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ECOLOGICAL DIVERSITY IN NORTH AMERICAN PINES[1]

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ABSTRACT

Ecological groups were identified from 34 North American species of pine using multivariate analysis of 18 ecological traits. Five adaptive modes are described: 1) fire-resistant species that are large, thick-barked, and have large cones and long needles; 2) tall, fast-growing mesophytic species with moderately high shade tolerance; 3) stress-tolerant species with animal-dispersed seeds, occurring mainly on cold or dry sites where fire is infrequent; 4) fire-resilient species that are precocious reproducers with small seeds, often in serotinous cones; and 5) species of southern mesic sites with fast growth, strong, heavy wood and short persistence of needles. Intermediates between these modes exist. Convergent evolution has occasionally occurred, as shown by high ecological similarity of species in different taxonomic sections within *Pinus*. However, the analogies between species are imperfect, suggesting the importance of constraint by shared ancestry and divergence produced by a diversity of environments.

DESPITE their economic and ecological significance, the ecological diversity of pines is often not fully appreciated. The genus is sometimes considered to have a narrow set of roles (e.g., Govindaraju, 1984) in the ecosystem: drought-tolerant pioneers on nutritionally poor sites. Yet the variation among species in morphology and life history is rich. Furthermore, there appears to be a striking recurrence of ecologically similar sets of species in different geographic areas—species analogs. For example, there are a number of seemingly analogous species between the northern Rocky Mountains and the Great Lakes states: *Pinus contorta* and *P. banksiana, P. monticola* and *P. strobus,* and *P. ponderosa* and *P. resinosa* (nomenclature follows Little and Critchfield, 1969). Are these and other potential species analogs supported by quantitative analyses of their similarities? Are there adaptive modes or syndromes, recurring suites of ecological traits?

This paper describes the ecological groups of North American pines as revealed through multivariate analysis of morphological and life history characters having probable ecological importance (in contrast to taxonomic characters having little ecological significance). Questions as to the origin of the species analogs are examined by comparing taxonomic groups of pines (Little and Critchfield, 1969) with the ecological groups of pines derived here. Did the variation in life history and morphology arise solely through a process of ecological and phylogenetic divergence, or has there been ecological convergence from distinct phylogenetic lines?

MATERIALS AND METHODS—Ecological traits for the North American pines (raw data in Appendix 1) were tabulated from the literature. Principal sources were Bowers (1942), Elias (1980), Fowells (1965), Munz and Keck (1959), Preston (1976), Sargent (1922), Shaw (1909), Sudworth (1917), U.S. Department of Agriculture (1948, 1974) and Ward (1963). All North American species north of Mexico were included except for three species with insufficient data (*Pinus engelmannii* = *P. apacheca*; *P. washoensis*; *P. strobiformis* is included here under *P. flexilis*). Recent segregates in the *P. cembroides* complex (*P. discolor* Bailey and Hawksworth, *P. johannis* M. F. Robert, *P. remota* (Little) Bailey and Hawksworth) are included under *P. cembroides.* The Great Basin bristlecone pine (*P. longaeva*) is part of *P. aristata* as used here. The Rocky Mountain subspecies *latifolia* of *P. contorta* was kept separate from subspecies *contorta* because of their different habitats (Critchfield, 1957; Fowells, 1965; *P. contorta* ssp. *murrayana* is included under *P. c.* ssp. *contorta*). *P. rigida* and *P. serotina* were also kept separate for this reason (Smouse and Saylor, 1973). Thirty-four taxa (henceforth "species") were thus included.

One goal of this study was to contrast ecological groups of species with phylogenetic groups of species. Therefore, certain characters

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TABLE 1. *Ecological characters used in multivariate analyses*

Variable name	Character	Type[a]	Units or coding[b]
ARMED	Cone scale armor	C	0 = none, 1 = stout prickles, 1.5 = large claw
BARKTH[c]	Bark thickness	C	cm
CLCONE	Closed cones at maturity	C	0 = never, 1 = often
COLGTH[c]	Cone length	C	cm
GRATE	Growth rate	M	0 = very slow, 1 = slow, 2 = moderate, 3 = fast
HEIGHT[c]	Height at maturity	C	m
LFLGTH[c]	Leaf length	C	cm
LFPER[c]	Leaf persistence	C	years
MINAGE[c]	Minimum seed-bearing age	C	years
MOISTR	Soil moisture of usual habitat	M	1 = very dry, 2 = dry, 3 = moist, 4 = wet
SEEDWT[c]	Seed weight	C	mg
SEEDLG	Seed length	C	cm
SPROUT	Vegetative sprouting from root collar	M	0 = none, 0.5 = only when young, 1 = persistent with age
TOLERN	Shade tolerance	M	0 = very intolerant, 1 = intolerant, 2 = intermediate or tolerant when young, 3 = tolerant
TWIGS	Twig thickness	M	0 = slender, 1 = stout, 1.5 = very stout
WINGLG	Seed wing length	C	cm
WOODST	Wood strength	C	0 = very weak, 1 = very strong
WOODWT[c]	Wood weight	C	0 = very light, 1 = very heavy

[a] C = continuous, M = ordered multistate.

[b] Units are given for continuous quantitative variables, coding is given for ordered multistate variables, and reference points are given for continuous characters (e.g., ARMED, CLCONE).

[c] Log transformed.

were excluded from the analysis that are traditionally important taxonomic characters but have questionable ecological significance. Number of needles per fascicle is the most important of these excluded characters: it occupies a central position in distinguishing the subdivisions of *Pinus* (Little and Critchfield, 1969). To the extent that ecological groups parallel taxonomic groups, spurious correlations between ecological factors and conservative taxonomic characters will be found. Yeaton (1981) postulated adaptive significance to needle number based on an observed correlation between site moisture and needle number in the Sierra Nevada. It is presumed here, however, that needle number is generally a conservative character (exception: needle number in the pinyon pines) reflecting shared ancestry rather than strong, direct selection.

The data set's ecological emphasis also derives from inclusion of characters that would probably be poor characters in a taxonomic study: for example, growth rate, sprouting ability, shade tolerance, and soil moisture of a species' usual habitat.

Evaluation of characters from the literature presented several problems. Both ordered multistate and quantitative characters were included (Table 1). Published ranges in quantitative variables were reduced to midpoints if no indication of the central tendency was given. An exception was minimum seed-bearing age, where the low end of the range was used to emphasize genetic potential rather than site effects. Characters were checked in several sources, and the consensus was entered into the data matrix. Some characters, such as height and growth rate, are not defined precisely (e.g., at what age? under optimum conditions?). Reported heights were quite variable among authors; hence, for consistency, values in Preston (1976) were used whenever possible. Some characters were excluded because of insufficient data (amount and variability of seed production, winter bud size) or markedly inconsistent evaluation by different authors (age of maturity, maximum age). The 18 traits used and their methods of coding are listed in Table 1.

The repeatability of the data was tested by comparing this data set with a similar, independently derived data set with only partial overlap in source literature. Four traits and 17 species are shared between this study and that of Strauss and Ledig (1985). These four traits were strongly correlated between the two studies (r^2 = 0.86, 0.51, 0.92, and 0.82 for mean height, tolerance index, minimum age of reproduction, and seed weight, respectively).

