.96***	.90***	.52*		.71***
10. Mean longevity	−.44*	.21	.45	.01	.85***	.69***	.72***	.22	.74***	

Note.—Larger values of the allometric coefficient indicate greater allocation to leaves; larger values of the tolerance index indicate lower tolerance of competition. For correlations among variables 2–7, n = 19–20, and for correlations with variable 1, n = 32, except as indicated below. Bristlecone pine was excluded from analyses involving longevity, maximum trunk circumference, and maximum size score. Bristlecone pine was excluded from longevity correlations because it was an outlier; its longevity was estimated to be about double the next most long-lived species. It was excluded from analyses involving trunk circumference because major portions of the trunk surface are dead; it is not comparable to the other species in this respect. Washoe and Afghan pines were excluded from analyses involving maximum size because these data were not available in the literature. For Washoe pine, data on tolerance and longevity were estimated from the closely related ponderosa and Jeffrey pines.

* $P < .1$.

** $P < .05$.

*** $P < .01$.

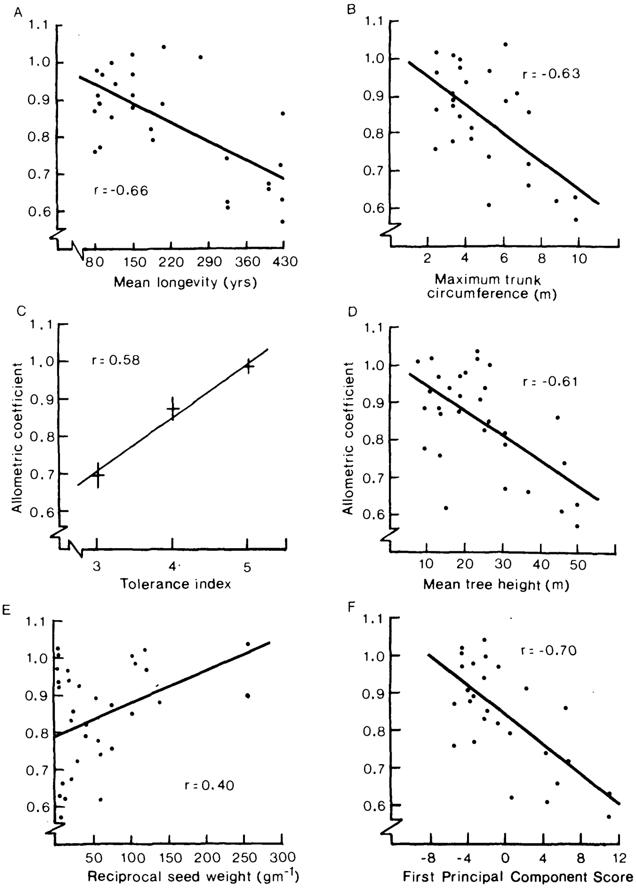

FIG. 1.—Relationships between the allometric coefficients for leaf to total biomass growth and life history traits. Nos. of observations (species in years) were *A* = 28, *B* = 27, *C* = 31, *D* = 32, *E* = 32, *F* = 27. All correlations, except *E*, were significant below the 1% level; for *E*, significance was between 1% and 5% (all 2-tailed significance tests). For *C*, bars indicate standard errors; the correlation was calculated from raw data, not class means. See note in table 1 for a description of the species omitted.

represented 56.4% of the total variance. Loadings reflected the interrelationships of variables suggested by the bivariate correlations (table 2*A*). When life history variables were considered alone, the first principal component represented 51.1% of the total variance (table 2*B*); regression of principal component scores on allometric coefficients was highly significant ($r = -0.70$; fig.1*F*). Results of a principal-components analysis of the hard pine subgenus paralleled that in the genus, except that tolerance index was unimportant because of its relative lack of variation among species. Regression of first-principal-component scores on the allometric coefficient was again significant ($r = -0.44$). Thus, life history traits can account for about one-fifth to one-half of the variance in the allometric

TABLE 2

LOADINGS FROM PRINCIPAL-COMPONENTS ANALYSES OF LEAF TO TOTAL ALLOMETRIC GROWTH AND LIFE HISTORY VARIABLES FOR A SAMPLE OF THE PINE GENUS

