

QUANTITATIVE ANALYSES OF THE GENETIC STRUCTURE OF CLOSELY RELATED CONIFERS WITH DISPARATE DISTRIBUTIONS AND DEMOGRAPHICS: THE *CUPRESSUS ARIZONICA* (CUPRESSACEAE) COMPLEX¹

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Seedling populations of seven *Cupressus* taxa were compared in common gardens to assess relationships among taxa and to elucidate the genetic structure of three taxa with different distributions and demographics. Discriminant analyses of 15 quantitative traits separated *C. sargentii* and *C. forbesii* from taxa within the *C. arizonica* complex (*C. arizonica*, *C. glabra*, *C. stephensonii*, *C. nevadensis*, and *C. montana*); aligned a population of *C. arizonica* from Sierra de Arteaga, Mexico, with families of the same taxon from southwestern United States; and described a close relationship between *C. nevadensis* and *C. glabra*, but nevertheless separated taxa within the *C. arizonica* complex. Analyses of wind-pollinated progenies of single trees showed the narrow endemic, *C. glabra*, to have a greater degree of population differentiation than the more broadly dispersed *C. arizonica*. In addition, genetic variances within the numerically small populations of *C. arizonica* were about the same as in the much larger populations of *C. glabra*. The results also suggested that genetic variability in *C. stephensonii*, a taxon occurring in a single population, may occur primarily among inbred lines. While the genetic structures of *C. arizonica* and *C. glabra* have counterparts among broadly dispersed conifers, that of *C. stephensonii* appears to be unique. Together, the results support the view that genetic structure primarily reflects the uncertain, chance events that are interspersed throughout evolutionary history.

Key words: Cupressaceae; *Cupressus arizonica*; ecological genetics; genecology; genetic variation; microevolution; systematics.

Allocation of genetic variability within and among populations produces a genetic structure that reflects adaptedness in contemporary environments and adaptability in evolutionary time. While being fundamental to developing sound managerial programs, genetic structure ordinarily is so poorly understood that inferences must be made from the concepts of evolutionary theory (see Mitton, 1995) and from general tendencies suggested by the allozyme literature (Hamrick and Godt, 1989; Hamrick, Godt, and Sherman-Broyles, 1992). Expectations are for (1) wind-pollinated conifers to have the greatest genetic variability, (2) broadly dispersed species to have the greatest variability among populations, and (3) numerically large populations to have the most variability within populations.

A brief survey of recent studies dealing with widespread and restricted congeners (Karron, 1987), Pleistocene refugium endemics (Lewis and Crawford, 1995), partial inbreeders (Charlesworth and Mayer, 1995), rare and scattered populations of an insect-pollinated perennial (Godt and Hamrick, 1993), a self-pollinating cosmopolitan (Wang, Wendel, and Dekker, 1995), an intercontinental weedy invader (Thébaud and Abbott, 1995),

and disjunct populations of conifers (Hamrick, Schnabel, and Wells, 1994) have provided so many exceptions to the expectations that genetic structure seems more a reflection of the contingencies of evolutionary history than ecology, life form, distribution, or breeding system (Karron, 1991; Hamrick, Schnabel, and Wells, 1994).

In the present study, quantitative traits were measured in common gardens on North American representatives of the genus *Cupressus* to (1) assess the relationships among taxa, (2) examine the genetic structure of taxa, and (3) compare genetic structures of taxa in reference to those of other forest tree species. The genus *Cupressus*, composed of wind-pollinated conifers, is part of a Mado-Tertiary geoflora that was widely distributed in the arid lands of western North America during the Pliocene (Axelrod, 1958). The genus currently includes five morphologically similar taxa (Table 1) that have a clouded taxonomy. The five, hereafter referenced collectively as the *C. arizonica* complex, have been considered by Wolf (1948) as separate species and by Little (1966, 1970) as varieties of *C. arizonica*. In addressing the relationships among taxa, the present paper also considers two additional taxa, *C. sargentii* and *C. forbesii*, which provide a basis for interpreting relationships among taxa within the complex. At the outset, this paper accepts the nomenclature of Wolf (1948; Table 1).

Taxa of the *C. arizonica* complex have much different distributions and demographics. Figure 1 shows that *C. arizonica* occurs in small, isolated populations in the southwest United States but also is dispersed throughout the mountains of northern Mexico; *C. glabra* and *C. nevadensis* occur in a small number of isolated populations;

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TABLE 1. Distinguishing characteristics (from Wolf, 1948) of taxa belonging to the *Cupressus arizonica* complex.