Data analysis—Multivariate analyses were used to assess similarity relationships among

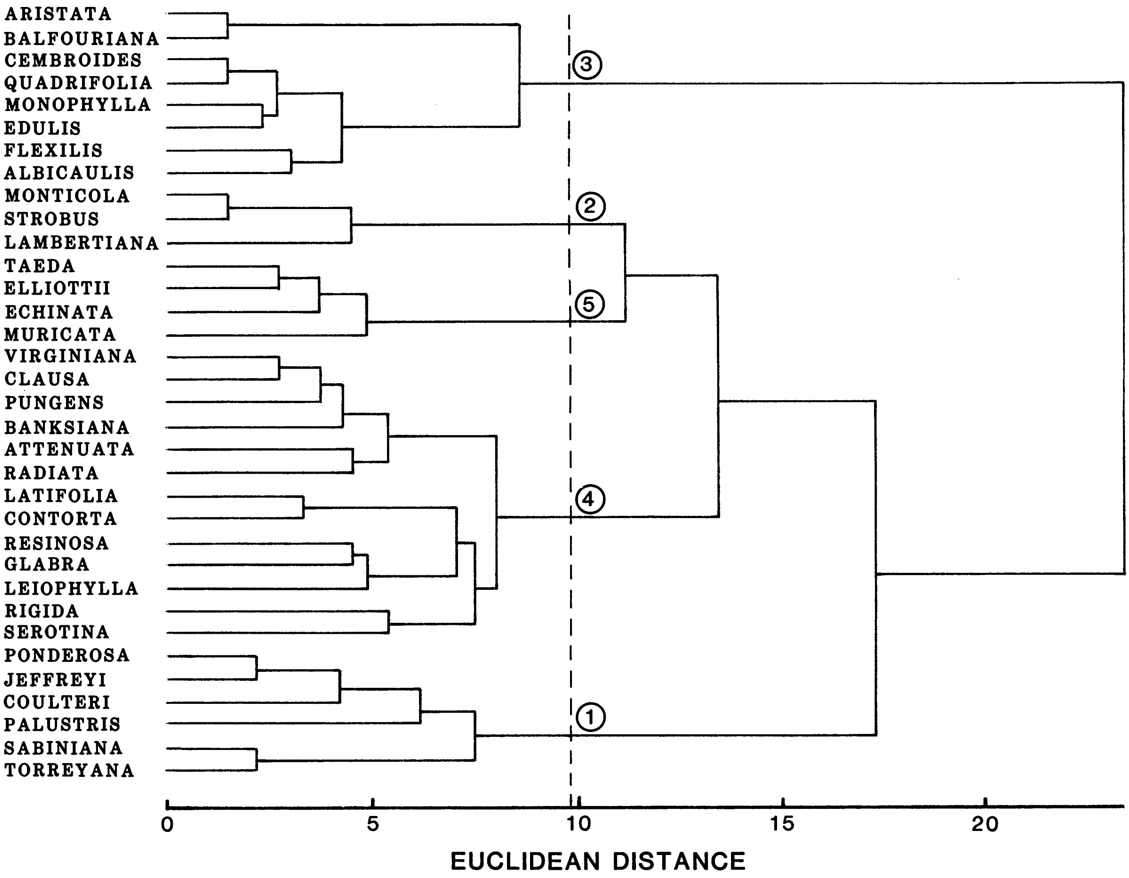

Fig. 1. Cluster analysis of species in ecological trait space (Euclidean distance, Ward's method of linkage [J. H. Ward, 1963]). The vertical dashed line indicates the five-group level used as the first approximation of the ecological groups of species.

species. The raw data matrix (18 characters × 34 species) was adjusted in two ways before analysis: 1) eight characters (Table 1) with strong positive skew were log-transformed to improve normality (Sokal and Rohlf, 1981, 419); 2) all characters were then relativized by their standard deviations (Sneath and Sokal, 1973, 153) to equalize their means and variances, so that all variables carried equal weight in the analyses.

Species were clustered (program CLUSTAR of Romesburg and Marshall, 1983) using a Euclidean distance matrix (Sneath and Sokal, 1973, 124) and Ward's linkage method (J. H. Ward, 1963), a sequential, agglomerative, hierarchic, nonoverlapping technique (Sneath and Sokal, 1973, 241). Clusters of species were then analyzed at the five-group level using multiple discriminant analysis (Nie et al., 1975) to clarify the differences between groups and to test for misclassified species. Discriminant analysis (DA) maximizes the separation of predefined groups, in this case on the basis of ecological characters. All of the ecological characters were entered simultaneously (method = DIRECT; Nie et al., 1975). Prior probabilities of group membership were assumed to be equal. Univariate *F* ratios were calculated for the differences in ecological traits among groups.

Standardized principal components analysis (PCA; Sneath and Sokal, 1973, 245; program PCA derived from PCAR, Department of Botany, University of Wisconsin, unpublished), using correlation as a resemblance measure, was used to summarize species relationships in ecological character space. PCA optimizes the representation of differences among species rather than difference among species groups as in DA. Species scores along successive ordination axes (components) were scaled by the proportion of variance explained by each axis.

Variation within species groups was analyzed with five standardized PCAs of species in ecological character space, one PCA for each ecological group. Like the full matrix, the data matrix for each group was relativized by standard deviations of characters within groups. Contributions of individual characters to

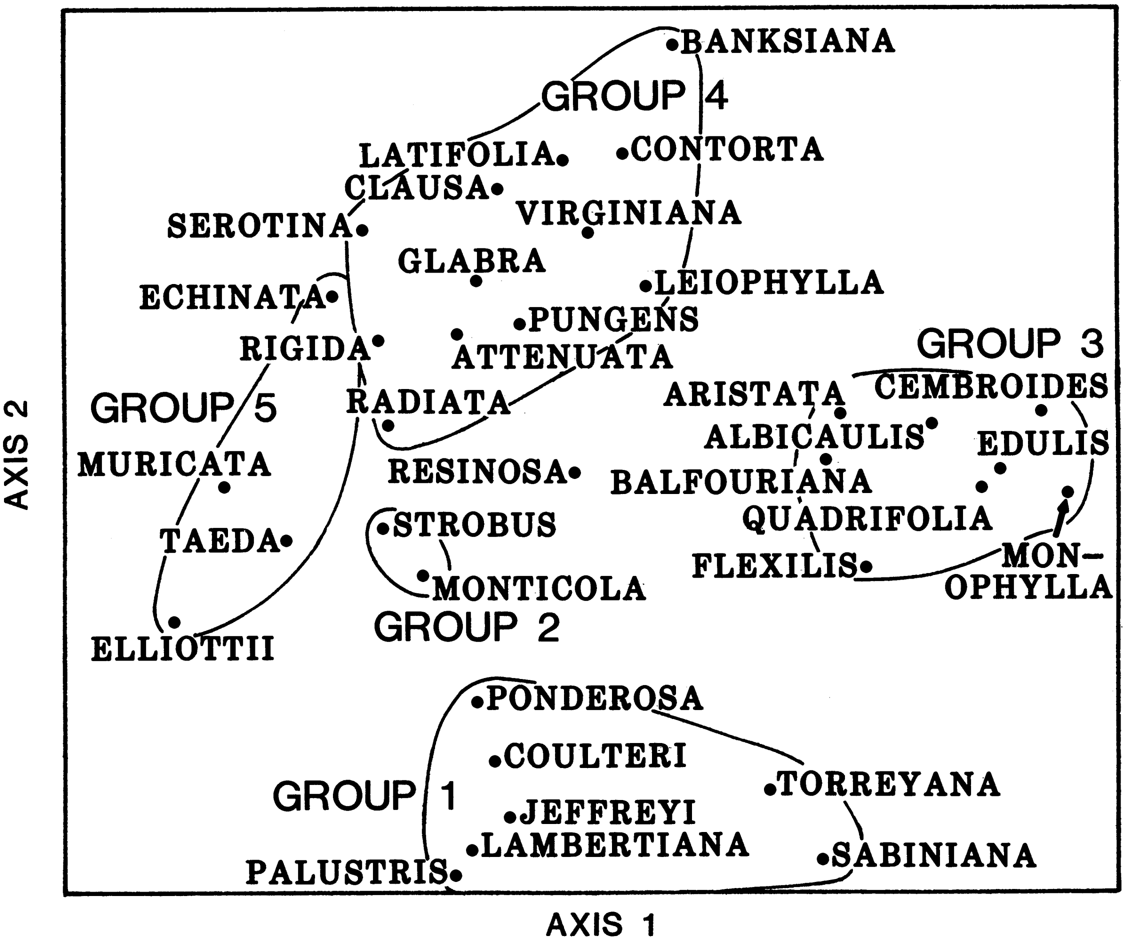

Fig. 2. Principal components analysis of species in ecological trait space. Species placement on the first two components (axes) represents 44% of the correlation structure among species. The five ecological groups are enclosed by loops. *Pinus resinosa* did not clearly belong to any one group.

species positioning on the ordination axes were evaluated with Pearson correlations and rank correlations (Kendall's Tau; algorithm based on procedures 3A and 4 in Sokal and Rohlf, 1969, 534–536).