Variable	*A*	*B*
1. Allometric coefficient	−.77	—
2. Reciprocal seed weight	−.50	−.43
3. Age at first reproduction	.59	.42
4. Tolerance index	−.60	−.54
5. Average tree height	.88	.88
6. Maximum tree height	.87	.85
7. Maximum trunk circumference	.82	.79
8. Maximum crown spread	.50	.54
9. Maximum size score	.95	.96
10. Longevity	.85	.79

NOTE.—See notes in table 1 for excluded species. Analyses were performed on standardized variables. Values are loadings for the first principal component. *A*, Loadings for analysis of allometric coefficients and life history data simultaneously for all species ($n = 27$); this component represented 56% of the total variance. *B*, Loadings for analysis of life history data alone ($n = 17$); this component represented 51% of the total variance.

coefficient. This analysis suggests that suites of life history traits have coevolved and are strongly related to division of vegetative growth in the seedling stage.

DISCUSSION

The correlations among life history parameters presented above are based on among-species rather than within-species covariance. They may not, therefore, describe the constraints on microevolution that operate within species (Lande 1982). Among-species patterns may be only a sample of a wider array of possible trait combinations, many of which are maladaptive and have been lost by extinction. Thus, the strength of the correlations we observed among species, especially when compared to the weak correlations often found within species (e.g., Bradley 1982; Brown 1983; Giesel et al. 1982), may be because other character combinations failed to persist. Because life history traits are major components of fitness, additive variance within populations will often be low and genetic correlations will be subject to large sampling errors. Vastly greater genetic variance and covariance would be expressed over the millennia available for species divergence. On a time scale of millions of years, correlations due solely to linkage can be broken and genetic changes can occur which minimize the cost of pleiotropy to total fitness. For these reasons, correlations among related species or other taxa may be a better means of quantifying the long-term constraints on life history evolution than studies of within-population genetic covariance. Comparative studies of among-taxa and within-taxon covariance would help test this hypothesis (e.g., Brown 1983).

The allometric coefficient varies from 0.54 to 1.02 in our sample. Because of the longevity and large size of tree species, such small differences could be of great biological importance. If we assume that the relative differences in allometric

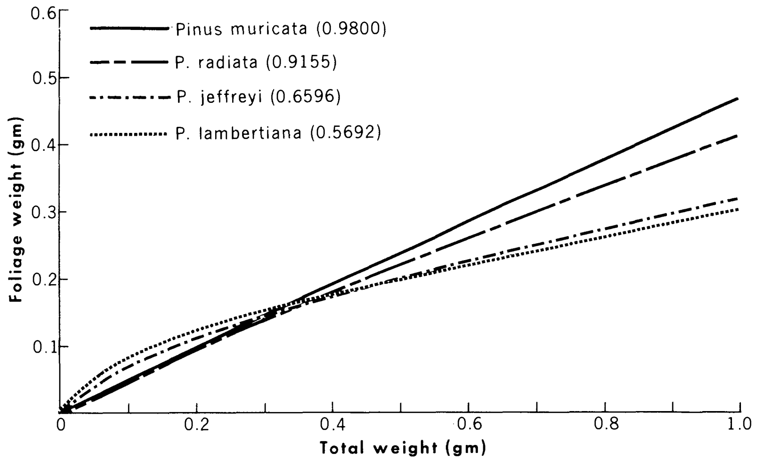

FIG. 2.—Allometric relationships between foliage dry weight and total plant dry weight for 4 species of pines (allometric coefficients shown in parentheses).

growth remain similar throughout life, as they seem to in pines (Ledig et al. 1970; Drew and Ledig 1980), the long-term impact can be calculated from the equations in Appendix B. However, in extrapolating to later years, estimates of allocation should be viewed as a measure of cumulative distribution rather than actual biomass fractions; death of leaves, branches, and roots will distort the biomass distribution from the seedling pattern, which has been disturbed little by tissue death and excision. As an illustration, Bishop pines invested strongly in foliage compared to seedlings of most other species (allometric coefficient = 0.98; fig. 2). If the allometric pattern remained stable, Bishop pines would have invested 40% of their growth in foliage by the time they were young saplings (total dry weight of 10^2 g). As mature trees (total dry weight of 10^6 g), investment in foliage would be 35%. In contrast, sugar pines invested less in foliage than seedlings of any other species in our sample (allometric coefficient in 1980 = 0.57; fig. 2). As young saplings, they would have invested 4% in foliage; as young trees, 0.08%. Thus, as saplings, Bishop pines would have invested about 10 times as much as sugar pines in foliage (40:4); as trees, they would have invested about 450 times more in foliage than sugar pines (35:0.08). Although the extrapolation is quite inexact, it suggests the potential impact of variations in allometric growth for large, long-lived organisms, and illustrates the magnitude of developmental variation that has accompanied life history evolution in pines.