Taxon	Bark	Cones	Leaf resin glands
<i>C. arizonica</i>	Fibrous, nonexfoliating	Serotinous	inactive
<i>C. glabra</i>	Smooth, exfoliating	Serotinous	active
<i>C. stephensonii</i>	Smooth, exfoliating	Serotinous	inactive
<i>C. nevadensis</i>	Fibrous, nonexfoliating	Serotinous	active
<i>C. montana</i>	Fibrous, exfoliating	Open	active

and *C. stephensonii* and *C. montana* occur at single localities. Of these taxa, the three whose genetic structure is to be considered in detail, *C. arizonica*, *C. glabra*, and *C. stephensonii*, differ demographically. Although few in number, populations of *C. glabra* tend to occupy large tracts of land (measurable in square kilometres) and contain thousands of individuals. Individuals within the more numerous populations of *C. arizonica*, however, tend to be linearly distributed in canyons and frequently are numbered in the tens or hundreds. And according to a 1978

census (J. L. Reveal, The autecology and status of Cuyamaca cypress, unpublished report held by the Cleveland National Forest, Alpine, CA), the single population of *C. stephensonii* contained < 500 individuals in the breeding population.

MATERIALS AND METHODS

Wind-pollinated cones were collected from 39 trees in eight populations of *C. arizonica*; 21 trees in five populations of *C. glabra*; and nine trees in the population of *C. stephensonii*. A mixture of cones from at least 25 trees was used to represent *C. nevadensis* and *C. forbesii*, while a mix of seeds from ten trees represented *C. montana* and *C. sargentii*. The tests also included a Mexican population of *C. arizonica*, Sierra de Arteaga, which was represented by seeds from only two trees. The location of the populations sampled are shown in Fig. 1. In this paper, the progenies of a single mother tree are referenced as a family, which, without coancestry, would be composed of half-sibs.

Common gardens were established at two field locations and in a shadehouse.

Field tests—To assess genetic differences in growth and development in natural environments, seedlings were grown in plastic containers (65

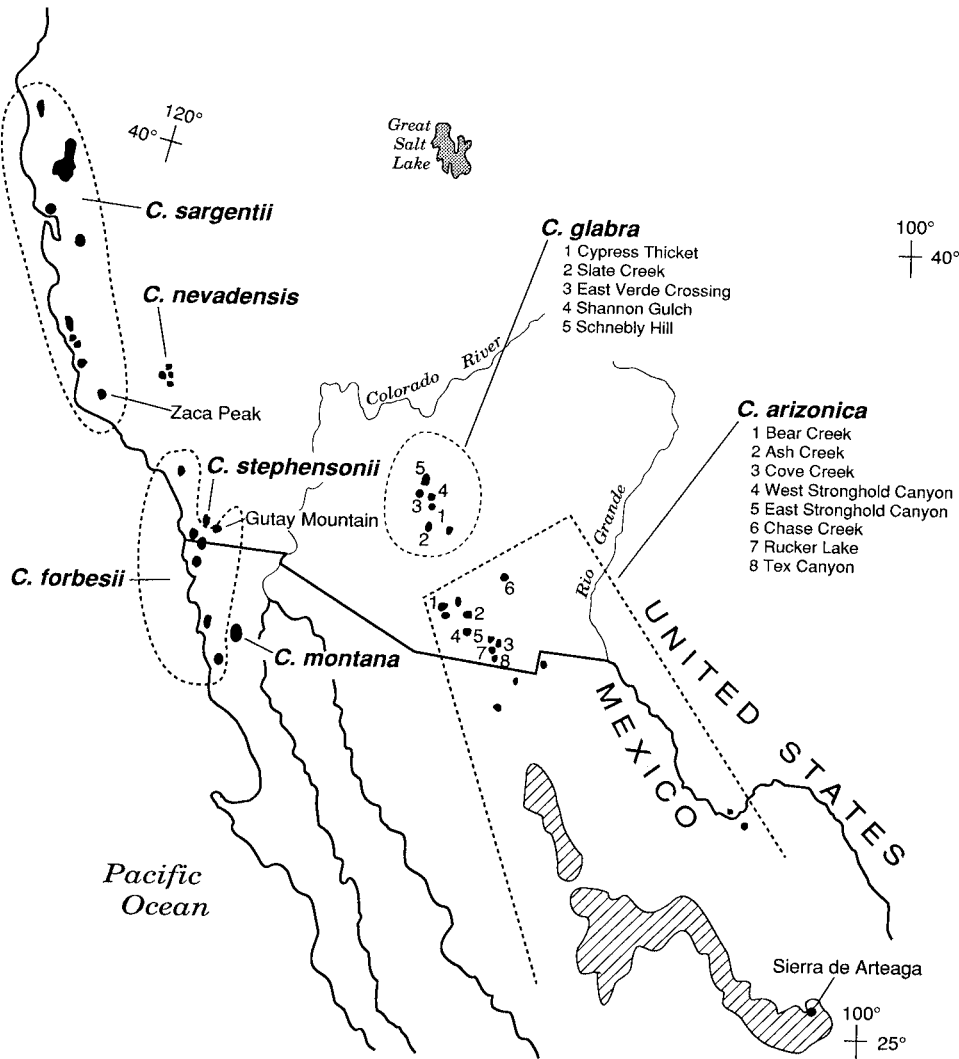


Fig. 1. Geographic distribution of seven *Cupressus* taxa and location of the populations sampled. Hatching represents the general distribution of *C. arizonica* in Mexico.

cm³) in a shadehouse at Moscow, Idaho, (latitude 46.7° N, longitude 117° W, elevation 690 m). First-year seedlings were planted in common gardens near Silver City, New Mexico (latitude 32.75°, longitude 108.25°), and Olympia, Washington (latitude 47.1°, longitude 122.9°). The New Mexico site was at an elevation of 1600 m where the frost-free period averages 120 d. The Olympia site was at an elevation of 100 m where the frost-free period averages 210 d (U. S. Department of Commerce, 1968).