RESULTS AND DISCUSSION—*Identification of groups*—Five groups of ecologically similar species can be distinguished. Fewer or more groups could have been distinguished, but the five-group level in the cluster analysis provides ecologically interpretable and fairly distinct groups (Fig. 1). The groups are considered as heuristic rather than a rigid formal classification.

The distinctness of the species groups can be qualitatively evaluated by examining their degree of isolation in the first two principal components (representing 44% of the variation among species; Fig. 2). Some of the species groups defined by cluster analysis are fairly distinct in this two-axis representation.

Pinus resinosa was withdrawn from Group 4 because its isolated central position in the PCA (Fig. 2) indicates that it combines features of several groups. *Pinus resinosa.* is the sole temperate representative of subsect. *Sylvestres* in America. It has the long leaves, thick bark, and delayed reproduction of Group 1, the small cones and seeds of Group 4, and the unarmed cones of Groups 2 and 3. Because it could not be comfortably placed in any of the groups, it was excluded from further analysis.

Although *P. lambertiana* clustered with Group 2, PCA revealed a stronger affinity with Group 1; hereafter, it is treated with Group 1. The similarities of *P. lambertiana* with these two groups are described under Group 1.

Another expression of the strength of the groups compares the average correlation among

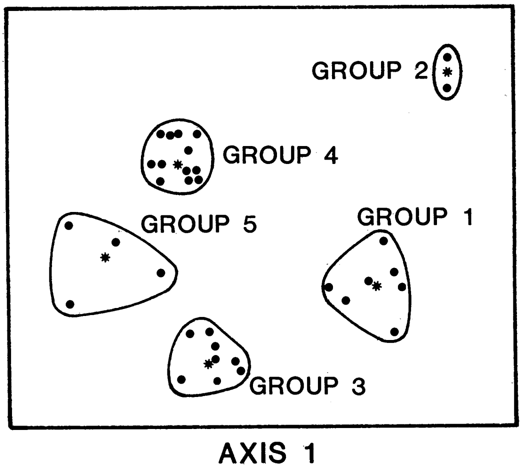

Fig. 3. Multiple discriminant analysis of ecological species groups in trait space. Points indicate position of individual species on the first two discriminant functions, stars indicate centroids of species groups.

species in the same group to the average correlation between species pairs in different groups. The average within-group correlation coefficients ($r_1 = 0.751$, $r_2 = 0.997$, $r_3 = 0.862$, $r_4 = 0.738$, $r_5 = 0.903$) are higher than the between-group average ($r = 0.654$).

Discriminant analysis and one-way analyses of variance were used to clarify the differences between groups (Fig. 3, Table 2). The first two discriminant functions (Fig. 3) expressed 72% of the variation among the five groups. All characters differed significantly ($P < 0.05$) among groups except for sprouting ability and site moisture (Table 3). Site moisture was the only borderline case ($P = 0.07$).

Ecological similarity among species in a group clearly increases as groups are narrowed from the whole genus to the 5-group level, then to individual species. Although the ecological groups discussed here are useful ecological subdivisions, and although the ecological similarities among species in the same group are often striking, the individuality of most species is impressive. And even within some species, the variation in ecological characteristics is broad (e.g., *P. rigida, P. contorta,* and *P. ponderosa*).

Description of the species groups—For each group, I describe the ecological characteristics shared within that group, followed by the departures of each species from the group norm. The strategy of each group is summarized in parentheses at the beginning of each description.

Group 1 (fire-resistant; coulteri, jeffreyi, lambertiana, palustris, ponderosa, sabiniana, torreyana*)*: Pines in this group are distinguished by characteristics increasing the likelihood of mature trees surviving fire: most are tall, with thick bark, long needles, and thick twigs (exceptions discussed below). In addition, they tend to have large, heavily armed cones (with stout sharp spines), large seeds with long wings, and are slow to initiate seed production (Table 3). Many of the species are fire-resistant (*P. lambertiana,* Fowells, 1965; *P. palustris,* Wahlenberg, 1946; *P. ponderosa,* Flint, 1930). Thick bark confers fire resistance in these species by insulating the cambium (Fahnestock and Hare, 1964; Wright and Bailey, 1982, 18). Also, thick twigs should have higher heat capacities than thin twigs, resulting in lower cambial temperatures during ground-surface fires. (They may also be the structural by-products of tufts of long needles on the branch ends.) Effective seed insulation is provided by thick cone scales in some pines (Linhart, 1978), but the literature lacked sufficient data to include that character in this study. The tufts of long needles at the end of the branches may insulate terminal buds, not only from fire but also from other microclimatic fluctuations. The potential for great height in these species tends to remove their crowns from the heat of surface fires.

These species may also have characteristics that promote surface fire. Mutch (1970) and Williamson and Black (1981) suggest that the fire-dependent species may produce litter that facilitates fire. Williamson and Black found that the long needles of *Pinus palustris* formed a deep, well-aerated litter layer beneath the pines that resulted in higher combustion temperatures than litter under other species (not pines) with lower fire tolerance. Because frequent surface fires favor fire-resistant species, characteristics that promote fire might have adaptive value to fire-resistant species. Mutch (1970) hypothesized that flammability of litter has evolved from direct selection by fire. Snyder (1984) noted, however, that flammability of fire-dependent species is not proof of Mutch's hypothesis.

At first glance, the large seeds and cones of

TABLE 2. *Effectiveness of the discriminant functions in separating species groups using ecological characters*

Function	Cumulative % of variance explained	Canonical correlation[a]
1	40.5	0.98
2	72.4	0.97
3	95.3	0.96
4	100.0	0.85

[a] In discriminant analysis the canonical correlation is a measure of each function's ability to discriminate among groups.

TABLE 3. *Average character value (untransformed) in each species group*

Character[a]	Species group. 1	2	3	4	5	P[b]
Armed cone scales	0.93	0.00	0.26	0.73	0.98	0.004
Bark thickness (cm)	5.2	3.2	1.8	2.0	5.3	0.001
Closed cones at maturity	0.13	0.00	0.00	0.60	0.25	0.007
Cone length (cm)	23.7	19.7	7.5	6.4	8.6	0.000
Growth rate	1.1	2.0	1.0	1.6	3.0	0.000
Height at maturity (m)	31.6	41.5	9.5	16.9	25.5	0.000
Leaf length (cm)	20.1	7.6	4.0	8.1	16.8	0.000
Leaf persistence (yr)	3.9	2.8	7.3	3.5	2.6	0.003
Minimum seed bearing age (yr)	16.3	6.0	19.4	6.8	5.5	0.000
Moisture of usual habitat	1.8	3.0	1.6	2.3	2.4	0.072
Seed weight (mg)	331.2	16.8	210.8	9.7	18.7	0.000
Seed length (cm)	1.3	1.3	1.2	0.5	0.6	0.000
Sprouting from root collar	0.03	0.00	0.00	0.30	0.13	0.166
Tolerance to shade	0.8	2.0	0.4	1.0	1.6	0.014
Twig thickness	1.21	0.00	0.86	0.42	0.63	0.002
Wing length (cm)	2.4	2.5	0.64	1.7	1.9	0.005
Wood strength	0.39	0.40	0.44	0.40	0.69	0.008
Wood weight	0.36	0.25	0.28	0.29	0.59	0.003

[a] See Table 1 for explanations of character coding.