The negative association between mature tree height and investment in foliage has bearing on an old hypothesis: the height that a tree can reach is ultimately limited by the height to which water can be lifted (Weber 1891). The height to which water can be lifted will be determined by the capacity of the root system to draw on soil moisture, and by the conductivity of the stem. Our observations indicate that the pine species which reach the greatest ultimate height are those that devote the greatest proportion of their growth to roots and stem as seedlings.

Our analysis has considered relationships among life history traits and seedling development, but has not considered the ecological factors that selected for these suites of traits. For example, seed weight is important for adaptation to drought and shading (Salisbury 1942; Baker 1972); the large deviations from regression shown by the relatively shade-tolerant sugar pine and the highly drought-tolerant bristlecone, Coulter, and Digger pines may reflect these ecological factors (fig. 1*E*). Among the heavier-seeded species, in fact, reciprocal seed weight seems unrelated to the distribution of growth between foliage and woody organs. Allocation of maternal reproductive effort for these species is probably best interpreted with a concept of life history evolution such as stress selection (*S*-selection; Grime 1977).

Among the pines, intraspecific competition may be more effective than drought in selecting for allocation to roots and stems. Baker's (1950) tolerance classes, the basis of our competition index, reflect potential stand density, tolerance of shading, and tolerance of root competition. In our sample, the species classed by Baker as being most intolerant of competition (i.e., Digger, bristlecone, and pinyon pines) occur in droughty habitats, where density is typically low and there is little competition for light. Contrary to our expectations for drought-tolerant species, they do not seem to invest heavily in roots and stem compared to species that are more tolerant of competition.

Longevity was the life history trait most strongly associated with species that invested heavily in roots and stems (fig. 1*A*). The distribution of longevity tends to be bimodal; one group of species clusters at a mean of 136 yr (SD = 61) and another clusters at a mean of 375 yr (SD = 59). The allometric coefficient shows a remarkable degree of correspondence with these longevity groups. Within groups, however, there seems to be little relationship between investment in woody organs and longevity. With the exception of pinyon pine, the shorter-lived, more ephemeral species are all hard pines. Pinyon pine, however, is by far the most long-lived species among the "ephemerals." The more long-lived group contains three hard pines and four soft pines. Thus, our sample suggests that soft pines tend to be more long-lived than hard pines and invest more in nonphotosynthetic tissues. Those hard pines which do attain long life, however, also show a relatively large investment in nonphotosynthetic tissues.

Size is a critical facet of life history evolution. Stearns (1984) found that the majority of variation in reptile life histories could be accounted for by size alone. In the present study, all life history traits and the allometric division of biomass were correlated with measures of size. Boyce (1979) demonstrated that seasonally fluctuating environments theoretically could result in selection for species with increased size. When resources are temporarily below the level required to maintain a stable population, large size may enable individuals to persist until conditions are again favorable for reproduction. In mammals, large body size provides for resource storage (fat), apparently buffers climatic variability, and results in a low intrinsic rate of increase because of the investment in large, and necessarily fewer, progeny. Similarly, large trees, with roots and trunks that hold storage pools and enable them to capture soil moisture and resources when limiting (Waring and Franklin 1979), are able to survive and maintain productivity under shade, drought, and other stresses that would adversely affect small plants. Like mammals, they also delay reproduction and produce larger propagules, presumably to aid in surviving the juvenile period. Under very severe or prolonged stress, however, small size is advantageous for surviving life-threatening periods (Grime 1977); small size reduces respiration and the demands on limited pools of water and nutrients. Thus, evolution of size may be a key means of adapting to a wide variety of biotic and abiotic stresses; other life history traits may be "prompted" to coevolve (cf. Stearns 1984).