Seven seedlings from each family or taxon were planted in row plots within each of three randomized complete blocks at Silver City and in two blocks at Olympia. Rows were separated by 1 m, while 0.6 m separated seedlings within rows. All sites were tilled and fenced before planting and were irrigated periodically during the first season after planting. After the 1st yr, the sites received only natural precipitation, ≈ 2 m at Olympia and 0.5 m at Silver City. Both sites were weeded periodically for two growing seasons. Testing was completed after the trees reached age 3.

Because environmental effects at the planting sites differentially affected growth and development, a different set and number of variables were measured at each site. At Silver City, severe winters associated with the high elevation coupled with low amounts of precipitation to influence growth and survival after the second growing season. This site provided the following variables: (1) 2nd-yr height (cm), a measure of growth potential before environmental effects became severe, (2) survival after the second winter, a measure of tolerance to the environmental stresses, and (3) stress response, 3rd-yr height adjusted by regression on 2nd-yr height after all trees that had died during the second winter had been given a 3rd-yr height of zero. This variable thus indexes cumulative environmental effects on growth and development, while taking into account the autocorrelation of successive height increments of trees.

The mild environmental conditions at Olympia yielded the following variables: (1) 3rd-yr height, a measure of growth potential under optimal conditions, (2) adjusted height, 3rd-yr height adjusted by regression on 2nd-yr height, a measure of the relative adaptedness of trees to the Olympia site during year 3, while taking into account autocorrelation of successive height increments, (3) crown shape index, the ratio of 3rd-yr height to crown width (the higher the ratio, the more narrow the shape of the crown), and (4) appressed branching index, the ratio of branch length to one-half the crown width (the higher the ratio, the more appressed the branching).

Shadehouse tests—Studies of genetic variation in shoot elongation, foliage color, and tolerance to freezing were carried out in a shadehouse at Moscow, Idaho. Seedlings were grown in plastic containers (740 cm³) in an experimental design that consisted of nine seedlings growing in row plots in each of two blocks. The containers were arranged in trays that held three plots of nine trees. Seedlings were grown for 6 mo in the shadehouse and were transferred to a greenhouse for the winter months where temperatures were maintained above -2° C. In early April of the second growing season, the trees were returned to the shadehouse where shoot elongation was measured 14 times at intervals of ≈ 15 d from 1 May until 5 October.

The periodic measurements allowed shoot elongation of individual trees to be modeled with a modified logistic function (Rehfeldt and Wykoff, 1981):

$$Y = [1 + be^{-rX + (c/X)}]^{-1}$$

where Y is the proportion of total increment attained by day X ; b , r , and c are regression coefficients; and e is the base of the natural logarithm. Regression statistics produced by this function allowed the initiation of shoot elongation to be defined as the day on which 2 cm of elongation had occurred, and cessation of elongation as the day on which all but 2 cm of elongation had occurred. Rate of shoot elongation was defined as the amount of elongation per day over the 40 d from 9 August to 18 September when trees of all taxa were elongating at max-

imal rates. The measurements thus provided five variables for describing shoot elongation: the amount, initiation, cessation, duration, and rate of elongation.

Foliage color was measured on each seedling after the second growing season according to the L*a*b* color space of a Minolta colorimeter. This procedure measures color according to three indices: L* measures lightness, with high values having the lightest tones; a* measures color along a red-green axis, with positive values coding red, while negative values code green; and b* measures color on a yellow-blue axis, with positive values coding yellow and negative values coding blue.

Freezing tests were conducted in late November of the second growing season on seedlings that acclimated in the Moscow shadehouse. Twigs 5 cm long were cut from the current year's growth, moistened, packaged in plastic bags, and frozen at a rate not exceeding 5°C/h to predetermined test temperatures. After freezing, the twigs were warmed at a rate not exceeding 5°C/h. The plastic bags were then placed on a laboratory bench for at least 3 d, and after air-drying, each twig was scored visually (values of zero or one) for injury as indicated by discolored and flaccid tissues. The tests were conducted in three stages: the first tested variation among taxa; the second, variation within *C. arizonica*; and the third, variation within *C. glabra*. Variation among families of *C. stephensonii* was not tested.

In the first stage, a subsample of the available trees was used to estimate the hardiness of each taxon at 12 temperatures ranging from -15°C to -26°C. For taxa not represented by individual families, a twig from each of the nine trees per plot was removed, and these were packaged together. For taxa represented by families, a twig from one tree in each of nine different families was packaged together for each block; a different combination of families was sampled for each test temperature. For each temperature, therefore, a taxon was represented by one nine-tree sample for each of two blocks.