[b] Probability of type I error, univariate F ratios for differences in characters among species groups (after transformation, as described in text).

this group would appear to support the general positive relationship between the size of organisms and the size of their offspring (Blueweiss et al., 1978). The relationship is, however, flawed within the pines. Consider the small seeds of the tall species *P. monticola* and *P. strobus* and the large seeds of the short species in Group 3; the generalization weakens further when other coniferous genera are included (e.g., the small seeds of *Sequoia*).

coulteri—Although less divergent from this group than *P. sabiniana* and *P. torreyana, P. coulteri* shares with these species some characteristics of both Group 3 (slow growth and somewhat smaller size) and Group 4 (partial seed retention; Minnich, 1980; Borchert, 1985). Although *P. coulteri* and *P. lambertiana* are in the same ecological group, the partial serotiny of *P. coulteri* appears to confer a reproductive advantage over *P. lambertiana* following wildfire in mixed stands (Griffin, 1982).

jeffreyi—*Pinus jeffreyi* is well represented by the average characteristics of Group 1 (Table 3). In comparison to the similar *P. ponderosa* with which it hybridizes (Munz and Keck, 1959), *P. jeffreyi* grows at higher elevations or on ultramafic substrates (Jenkinson, 1980) and has longer needle retention and larger cones.

lambertiana—This species differs from the rest of this group in its short leaves, faster growth, slender twigs, and a tendency to be found on more mesic sites. These are all characteristics of the taxonomically related *P. strobus* and *P. monticola* (ecological Group 2, taxonomic subsection *Strobi*). However *P. lambertiana* is a tall, thick-barked, large-seeded species, like most other members of Group 1. The ecological divergence of *P. lambertiana* from Group 2 is not surprising, considering its probable phylogenetic affinities with Asian species (Axelrod, 1986).

palustris—*Pinus palustris* differs from the rest of this group in its stronger, heavier wood, longer seed wings, and a weak capacity to resprout vegetatively when young. This species also has perhaps the most strongly developed characteristics for fire tolerance: besides extremely long needles, it has a persistent juvenile "grass stage" (a tuft of needles surrounding a short shoot) followed by a stage of rapid shoot elongation (Wahlenberg, 1946). In this fire-resistant stage the tree develops its root system and stores resources to allow fast height growth. This fast growth moves shoot apices rapidly above the zone of highest temperature that occurs during surface fires.

Although omitted from the quantitative analysis for lack of data, *P. engelmannii* in the Southwest is similar in many ways to *P. palustris*. It, too, has a persistent grass stage (Mirov, 1967).

ponderosa—Like the closely related (both taxonomically and ecologically) *P. jeffreyi, P. ponderosa* is a typical, central species of this group.

sabiniana—Pinus sabiniana and *P. torreyana* are two Californian species that are intermediate between the fire-resistant Group 1 and the stress-tolerant Group 3. More details are given under *P. torreyana.*

torreyana—Pinus torreyana and *P. sabiniana* do not fit well into this or any other single group. The affinity of these species to Group 1 derives from their long needles and moderately thick bark and twigs. They are ecologically similar to Group 3 (Fig. 2) in their small stature, slow growth, delayed reproduction, and short, probably nonfunctional seed wings. They have some affinity with Group 4 in their tendency for delayed seed release, although they are not true closed-coned species (McMaster and Zedler, 1981).

Group 2 (Relatively shade-tolerant, mesophytic species; monticola, strobus*):* Higher shade tolerance than other pines, thin twigs, unarmed cone scales, mesic sites, fast growth, tall habit, short needle retention, precocious reproduction. These two species are closely related both ecologically and taxonomically.

The fast growth of these more tolerant species contrasts with the usual observation that shade-tolerant species have slower growth. This discrepancy can be reconciled by considering the scope of the comparison. When comparing species that share sites, tolerant species grow more slowly than intolerant (Horn, 1971; Bormann and Likens, 1979; Spurr and Barnes, 1980). Comparing pines across a variety of sites, however, results in the opposite trend because the more shade-tolerant pines are found primarily on mesic sites where faster growth is possible.

The western *P. monticola* is ecologically close to its eastern analog (and homolog), *P. strobus,* but differs in having longer cones and longer needle retention. *Pinus strobus* more often grows with deciduous competitors.

Group 3 (stress-tolerant; albicaulis, aristata, balfouriana, cembroides, edulis, flexilis, monophylla, quadrifolia*):* Short stature, long persistence of leaves, mostly with large seed but with the wing short or lacking, thin bark, slow growth, many years required before seed is produced, dry sites. Group 3 is the most cohesive and distinct of the species groups (Fig. 3). *Pinus aristata* and *balfouriana,* however, form a fairly distinct subgroup having small seeds with long wings.

The long persistence of leaves (average = 7 years) can be considered an extreme expression of evergreenness. The two primary advantages of evergreens are usually thought to be 1) nutrient conservation and 2) energetic opportunism, the capability of taking advantage of short

TABLE 4. *Correlation coefficients among ecological characters (after transformation) of North American pines*

	Ecological characters[a]																	
	WOODWT	WOODST	WINGLG	TWIGS	TOLERN	SPROUT	SEEDLG	SEEDWT	MOISTR	MINAGE	LFPER	LFLGTH	HEIGHT	GRATE	COLGTH	CLCONE	BARKTH	ARMED
ARMED	0.29	0.10	0.42	0.33	−0.12	0.12	−0.15	−0.12	−0.05	−0.37	−0.03	0.49	0.09	0.16	0.13	0.25	0.29	—
BARKTH	0.20	0.10	0.37	0.27	0.36	−0.47	0.17	0.21	0.17	0.12	−0.18	0.51	0.47	0.24	0.60	−0.17	—	
CLCONE	−0.07	−0.18	0.14	−0.10	0.01	0.06	−0.36	−0.38	0.04	−0.58	−0.19	0.05	−0.09	0.16	−0.15	—		
COLGTH	0.09	−0.20	0.56	0.21	0.21	−0.26	0.46	0.44	0.05	0.18	−0.12	0.52	0.50	0.12	—			
GRATE	0.27	0.22	0.36	−0.37	0.46	0.08	−0.29	−0.32	0.15	0.43	−0.41	0.36	0.34	—				
HEIGHT	0.32	−0.08	0.57	−0.20	0.51	−0.04	−0.16	−0.21	0.39	−0.10	−0.40	0.45	—					
LFLGTH	0.52	0.04	0.55	0.30	0.20	0.15	0.12	0.17	0.09	−0.14	−0.42	—						
LFPER	−0.11	−0.08	−0.24	0.23	−0.45	−0.20	0.06	−0.13	−0.13	0.40	—							
MINAGE	−0.10	−0.04	0.42	0.27	−0.16	−0.19	0.42	0.59	−0.24	—								
MOISTR	0.20	0.19	0.20	−0.11	0.48	0.22	−0.38	−0.43	—									
SEEDWT	−0.15	−0.28	−0.22	0.46	0.22	−0.32	0.90	—										
SEEDLG	−0.24	−0.28	−0.17	0.40	−0.18	−0.35	—											
SPROUT	0.21	−0.03	0.08	−0.06	−0.21	—												
TOLERN	−0.05	0.08	0.26	−0.40	—													
TWIGS	0.23	0.13	0.10	—														
WINGLG	0.45	0.04	—															
WOODST	0.53	—																
WOODWT	—																	

[a] Character codes are defined in Table 1.

favorable conditions within a generally unfavorable period (Moore, 1984). Both characteristics can be considered adaptations to stress, defined by Grime (1979, 21) as "the external constraints which limit the rate of dry matter production of all or part of the vegetation." These pines grow in habitats that are either cold (*P. flexilis, P. albicaulis, P. balfouriana*) or dry (*P. cembroides, P. edulis, P. monophylla, P. quadrifolia*), or both (*P. aristata*). Fuel loads in their habitats are generally discontinuous and light, resulting in lower fire frequencies than most other pines experience.