The associations of life history characteristics and distribution of biomass are consistent with several theories of life history evolution, such as *r*- and *K*-selection, *S*-selection, and selection in expanding or declining populations (Grime 1977; Stearns 1977; Boyce 1979; Caswell 1982). Our data, unfortunately, permit only a tentative choice among competing theories. When carrying capacity, *K*, is defined in terms of biomass or number of meristems (White 1980), our data fit well with traditional notions of *r*- and *K*-selection. The effects of stress from drought and shading, however, have a strong influence on the observed character complexes, for example, on the way maternal resources are allocated (i.e., on reciprocal seed weight) and on measures of size. Thus, theories of life history evolution that explicitly accommodate chronic stresses as evolutionary agents (e.g., Grime 1977; Boyce 1979) seem to provide superior frameworks for understanding life history evolution in pines.

We offer the following as a testable hypothesis to account for the associations between distribution of biomass and life history in pines, and perhaps for perennials in general. Frequently disturbed, ephemeral habitats place a premium on early reproduction (e.g., Solbrig 1971), probably at the expense of root growth and supportive stem tissue. Such a tactic is likely to limit ultimate size and perhaps longevity because a large stem and root system is needed for physical support of aboveground biomass, for storage, and for scavenging light, soil moisture, and nutrients as a site becomes fully occupied with competitors. Thus, rapid early development to maturity reduces the potential for attainment of large size, a prerequisite for competition later in life. Conversely, allocation to structural tissues reduces relative growth rate when conditions are favorable; the investment in photosynthetic machinery is compounded less rapidly and the ratio of respiring tissue to photosynthetic tissue is highest in species that devote the largest proportion of resources to roots and stems (Ledig 1976). This may place a potentially long-lived species at an early height disadvantage, therefore requiring increased seed size, greater tolerance of shade, and a delayed reproductive effort to improve chances for survival. In this way, juvenile strategies for allocation of vegetative growth may constrain reproductive behavior and limit the life span.

Suites of life history and reproductive characteristics have evolved in pines and are associated with the distribution of vegetative growth in the juvenile or prereproductive phase. At one extreme are long-lived species and species of late seral stages. At the other extreme are species described by an array of adjectives (not entirely synonymous) such as early-seral, opportunistic, fugitive, or colonizing. Early-seral species reach reproductive maturity at an early age, grow rapidly in the juvenile stage, are intolerant of competition, small at maturity, limited in life span, and frequently small seeded. To this, we add that in the juvenile phase they invest more strongly in foliage relative to other tissues; a preferential investment in energy-harvesting potential. Our results suggest that allocation of growth among vegetative organs may be a fundamental aspect of life history evolution. Architectural patterns established during the first few months of life are indicative of development decades to centuries later, when the plant has increased a millionfold in size.

SUMMARY

Partition of biomass between photosynthetic and structural tissues of seedlings was measured by allometry in 20 species of pines. The division of growth during the seedling, or vegetative, phase of development foreshadows life history characteristics which develop much later in the reproductive phase. Species with life histories characterized by small size at maturity, small seeds, low tolerance of competition, early reproduction, and short life spans invested heavily in foliage as a proportion of total biomass. Species with the opposite constellation of characteristics invested more heavily in structural and conductive organs, roots, and stem. These character associations define a trend from fugitive species to species of later seral stages, and generally conform to expectations of *r*- and *K*-selection theory. Species adapted to severe stresses may deviate, however, from these trends. Theories of life history evolution which do not incorporate ecological stresses as selective factors seem inadequate for pines.