For tests of variation among families within *C. arizonica* and *C. glabra*, the nine seedlings from each plot were packaged together according to block. The tests, therefore, contained one nine-tree sample of each family for each of two blocks for each freezing treatment. Variation within *C. arizonica* was tested at eight temperatures between -18°C and -25°C, while that for *C. glabra* was tested at eight temperatures between -16°C and -25°C.

Statistical analyses—The tests described above provided 16 variables for assessing genetic variation.

Analyses of variance for testing differentiation of taxa used the following model for all variables except freezing injury:

$$Y_{ijkl} = \mu + B_i + S_j + BS_{ij} + e_{ijkl},$$

where Y is the performance of an individual, μ is the mean, B is the effects of blocks; S is the effects of taxa; BS is the interaction of blocks and taxa, an experimental error; and e is the residual. All variates were assumed to be random.

Analyses of freezing injury of taxa used the model:

$$Y_{ijkl} = \mu + B_i + T_j + S_k + TS_{jk} + BT_{ij} + BS_{ik} + BTS_{ijk} + e_{ijkl},$$

where, in addition to the symbols defined above, T is the effect of temperatures. Temperature was assumed to be a fixed variate, and all others were random. All effects involving the interaction of blocks were summed together into an experimental error.

Analyses of genetic variation in *C. arizonica* and *C. glabra* used the following model for all variables except freezing injury:

$$Y_{ijkl} = \mu + B_i + P_j + M_{k(j)} + BP_{ij} + BPM_{ik(j)} + e_{ijkl},$$

where, in addition to the symbols defined above, P represents the effects of populations and M the effects of maternal families within populations. The two effects involving block interactions were bulked into an experimental error. All effects were assumed to be random.

Analyses of genetic variation in freezing injury for families of *C. arizonica* and *C. glabra* followed the model:

$$Y_{ijklm} = \mu + B_i + T_j + P_k + M_{j(k)} + TP_{jk} + TM_{j(k)} + BT_{ij} + BP_{ik} \\ + BM_{j(k)} + BTP_{ijk} + BTM_{j(k)} + e_{ijklm},$$

the symbols for which are defined above. The five terms involving the interaction of blocks were combined into an experimental error. All effects except temperatures were assumed to be random.

Results of analyses of variance are presented as intraclass correlations, calculated as the ratio of components of variance for either taxa, populations, or families within populations to the total phenotypic variance. The latter term was defined as the sum of variance components for effects of taxa, populations, and families; the experimental error; and the residual variance.

Relationships among taxa were assessed with canonical discriminant analyses that used all variables except freezing injury. The analyses used family means for *C. arizonica*, *C. glabra*, and *C. stephensonii*; the population mean for the Sierra de Arteaga population of *C. arizonica*; and taxon means for *C. nevadensis*, *C. montana*, *C. forbesii*, and *C. sargentii*. Data on freezing injury were not used because taxa, families of *C. arizonica*, and families *C. glabra* were tested at different temperatures.

Genetic variation within *C. arizonica* and *C. glabra* was related to environmental gradients by regressing family means on the elevation of the mother tree. These regressions tested both the first and second powers of elevation as independent variables.

All analyses used software of SAS (1985).

RESULTS

The results consider variation among taxa and variation within *C. arizonica*, *C. glabra*, and *C. stephensonii*.

Variation among taxa—Significant effects of taxa were detected for all variables except adjusted height measured at Olympia (Table 2). Intraclass correlations were as high as 0.73, averaged 0.36, and thus described pronounced differentiation of taxa. The lack of differences among taxa for adjusted height merely suggested a continuation throughout year 3 of the genetic differences in growth potential that had been expressed by year 2.

Outstanding among the array of mean values were: (1) the high growth potentials of *C. sargentii* and the Sierra de Arteaga population of *C. arizonica*, and the low growth potentials of *C. stephensonii* and *C. montana*; (2) the early initiation of shoot elongation of *C. forbesii* and the late initiation for *C. montana*; (3) the late cessation of elongation for *C. sargentii*; (4) the short duration of elongation of *C. montana* and the long durations for *C. forbesii* and *C. sargentii*; (5) the slow rate of elongation of *C. stephensonii*; (6) the high injuries from freezing for *C. sargentii*, *C. forbesii*, and *C. nevadensis*; (7) the low survival and large responses to stress (negative residuals) of *C. sargentii* and *C. forbesii* at Silver City; (8) the appressed branching of *C. montana* and *C. sargentii*, and the strongly horizontal branching of *C. arizonica*; (9) the strongly columnar shapes of *C. sargentii* and *C. nevadensis* and the broadly spreading shape of *C. stephensonii*; and (10) the bright green foliage (high L* and high b*) of *C. sargentii* and the silver-blue (high L* and low b*) foliage of the Sierra de Arteaga population of *C. arizonica*.

By describing for *C. sargentii* and *C. forbesii* a high

TABLE 2. Mean values, variance components, phenotypic variances, and intraclass correlations of *Cupressus* taxa.