Slow growth is typical of stress-tolerant plants (Grime, 1979). Delayed sexual maturity may be a consequence of the longer time needed to achieve some critical size necessary for reproduction (Harper, 1977, 687), or of a conservative strategy that promotes individual survival by avoiding the cost of early reproduction (Willson, 1983).

Long lifespans are characteristic of plants in stressful habitats (Grime, 1979). Although longevity data were not included in this study, Group 3 contains the longest-lived pines. It includes the longest-lived organism known (*P. aristata* sens. lat.) as well as other very long-lived species (e.g., *P. flexilis* to 2000 years; Lanner, 1984).

In angiosperms, large seeds are most often explained as an adaptation to some form of stress such as drought or shade (Salisbury, 1942; Baker, 1972, and many others). This same reasoning has been applied to the pines (Strauss and Ledig, 1985). Turner (1985) implied that the large seeds of *P. albicaulis* are an adaptation for mechanical strength of seedlings to the stress of high snow and litter accumulations. In addition to these two abiotic environmental explanations, a large body of literature establishes the association of large-seeded pines with seed dispersal by birds.

Effective dispersal of the large wingless or nearly wingless seeds is mainly by Clark's Nutcrackers and jays. Bird dispersal has been observed in *P. albicaulis* (Tomback, 1981; Lanner, 1982), *P. edulis* (Vander Wall and Balda, 1977; Ligon, 1978), and *P. flexilis* (Lanner and Vander Wall, 1980). The short wing sometimes found on *P. flexilis* is ineffective in aiding wind dispersal (Lanner, 1985). Bird dispersal is also likely for the large wingless seeds of *P. cembroides* and *P. quadrifolia.* Other features associated with bird dispersal include prominent display of cones, indehiscent cones, and thin fracture zones in the cone scales that make scale removal easy (Vander Wall and Balda, 1977; Lanner, 1982). A multistemmed habit often results from simultaneous establishment from seed caches (Tomback, 1981; Linhart and Tomback, 1985).

Birds also eat winged pine seeds of small to moderate size (*P. aristata,* Peattie, 1953; Vander Wall and Balda, 1977; *P. attenuata,* Vogl, 1973; *P. leiophylla,* Wetmore, 1935; *P. palustris,* personal observation; *P. ponderosa* and *P. jeffreyi,* Smith and Balda, 1979; Lanner, Hutchins, and Lanner, 1984), but it is not clear that this activity contributes significantly to effective dispersal and establishment of these species.

Both *P. balfouriana* and *P. aristata* are more likely to be wind-dispersed, having small seeds relative to the wing. However, the frequently multistemmed habit of *P. aristata* suggests a possible dispersal role of birds (Lanner et al., 1984). In other respects, however, *P. balfouriana* and *P. aristata* share many characteristics with the bird-dispersed species.

albicaulis—This species lies close to the central tendency of Group 3.

aristata—In contrast to the usual vertebrate-mediated seed dispersal in this group, *P. aristata* can be dispersed by wind, having smaller seeds and larger wings than most species in this group. In these respects, *P. aristata* and *P. balfouriana* form a distinct subgroup. Apart from the difference in dispersal mode, however, these two species are much like the more northern members of this group (*albicaulis, flexilis*) and the pinyon pines.

balfouriana—See comments under the similar *P. aristata.*

cembroides—*Pinus cembroides* has the shortest stature of species in Group 3. It also differs from this group in having more slender twigs. This species and two other pinyon pines (*monophylla* and *quadrifolia*) occur on the driest sites occupied by North American pines.

edulis—*Pinus edulis* is close to the central tendency of Group 3. Among the pinyon pines it is generally taller, grows on more moist sites, and produces lighter seeds.

flexilis—This species departs from the characteristics of Group 3 in having some features of Group 1: *Pinus flexilis* has larger cones, thicker bark, and smaller seeds than most other Group 3 species. The relatively thick bark is perhaps related to the occurrence of this species on the fire-prone east-slope foothills of the Rocky Mountains.

monophylla—This species is similar to the other pinyon pines, but differs in its longer needle retention.

quadrifolia—This species of warm, arid habitats has less persistent leaves than related species at higher elevations in more northern latitudes. Otherwise it is quite similar to the other bird-dispersed species in this group.

Group 4 (Fire-resilient; attenuata, banksiana, clausa, contorta, contorta *ssp.* latifolia, glabra, leiophylla, pungens, radiata, rigida, serotina, virginiana*):* Group 4 is distinguished by a high degree of cone serotiny, small seed, and precocious reproduction. Mature individuals have a low-to-moderate tolerance of fire, but populations are fire-resilient through abundant seed reproduction and delayed seed release. Populations of these species tend to survive as seeds through infrequent catastrophic fire.

Cone serotiny results in storing many years of seed production, then releasing the seed after fire. However, most (all?) species showing cone serotiny are polymorphic for that trait (*attenuata, muricata, radiata,* and *torreyana,* McMaster and Zedler, 1981; *banksiana,* Rudolph, Libby, and Pauley, 1957; Roe, 1963; Teich, 1970; *clausa,* Little and Dormann, 1952; D. B. Ward, 1963; *contorta* ssp. *latifolia,* Clements, 1910; Lotan, 1975; Perry and Lotan, 1979; Critchfield, 1980; Muir and Lotan, 1985; *rigida,* Ledig and Fryer, 1972; Givnish, 1981). The polymorphism allows establishment on sites not recently burned; e.g., after insects, disease, or avalanche for *P. contorta* (Muir and Lotan, 1985) or on sand dunes for *P. clausa* (W. J. Platt, personal communication, 1986).

The combination of low probability of adult survival with high potential for explosive reproduction is consistent with interpretation of this group as *r*-selected. The small, readily dispersed seeds of this group are typical of pioneer species (Clements, 1905; Gleason, 1910; also *r*-strategists of MacArthur and Wilson, 1967; ruderals of Grime, 1979). Some of these pines are thought to be particularly consistent and prolific seeders (e.g., *P. contorta* ssp. *latifolia*, Fowells, 1965; Lotan, 1975; Smith and Balda, 1979; Critchfield, 1980; and *P. glabra,* W. J. Platt, personal communication, 1986). Published data on variability in seed production are insufficient for a genus-wide verification of this observation.