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APPENDIX A

Life History Statistics Used in Analyses

Common Name	Scientific Name	Seed Weight (mg)	Age at Reprod. (yr)	Tol. Index	Size Score	Mean Height (m)	Max. Circ. (m)	Max. Height (m)	Max. Spread (m)	Mean Longev. (yr)
1. Virginia pine	*Pinus virginiana* Mill.	8.2	5	4	190	22.9	2.4	25.9	16.2	150
2. Pitch pine	*P. rigida* Mill.	7.4	3	4	245	18.3	3.3	29.2	15.2	150
3. Loblolly pine	*P. taeda* L.	25.0	7	4	353	30.5	4.3	49.4	22.2	187
4. Ponderosa pine	*P. ponderosa* Laws.	37.9	18	4	527	44.2	7.3	68.0	20.7	425
5. Knobcone pine	*P. attenuata* Lemm.	17.9	6	4	269	9.8	3.3	35.7	20.1	87
6. Digger pine	*P. sabiniana* Dougl.	789.3	17	5	379	18.3	5.2	48.8	24.4	92
7. Table Mountain pine	*P. pungens* Lamb.	13.3	5	4	178	13.7	2.4	23.2	13.4	80
8. Spruce pine	*P. glabra* Walt.	9.9	10	4	260	25.9	3.7	28.3	25.6	112
9. Lodgepole pine	*P. contorta* var. *murrayana* Dougl.	3.9	6	4	355	22.9	6.1	33.5	11.3	207
10. Afghan pine	*P. eldarica* Medw.	49.9	8	—	—	25.0	—	—	—	—
11. Coulter pine	*P. coulteri* D. Don	326.6	14	4	306	15.8	4.0	41.8	12.2	117
12. Monterey pine	*P. radiata* D. Don	34.2	7	3	412	23.7	6.7	38.1	27.7	85
13. Bishop pine	*P. muricata* D. Don	9.7	5	4	278	19.8	3.7	36.9	13.7	84
14. Washoe pine	*P. washoensis* Mason & Stockwell	52.0	15	4	—	30.5	—	—	—	400
15. Jeffrey pine	*P. jeffreyi* Grev. & Balf.	123.0	8	4	480	36.6	7.3	53.3	26.5	400
16. Bristlecone pine	*P. aristata* Engelm.	217.9	20	5	529	10.7	11.9	14.3	12.5	723
17. Sugar pine	*P. lambertiana* Dougl.	218.0	60	3	617	49.4	9.8	65.8	20.7	425
18. Eastern white pine	*P. strobus* L.	17.2	7	3	387	45.7	5.2	48.2	23.8	325
19. Limber pine	*P. flexilis* James	92.8	30	4	405	15.2	8.8	13.1	14.0	300
20. Pinyon pine	*P. edulis* Engelm.	238.8	50	5	180	7.6	3.3	10.4	13.7	275

Note.—Nomenclature follows Critchfield and Little (1966). Reprod. = first reproduction; tol. = tolerance; max. = maximum; circ. = circumference; longev. = longevity. Dashes indicate that data were unavailable. Seed weight, age at first reproduction, and mean height are from U.S. Department of Agriculture (1974) and Wells (1964); tolerance index is adapted from Baker (1950); size score and maximum circumference, height, and spread are from Hartman (1978); mean longevity is based on data in Sudworth (1908), Metcalf (1921), Altman and Dittmer (1962, 1972), Forde (1963), Clark and Saucier (1969), Harlow and Harrar (1969), Zobel (1969), Beasley (1972), and Clepper (1982).

APPENDIX B

Estimates of Parameters of the Allometric Relationship, Foliage Biomass = a(Total Biomass)^b, for 20 Species of Pines

Species	1980		1979	
	a	*b*	*a*	*b*
1. Virginia pine	.5462	1.0242	.3279	.8481
2. Pitch pine	.4273	.9159	.2562	.7873
3. Loblolly pine	.3249	.7942	.2552	.7305
4. Ponderosa pine	.3251	.7200	.2814	.7712
5. Knobcone pine	.3973	.8945	.2426	.6865
6. Digger pine	.4030	.9668	—	—
7. Table Mountain pine	.4206	.8686	.2355	.6730
8. Spruce pine	.4521	.9994	.2509	.7564
9. Lodgepole pine	.2522	.8867	.3172	.9490
10. Afghan pine	.3815	.8296	.3556	.8644
11. Coulter pine	.4261	.9426	—	—
12. Monterey pine	.4111	.9155	—	—
13. Bishop pine	.4644	.9800	—	—
14. Washoe pine	.2025	.6657	—	—
15. Jeffrey pine	.3120	.6596	—	—
16. Bristlecone pine	.5734	1.0244	.2760	.8442
17. Sugar pine	.2993	.5692	.3350	.5428
18. Eastern white pine	.1652	.6072	.1959	.6532
19. Limber pine	.1506	.6173	—	—
20. Pinyon pine	.4836	1.0144	—	—

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