Variable	Mean	σ^2_{TX}	σ^2_{PH}	r_T
Shadehouse test				
2-yr elongation	433.8 mm	4 579.5‡	7 959.2	0.58
Initiation	44.9 d	103.36‡	157.34	0.66
Cessation	191.2 d	161.44‡	296.42	0.54
Duration	146.3 d	521.85‡	715.97	0.73
Rate	2.8 mm/d	0.30†	0.68	0.44
Color L*	45.6	10.44‡	20.43	0.51
Color a*	14.4	0.52‡	2.16	0.24
Color b*	21.1	9.44‡	20.96	0.45
Freezing injury	54.1%	0.06‡	0.217	0.27
Olympia test				
3-yr height	100.1 cm	101.4‡	525.2	0.19
Adjusted height	100.1 cm	2.38	207.8	0.01
Shape index	2.07	0.04†	0.272	0.14
Appressed index	1.61	0.11‡	0.274	0.38
Silver City test				
2-yr height	51.7 cm	50.3‡	273.1	0.18
Stress response	61.7 cm	92.28‡	624.6	0.14
Survival	88.4%	0.02‡	0.109	0.19

† Significance of *F* value at $0.05 \leq P \leq 0.01$.

‡ Significance of *F* value at $P \leq 0.01$.

Note: σ^2_{TX} is the variance component for the effects of taxa; σ^2_{PH} is the total phenotypic variance; and r_T is the intraclass correlation for the effects of taxa. Indices are without units.

growth potential, late cessation of shoot elongation, low freezing tolerance, poor survival, and large stress response, these results demonstrate the adaptation of these two taxa to milder climates than those in which taxa of the *C. arizonica* complex occur.

Large mean differences among taxa enabled the canonical discriminant function to readily separate the taxa (Fig. 2). Of the seven canonical vectors, the first four accounted for 95% (43, 33, 15, and 4%, respectively) of the variance among taxa. The last three vectors individually accounted for <2%, did not contribute to understanding the interrelationships among taxa, and hereafter are ignored.

Ordination of mean values (Fig. 2, left) for vectors 1 and 2 disassociated *C. forbesii* and *C. sargentii* from taxa of the *C. arizonica* complex; separated the families of *C. arizonica*, *C. glabra*, and *C. stephensonii* into discrete groups; aligned the Sierra de Arteaga population of *C. arizonica* on the periphery of the families of the same taxon from southwestern U.S.; associated *C. nevadensis* with the families of *C. glabra*; and associated *C. montana* with the families of *C. stephensonii*.

Ordination of taxa for vectors 3 and 4 (Fig. 2, right) provided further separation of *C. forbesii* and *C. sargentii* from each other and from taxa in the *C. arizonica* complex; separated *C. montana* from the families of *C. stephensonii*; and suggested a relationship between *C. glabra* and *C. nevadensis* that was only slightly more distant than that involving the Sierra de Arteaga population of *C. arizonica* and southwestern U.S. families of the same taxon.

It is possible that the separation of *C. nevadensis* from *C. glabra* would have been enhanced if data on freezing injury could have been included in the canonical analyses. Mean injuries for *C. nevadensis* averaged 74%, while