Several members (*leiophylla, rigida, serotina,* and *virginiana*) of Group 4 have the capacity to resprout vegetatively from the root collar or along the stem (Stone and Stone, 1954), an additional means of persistence through disturbance. The ability to resprout is generally restricted to seedlings and saplings (Stone and Stone, 1954). This may provide a mechanism for improved survival of fire-susceptible species on sites subject to fire-free intervals shorter than required for plentiful seed reproduction.

attenuata—Pinus attenuata and *P. radiata* have larger cones and more massive cone scales than is typical for Group 4. However, as compared to *P. radiata, P. attenuata* is shorter, has more persistent leaves, thinner bark, sharper cone armor, and lower shade tolerance. These Group 3 characteristics suggest more stressful environments than those of *P. radiata* and perhaps less frequent fire in its dry, rocky habitats. This mainly inland species differs from its coastal relatives, *P. radiata* and *P. muricata,* in its tendency to grow in "dry, submarginal forest sites" (Critchfield, 1967). Of the serotinous pines, *P. attenuata* is apparently most consistent in this character (Vogl, 1973; McMaster and Zedler, 1981).

banksiana—Closely related to *P. contorta* and *P. contorta* ssp. *latifolia,* this species has the lightest seeds of the North American pines. Light seeds with a substantial seed wing gives these species good potential for wind dispersal. *Pinus banksiana* differs from most species in Group 4 in having cones that are virtually unarmed. Although *P. banksiana* readily hybridizes with *P. contorta* (Duffield, 1952; Critchfield, 1967), the two have had distinct ecological histories for the tens of thousands of years since their probable divergence in the Pleistocene (Critchfield, 1985), and have several ecological differences (see under *P. contorta* ssp. *latifolia*).

clausa—Pinus clausa lies close to the central tendency of Group 4. In contrast to other pines of the extreme Southeast, *P. clausa* grows well on xeric, deep-sand sites (Brendemuehl, 1981).

contorta ssp. *contorta*—Similar to *P. banksiana* and *P. contorta* ssp. *latifolia, P. c.* ssp. *contorta* has small seeds. It differs from ssp. *latifolia,* however, it its short stature, short and more persistent leaves, generally nonserotinous cones, and its tendency toward wetter habitats (occurring in coastal sphagnum bogs, sand dunes, and barrens as well as moist sites at high elevations along the Sierra Nevada-Cascade axis [Critchfield, 1957]).

contorta ssp. *latifolia*—This taxon is ecologically similar to *P. contorta* ssp. *contorta* and *P. banksiana.* Differences from *P.c.* ssp. *contorta* are given under that taxon. The ssp. *latifolia* differs from *P. banksiana* in its greater height, longer needles, longer leaf persistence, and sharp spines on the cone scales.

glabra—*Pinus glabra* is unusual for Group 4 in having the shade tolerance and slender twigs of Group 2. It is also unusual for Group 4 in its lack of cone serotiny and weakly armed cone scales. In other seed and cone characteristics it is fairly typical of Group 4. The lack of cone serotiny in this species may reflect a high frequency of nonfire disturbance by hurricanes. Age structures tend to consist of discrete age classes corresponding to dates of hurricanes (W. J. Platt, personal communication, 1986).

leiophylla var. *chihuahuana*—Among the North American pines this species has the best-developed ability to sprout from stumps. In contrast to the other species, this sprouting ability is often retained in mature trees (Shaw, 1909; Stone and Stone, 1954). Although seeds may be retained in mature cones for several years (Shaw, 1909), this taxon is apparently not truly serotinous.

pungens—The cones, seeds, and seed wings of *P. pungens* are large for Group 4. The heavily armed cones of this species approach the extremes found in *P. sabiniana, P. coulteri* and *P. torreyana,* but in most other respects, *P. pungens* is similar to Group 4.

radiata—Some similarities of *P. radiata* to *P. attenuata* are given with the latter. *Pinus radiata* is more shade tolerant than *P. attenuata* and most other species in Group 4. The high potential growth rate of *P. radiata* is similar to that found in Group 5.

rigida—In its relatively long needles and thick bark, *P. rigida* has ecological affinities to Group 1. It appears to have compromised between the fire tolerance of Group 2 and the resilience to fire of Group 4. *Pinus rigida* is usually not serotinous, in contrast to its more frequently serotinous relative, *P. serotina,* to the south. Ledig and Fryer (1972) found that the higher level of serotiny on the coastal plain was probably a result of the higher fire frequency in that area, rather than a result of hybridization and gene flow from *P. serotina.* Givnish (1981) found that clinal variation in the cone-type polymorphism was related to clinal variations in the fire regime.

serotina—*Pinus serotina* grows on wetter sites than most species in Group 4. Like *P. rigida,* its leaves are unusually long for this group and it has some resprouting capability. Its occurrence in warm climates and on moist sites allows the extra energetic expenditure in heavier wood, despite the faster growth rate than *P. rigida.* This apparently high net production is more typical of the Southern pines of moist sites in Group 5.

virginiana—*Pinus virginiana* is a typical species of Group 4 except that it lacks serotinous cones and occasionally resprouts vegetatively from young cut stems (Stone and Stone, 1954).

Group 5 (Southern, mesic sites; *echinata, elliottii, muricata, taeda*): Fast growth; strong, heavy wood; mostly long leaves with short persistence; moderately shade tolerant. This group of Southern pines has characteristics of both Groups 1 and 2 (and Group 4 in the case of *P. echinata*). These share with Group 2 short needle retention and growth on mesic sites. However, Group 5 has strong, heavy wood and long needles more characteristic of Group 1.

Outside of Group 5, fast growth and short needle retention appear to trade off with the energetic investment in heavy wood and long needles, respectively. Species in Group 5, however, are apparently able to transcend these trade-offs because of the favorable warm, moist conditions of their habitats. This comparison is particularly clear with Group 2 (*P. strobus* and *P. monticola*), fast-growing mesophytic northern species with relatively short needles and light wood. In the Southeast, *P. elliottii* grows on poorly drained flats, low terraces, and moist hammocks, often in association with *P. echinata* and *P. taeda* (Mirov, 1967; D. B. Ward, 1963).

echinata—*Pinus echinata* is intermediate between Groups 5 and 4 in many respects. Compared with the other species in Group 5, *P. echinata* generally has smaller seeds, cones, and leaves; is less shade tolerant; grows on drier sites and generally more slowly than *elliottii* and *taeda;* has more slender twigs; and has some ability to resprout vegetatively when young.

elliottii—*Pinus elliottii* is exceptional in its strong, heavy wood and fast growth. It also tends to be tolerant of salt spray and saline soils and is often found near the coast (Mirov, 1967). Although fire clearly plays a role in its life history, *P. elliottii* is apparently less fire resilient and less fire tolerant than some associated pine species (*P. clausa* and *P. palustris* respectively; Myers and Deyrup, 1984). Seedlings have a persistent "grass stage" similar to *P. palustris* that apparently confers some fire tolerance (D. B. Ward, 1963).

muricata—The only pine in Group 5 not from the Southeast, *P. muricata* also differs from this group in its unusually thick bark, partial serotiny (McMaster and Zedler, 1981; Millar, 1986), and lighter wood, but shares the strong wood and apparently the potential for fast growth of this group. In contrast to its inland relative in subsection *Oocarpae, P. attenuata,* it occurs in coastal habitats. Its other close relative, *P. radiata,* shares many characteristics with this group, as well as Groups 4 and 5 (Fig. 2). *Pinus muricata* has heavier wood, thicker bark, and lighter seeds than *P. radiata*; otherwise, they are quite similar.

taeda—Pinus taeda is typical of Group 5 except for its lower shade tolerance and weaker wood. It has similarities to Group 1 in features conferring fire resistance (Wade, 1985).

Cone predation—Although most of the ecological characters showed clear patterns among the species groups, cone armor did not. Cone armor would appear to provide defense against such cone predators as birds and squirrels. Although cone predation by birds results in effective seed dispersal in some pines (see under Group 3 above), predation by squirrels is considered less effective in disseminating seeds to sites favorable for germination (Tomback, 1982; Hutchins and Lanner, 1982; Benkman, Balda, and Smith, 1984). A variety of defenses against cone predation by squirrels has been proposed, including asymmetric cone structure and attachment, thick cone scales, cone scales armed with sharp spines, and cone serotiny (Smith, 1970; Elliott, 1974; Linhart, 1978). Of these characters, only cone serotiny and arming of cone scales are included in this study. While cone serotiny affords some defense against predation, its role in the fire ecology of pines confounds its interpretation as a defense against predators. Cone armor appears to be more clearly related to predation alone; indeed, it showed little consistent pattern in relationship to the other characters. However, the distribution of cone armor among the pines is puzzling. The lack of spines on cones of large-seeded species that rely on bird dispersal makes ecological sense, but what of the seemingly defenseless species such as *P. banksiana, P. glabra,* and *P. monticola,* that have small seeds with substantial wings and, in some cases, share habitats with pines having heavily armed cones? Do these species avoid seed predation in some other way or is cone armor a largely ineffective deterrent to predation?

Life history strategies—Ecological divergence in the North American pines fits fairly well into Grime's (1979) triangular summary of plant life history strategies. Groups 1, 2, and 3 represent three kinds of stress-tolerance: Group 1 is tolerant of frequent ground-surface fires and reacts to fire more as a stress than as a disturbance; Group 2 is more tolerant of shade stress than most other pines; and Group 3 is more tolerant of temperature and moisture stress. Group 4, the largest group, falls toward the "ruderal" vertex: its species are relatively short-lived, precocious and abundant reproducers, and generally of low successional persistence. Species in ecological Groups 2 and 5 have features that, relative to other pines, fall toward the "competitive" vertex of Grime's triangle. Yet because the habitats of these species have elements of stress and disturbance, these species do not have an extreme competitive strategy. They are perhaps best placed as "C-S-R strategists" (Grime, 1979, 56), species adapted to habitats where the level of competition is restricted by moderate intensities of both stress and disturbance.

While the pines certainly do not span the whole range of life histories, the apparent trends in the pines are similar to those in all plants. Because the pines are not extreme in their expression of one strategy or another, comparison of the ecological group characteristics of the pines with Grime's table of characteristics of competitive, stress-tolerant, and ruderal plants does not afford a perfect match. Nevertheless, the trends are similar enough that it is reasonable to envision the ecological diversity of pines as occupying a smaller triangle within Grime's triangle.

Perhaps the greatest difficulty with fitting the pines into Grime's system is the juxtaposition of three quite different groups of pines toward the stress-tolerant apex. However, if the pines are placed in the triangle on the basis of production (as Grime advises) rather than by his environmental interpretations of the triangle, these three groups (and therefore the three kinds of stress) would be more widely separated.

Convergent evolution and phylogenetic constraint—High ecological similarity in phylogenetically divergent groups is considered a manifestation of convergent evolution. It is assumed that the taxonomic subdivisions of *Pinus* (Little and Critchfield, 1969) reflect the phylogeny of the genus. Given these two assumptions, a comparison of the taxonomic groups and the ecological groups suggests that convergent evolution has occasionally occurred in the pines (Fig. 4).

Convergence appears to have involved subsections *Strobi, Australes,* and *Oocarpae. Pinus flexilis* and *P. albicaulis* diverged from the other two species in section *Strobus,* toward ecological characteristics more typical of section *Parrya* (ecological Group 3: stress-tolerant and typically bird-dispersed). *Pinus lambertiana* has diverged from the other members of subsection

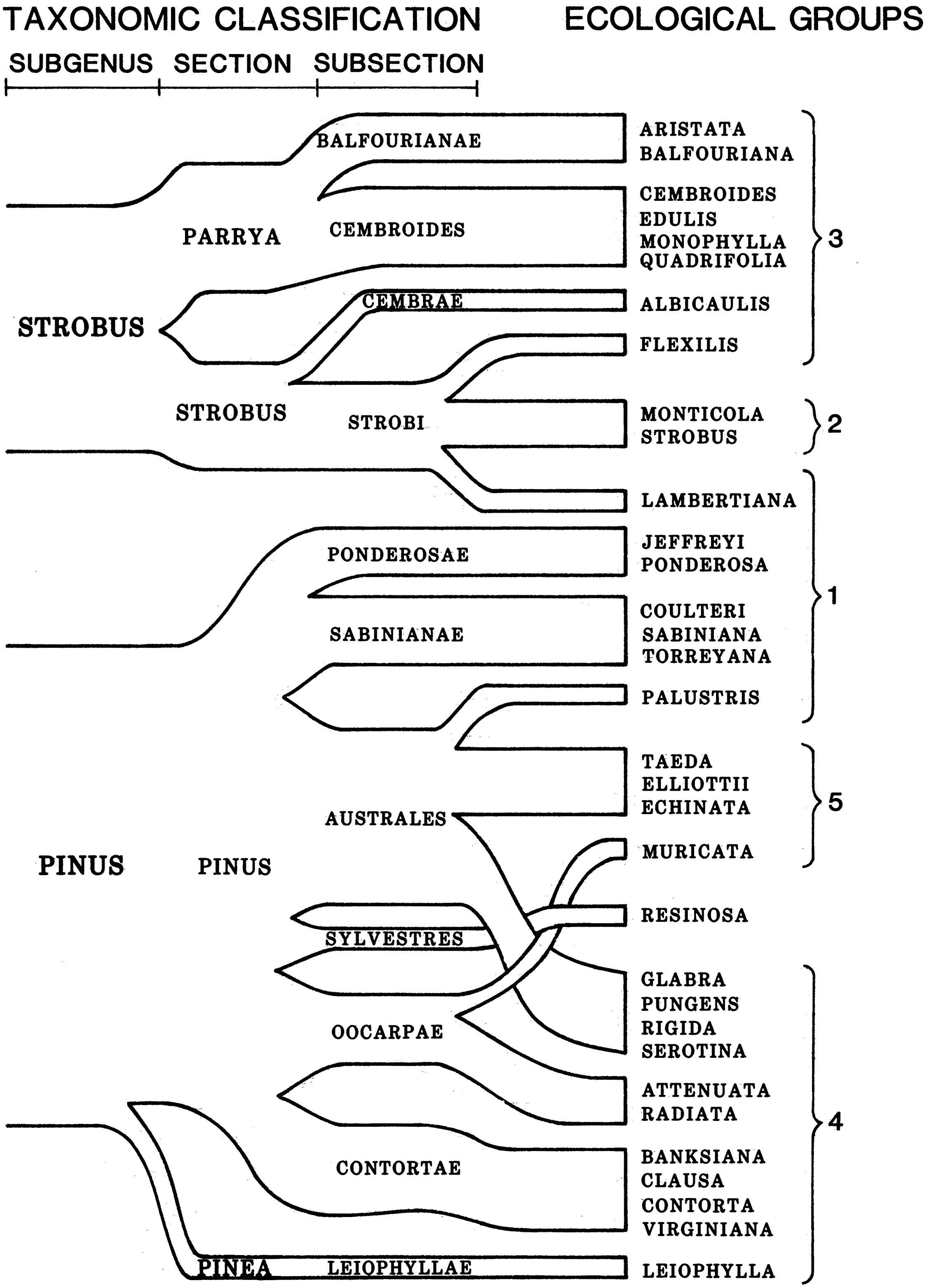

Fig. 4. Comparison of taxonomic subdivisions of *Pinus* (Little and Critchfield, 1969) with ecological groups.

Strobi, toward the fire-tolerant ecological Group 1.

The members of subsection *Australes* have diverged into three of the ecological groups (Fig. 4). Four species (*glabra, pungens, rigida,* and *serotina*) have characteristics of Group 4 (fire resilient). *Pinus palustris* has the fire tolerance of Group 1, typified by *P. ponderosa* and *P. jeffreyi.* The remainder of subsection *Australes* forms the core of ecological Group 5 (Southern mesic sites).