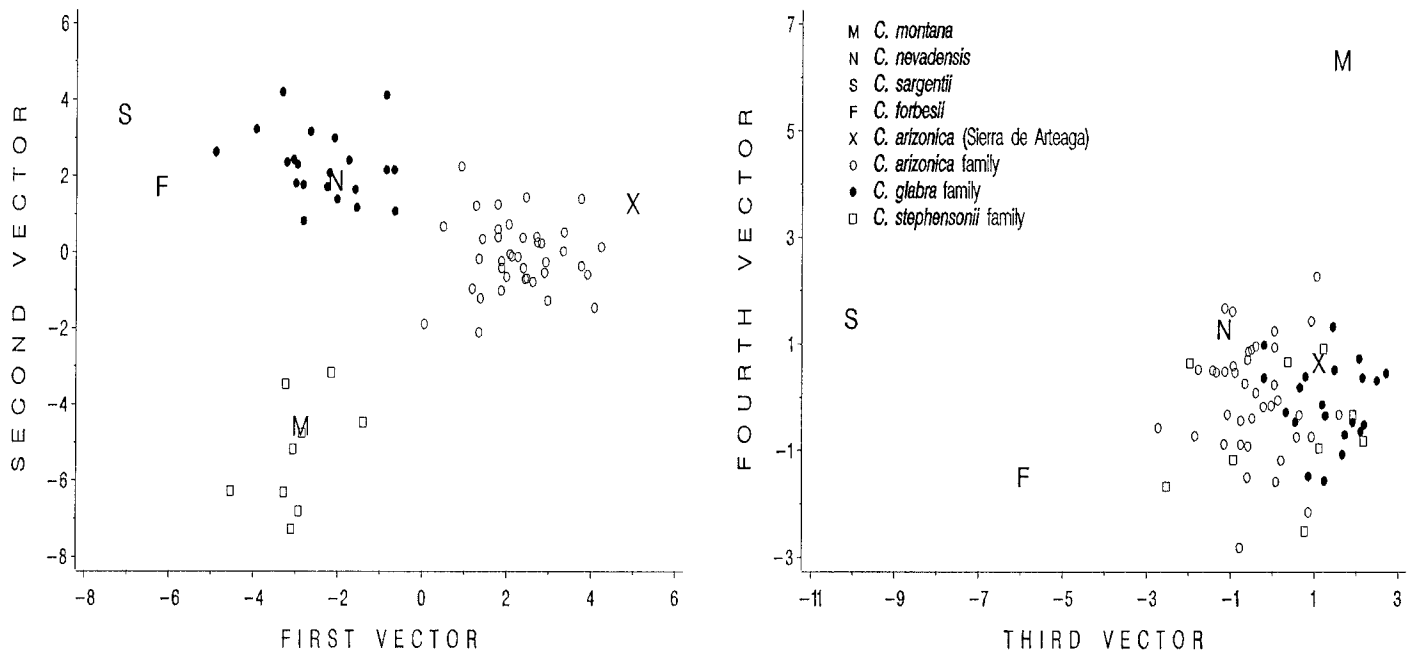


Fig. 2. Ordination of *Cupressus* taxa according to the first four vectors from a canonical discriminant function.

that for *C. glabra* was 34%. A range of family means for *C. glabra* of 51% quite likely would not have included the mean of *C. nevadensis*.

Variation within *C. arizonica*—Genetic variation was detected for 11 of the 16 variables analyzed (Table 3), but population effects were significant for only the appressed branching index, the crown shape index, and the cessation and duration of shoot elongation. Although accounting for $\approx 10\%$ of the phenotypic variance for these

four variables, population effects on the average accounted for only 3% of the phenotypic variance for all variables analyzed.

Most of the differences among populations involved the Tex Canyon population from the Chiricahua Mountains (Fig. 1). Trees from this area had the most columnar crown shape, most appressed branching, and a duration of shoot elongation that averaged 5 d longer than that of any other population. Tex Canyon, however, was represented by only two families, and it is uncertain whether

TABLE 3. Mean values, variance components, phenotypic variances, and intraclass correlations for families and populations of *Cupressus arizonica*.

Variable	Mean	σ^2_p	σ^2_F	σ^2_{PH}	r_p	r_F
Shadehouse test						
2-yr elongation	438.5 mm	-82.9	777.3 \ddagger	3553.4	0.00	0.22
Initiation	47.3 d	0.9	3.0 \ddagger	33.9	0.03	0.09
Cessation	187.4 d	6.8 \ddagger	4.3	91.2	0.08	0.05
Duration	140.1 d	10.3 \ddagger	-1.3	127.7	0.08	0.00
Rate	2.9 mm/d	-0.02	0.06 \ddagger	0.41	0.00	0.15
Color L*	46.1	0.22	0.25	10.2	0.02	0.02
Color a*	14.2	0.00	0.15 \ddagger	1.3	0.00	0.12
Color b*	20.4	0.16	2.3 \ddagger	11.2	0.01	0.21
Freezing injury	34.2%	-0.00	0.02 \ddagger	0.21	0.00	0.11
Olympia test						
3-yr height	99.3 cm	-0.7	60.1 \ddagger	428.6	0.00	0.14
Adjusted height	99.3 cm	1.2	10.3	205.6	0.01	0.05
Shape index	2.00	0.03 \ddagger	0.02	0.21	0.13	0.09
Appressed index	1.37	0.01 \ddagger	0.01 \ddagger	0.12	0.11	0.10
Silver City test						
2-yr height	50.5 cm	4.5	7.9	259.0	0.02	0.03
Stress response	65.1 cm	21.1	-4.5	428.9	0.04	0.00
Survival	91.6%	0.001	0.00	0.08	0.02	0.03

\ddagger Significance of F value at $0.05 \leq P \leq 0.01$.

\ddagger Significance of F value at $P \leq 0.01$.

Note: σ^2_p and σ^2_F are the variance components for the effects of populations and families, respectively; σ^2_{PH} is the total phenotypic variance; r_p and r_F are the intraclass correlations for populations and families, respectively. Indices are without units.

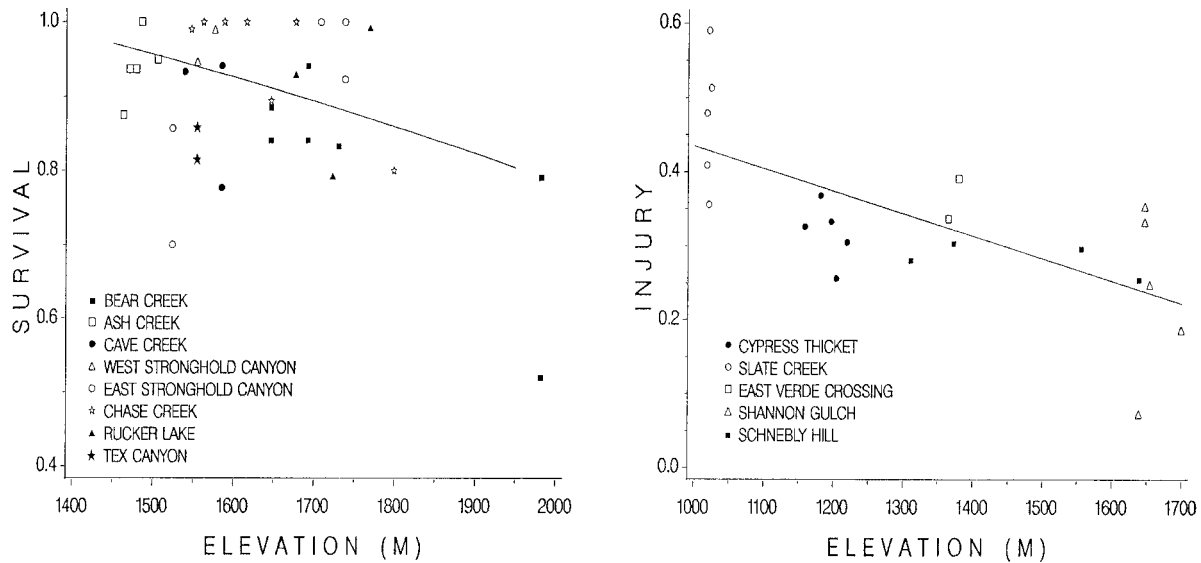


Fig. 3. Regression lines describing the relationship of the average proportion of trees surviving for *C. arizonica* families at Silver City (left) and average proportion of trees injured from freezing of *C. glabra* families (right) with the elevation of the mother tree. Family means are plotted according to population.

the performance of these families reflected the population as a whole or effects of sampling.

Genetic variance among families within populations was detected for eight variables, and for these eight, intraclass correlations averaged 0.14. Family effects were particularly strong for the amount of 2-yr shoot elongation, 3-yr height, the rate of shoot elongation and the relative amounts of either yellow or blue in the foliage (color index b*). For all variables analyzed, intraclass correlations averaged 0.09.

The regression of family means on the elevation of the mother tree produced four relationships that were statis-

tically significant ($P < 0.05$). These four described slightly negative associations of elevation with the color index b*, the appressed branching and crown shape indices, and survival at Silver City. The best-fitting of these relationships ($R^2 = 0.16$) involved survival (Fig. 3, left); statistical significance of the relationship, however, obviously was dependent on the family from a high elevation at Bear Creek that had the lowest survival.

Variation within *C. glabra*—Genetic variation was detected for ten of the 16 variables analyzed (Table 4). Population effects were significant for only four of the vari-

TABLE 4. Mean values, variance components, phenotypic variances and intraclass correlations for families and populations of *Cupressus glabra*.

Variable	Mean	σ^2_P	σ^2_F	σ^2_{PH}	r_P	r_F
Shadehouse test						
2-yr elongation	443.9 mm	-21.9	314.1	3 128.7	0.00	0.10
Initiation	39.5 d	-1.4	11.4‡	47.1	0.00	0.24
Cessation	197.7 d	1.9	18.6‡	131.0	0.01	0.14
Duration	158.6 d	1.3	46.4‡	201.3	0.01	0.23
Rate	2.7 mm/d	0.01	-0.01	0.34	0.04	0.00
Color L*	46.2	0.05	-0.11	10.1	0.00	0.00
Color a*	14.8	0.03	0.09	1.21	0.02	0.07
Color b*	22.4	-0.10	2.3‡	12.1	0.00	0.19
Freezing injury	33.5%	0.025‡	0.004‡	0.18	0.14	0.02
Olympia test						
3-yr height	107.2 cm	-20.2	133.8‡	474.8	0.00	0.28
Adjusted height	107.2 cm	-9.6	34.8‡	233.7	0.00	0.15
Shape index	2.20	-0.01	0.01	0.24	0.00	0.04
Appressed index	1.92	0.01	-0.00	0.22	0.02	0.00
Silver City test						
2-yr height	57.7 cm	15.7†	15.8	228.8	0.07	0.07
Stress response	66.9 cm	311.3‡	-13.1	799.2	0.39	0.00
Survival	88.5%	0.04‡	0.00	0.11	0.32	0.00

† Significance of *F* value at $0.05 \leq P \leq 0.01$.

‡ Significance of *F* value at $P \leq 0.01$.

Note: σ^2_P and σ^2_F are the variance components for the effects of populations and families, respectively; σ^2_{PH} is the total phenotypic variance; r_P and r_F are the intraclass correlations for populations and families, respectively. Indices are without units.

ables but were particularly strong for freezing injury, the response to stress, and survival at Silver City. Intraclass correlations for these variables averaged 0.25, but for all variables the same statistic averaged 0.07.

Mean values showed that nearly all of the genetic differences among populations could be ascribed to the performance of families from Slate Creek (Fig. 1). Survival for the five families from this population ranged from 45 to 77% and averaged 56%; the lowest mean survival of any other family was 86%. Likewise, the response to stress for this population was indexed by a value of -32 cm (3-yr height was 32 cm less than would be expected according to 2-yr height), while that for other populations was ≈ 6 cm. This same population had a freezing injury (47%) that was 11% greater than that of any other population.

Genetic variation among families within populations was detected for seven variables, and for these seven, intraclass correlations averaged 0.18. Family effects were particularly strong for 3-yr height and the initiation and duration of shoot elongation. For all variables, intraclass correlations averaged 0.10.