Pinus muricata of subsection *Oocarpae* has diverged ecologically from the other species in this group toward Group 5.

The variability in combinations of ecological characteristics within groups suggests no evidence of a restricted set of optimal combinations of ecological characters toward which North American pines are evolving. In other words, convergent evolution has not produced a set of strict analogs. The analogies are imperfect for at least two reasons. First, the ecological diversity of the pines reflects characters conferred both by shared ancestry (homology) and by similar patterns of adaptation in different evolutionary lines (analogy); that is, two species in the same taxonomic subdivision that have diverged ecologically will still share numerous characteristics by virtue of their shared ancestry. Second, few of the many local environments in North America are closely matched in other areas of the continent.

A logical extension of this work is to search for species analogs on different continents. Expanding the geographic scale should decrease the relative importance of constraint by shared ancestry (assuming that phylogenetic divergence between species was earlier, the more distant the species) while affording an opportunity for more precisely matched climates.

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APPENDIX 1. *Raw data for North American pines, sorted by ecological groups. See Table 1 for explanation of character coding*

	Ecological character																
Species	HEIGHT	LFLGTH	LFPER	COLGTH	CLCONE	ARMED	SEEDL	WINGLG	TWIGS	BARKTH	WOODWT	WOODST	TOLERN	GRATE	SPROUT	MOISTR	SEEDWT	MINAGE
coulteri	45.	9.00	3.5	12.00	0.3	1.5	0.50	1.20	1.50	1.75	0.30	0.25	1.0	1.0	0.0	2.0	336.7	8.
jeffreyi	140.	6.50	7.5	10.00	0.0	1.0	0.45	1.00	1.00	3.00	0.40	0.40	1.0	1.0	0.0	2.0	113.6	8.
lambertiana	187.	3.00	2.5	18.00	0.0	0.0	0.45	1.00	0.50	2.75	0.25	0.40	2.0	2.0	0.0	3.0	216.5	40.
palustris	100.	13.00	2.0	8.00	0.0	1.0	0.50	1.50	1.50	1.10	0.70	0.75	0.0	1.0	0.2	1.0	98.8	20.
ponderosa	165.	5.50	5.0	4.25	0.0	1.0	0.25	1.00	1.00	3.00	0.40	0.40	1.0	1.0	0.0	2.0	37.9	16.
sabiniana	45.	8.50	3.5	8.00	0.3	1.0	0.80	0.38	1.50	1.75	0.25	0.25	0.0	1.0	0.0	1.0	606.0	10.
torreyana	43.	10.00	3.5	5.00	0.3	1.0	0.75	0.40	1.50	1.00	0.25	0.25	1.0	1.0	0.0	2.0	909.0	12.
monticola	135.	3.00	3.5	9.50	0.0	0.0	0.50	1.00	0.00	1.25	0.25	0.40	2.0	2.0	0.0	3.0	16.8	7.
strobus	135.	3.00	2.0	6.00	0.0	0.0	0.50	1.00	0.00	1.25	0.25	0.40	2.0	2.0	0.0	3.0	16.8	5.
albicaulis	32.	2.25	5.5	2.25	0.0	0.8	0.40	0.00	1.00	0.50	0.20	0.50	0.0	1.0	0.0	2.0	126.3	20.
aristata	35.	1.25	13.5	3.25	0.0	0.8	0.30	0.60	1.00	0.62	0.40	0.50	0.0	1.0	0.0	2.0	19.8	20.
balfouriana	35.	1.25	13.5	4.00	0.0	0.5	0.30	1.00	1.00	0.62	0.40	0.40	0.0	1.0	0.0	2.0	26.9	20.
cembroides	17.	1.50	3.5	1.75	0.0	0.0	0.60	0.00	0.40	0.50	0.25	0.40	0.5	1.0	0.0	1.0	413.2	15.
edulis	45.	1.10	6.0	2.00	0.0	0.0	0.55	0.00	1.00	0.62	0.25	0.40	0.5	1.0	0.0	2.0	239.2	25.
flexilis	32.	2.25	5.5	6.50	0.0	0.0	0.40	0.00	1.00	1.50	0.20	0.50	1.0	1.0	0.0	2.0	103.3	20.
monophylla	17.	1.50	8.0	2.00	0.0	0.0	0.60	0.30	0.75	0.75	0.25	0.40	0.5	1.0	0.0	1.0	378.8	20.
quadrifolia	35.	1.40	3.0	2.00	0.0	0.0	0.60	0.10	0.75	0.60	0.25	0.40	0.5	1.0	0.0	1.0	379.0	15.
attenuata	40.	5.00	4.5	4.50	1.0	1.5	0.25	1.25	0.00	0.38	0.25	0.25	1.0	3.0	0.0	1.0	15.7	5.
banksiana	50.	1.10	2.5	1.75	0.9	0.1	0.08	0.33	0.00	0.50	0.25	0.40	0.0	1.0	0.0	1.0	3.5	3.
clausa	60.	2.75	3.5	2.70	1.0	1.0	0.20	0.60	0.00	0.40	0.25	0.40	1.0	2.0	0.0	2.0	6.1	5.
contorta	20.	1.25	5.0	1.38	0.3	0.8	0.17	0.50	1.00	0.87	0.25	0.75	1.0	1.0	0.0	3.0	3.4	4.
glabra	90.	2.50	2.5	1.80	0.0	0.3	0.13	0.60	0.00	0.60	0.25	0.40	3.0	1.0	0.0	3.0	6.3	10.
latifolia	75.	2.00	5.0	1.38	1.0	1.0	0.17	0.50	1.00	0.40	0.25	0.60	1.0	1.0	0.0	2.5	4.5	5.
leiophylla	45.	3.50	4.0	1.75	0.0	0.5	0.13	0.33	0.00	1.25	0.25	0.40	1.0	1.0	1.0	2.0	11.4	28.
pungens	60.	2.00	2.5	3.00	1.0	1.0	0.25	1.00	1.00	0.75	0.25	0.20	1.0	1.0	0.4	2.0	12.6	5.
radiata	70.	5.00	3.0	5.00	1.0	0.0	0.25	0.75	0.00	1.75	0.25	0.25	2.0	3.0	0.0	2.0	28.4	5.
rigida	50.	4.00	2.5	2.50	0.0	1.0	0.25	1.00	1.00	1.20	0.25	0.40	0.5	3.0	1.0	2.0	7.3	3.
serotina	45.	7.00	3.5	2.25	1.0	0.5	0.13	0.75	1.00	0.62	0.75	0.40	0.0	1.0	1.0	4.0	8.4	4.
virginiana	60.	2.25	3.5	2.25	0.0	1.0	0.25	0.30	0.00	0.50	0.25	0.30	1.0	1.5	0.2	2.5	8.6	5.
echinata	90.	4.00	3.0	2.00	0.0	0.9	0.19	0.50	0.00	0.82	0.60	0.70	1.0	3.0	0.5	2.0	9.5	5.
elliotii	90.	10.00	2.0	4.25	0.0	1.0	0.25	1.00	1.00	1.20	0.75	0.75	2.5	3.0	0.0	2.5	31.3	7.
muricata	55.	5.00	2.5	3.00	1.0	1.0	0.25	0.80	1.00	5.00	0.40	0.70	2.0	3.0	0.0	2.5	9.1	5.
taeda	100.	7.50	3.0	4.25	0.0	1.0	0.25	0.75	0.50	1.38	0.60	0.60	1.0	3.0	0.0	2.5	24.7	5.
resinosa	70.	5.00	4.5	1.90	0.0	0.0	0.19	0.67	1.00	1.25	0.40	0.40	1.0	2.0	0.0	2.0	8.7	20.