The regression of family means on the elevation of the mother tree produced five statistically significant ($P < 0.05$) relationships. As elevation increased, the amount of freezing injury decreased ($R^2 = 0.49$); the response to stress lessened ($R^2 = 0.64$); survival at Silver City increased ($R^2 = 0.52$); and the duration of shoot elongation became shorter ($R^2 = 0.18$), largely because the cessation became earlier ($R^2 = 0.18$). Family means for freezing tolerance, the response to stress, and survival were interrelated with simple correlations > 0.7 .

Figure 3 (right) illustrates the relationship between freezing injury and the elevation of the mother tree. This relationship is driven by (1) high injury to trees from Slate Creek, the population from the lowest elevation and (2) low injury to trees from Shannon Gulch, which was from the highest elevation. The slope of the regression line predicts that injury increases by $\approx 3\%$ as the elevation of the mother tree increases by 100 m.

Variation within *C. stephensonii*—Genetic variation among families was detected for eight of the 15 variables analyzed (Table 5). Intraclass correlations showed that family effects accounted for as much as 38% of the total variance, while averaging 0.28 for the significant variables and 0.17 for all variables. These intraclass correlations are nearly twice as large as those estimated among families of *C. arizonica* and *C. glabra*.

Among the significant family effects, those for measures of growth potential, survival at Silver City, and the response to stress were the most pronounced (Table 5). One family was the shortest at both Olympia (66 cm) and Silver City (31 cm), had the lowest survival (39%, as compared to a taxon mean of 85%) at Silver City, and had a large response to stress (-22 cm). Another family exhibited the greatest growth potential (107 cm in 3rd-yr height at Olympia; 53 cm in 2nd-yr height at Silver City) but also had the largest response to stress (-25 cm) and a relatively low survival (76%) at Silver City.

The large family effects detected for the index to crown shape resulted from the progenies of one family that exhibited a low growth potential, forking at the

TABLE 5. Mean values, variance components, phenotypic variances, and intraclass correlations for families of *Cupressus stephensonii*.

Variable	Mean	σ^2_F	σ^2_{PH}	r_F
Shadehouse test				
2-yr elongation	365.5 mm	680.8†	3 002.9	0.23
Initiation	49.1 d	7.5†	41.2	0.18
Cessation	189.6 d	-11.3	186.9	0.00
Duration	140.5 d	2.0	236.0	0.01
Rate	2.3 mm/d	-0.01	0.36	0.00
Color L*	43.2	1.09	0.32	0.12
Color a*	14.0	0.13	9.1	0.06
Color b*	21.2	0.75	2.3	0.07
Freezing injury	—	—	—	—
Olympia test				
3-yr height	84.0 cm	141.4‡	372.3	0.38
Adjusted height	84.0 cm	31.6†	167.4	0.19
Shape index	1.80	0.05†	0.20	0.26
Appressed index	1.72	0.02	0.17	0.12
Silver City test				
2-yr height	42.8 cm	42.4‡	134.1	0.32
Stress response	42.8 cm	90.5‡	402.4	0.22
Survival	85.3%	0.05‡	0.13	0.37

† Significance of F value at $0.05 \leq P \leq 0.01$.

‡ Significance of F value at $P \leq 0.01$.

Note: σ^2_F is the variance component for the effects of families; σ^2_{PH} is the total phenotypic variance; and r_F is the intraclass correlation for families. Indices are without units.

ground surface, and an asymmetric, two-dimensional crown. This unusual phenotype was apparent in all seedlings of the family, regardless of test site.

DISCUSSION

Genetic variation was detected among taxa for 15 of the 16 variables measured, and large intraclass correlations for many of these variables suggested that differentiation was pronounced. Mean values involving growth potential and cold hardiness were readily interpreted as reflecting (1) the adaptation of *C. forbesii* and *C. sargentii* to the mild climates along the Pacific Coast and (2) the adaptation of taxa in the *C. arizonica* complex to harsher montane environments. As a result, canonical discriminant functions readily separated *C. forbesii* and *C. sargentii* from each other and from taxa of the *C. arizonica* complex. The same functions described a relationship between *C. nevadensis* and *C. glabra* that was only slightly more distant than that involving the Sierra de Arteaga population and southwestern U.S. families of *C. arizonica*, but otherwise readily separated taxa within the *C. arizonica* complex.

If one accepts Mallet's (1995) argument, species can be defined in a Darwinian sense as morphologically distinguishable groups of individuals, particularly when genetic analyses demonstrate the clustering of genotypes. While the work of Wolf (1948) provides the morphological foundation, the present results readily clustered genotypes into divergent groups. The proximal association of *C. nevadensis* and *C. glabra* notwithstanding, these results thus support the nomenclature of Wolf (1948) who described the five taxa within the *C. arizonica* complex as individual species.

Genetic structure of *Cupressus taxa*—The analyses readily detected genetic variability in *C. arizonica*, *C. glabra*, and *C. stephensonii*. However, the genetic structure of these taxa differed greatly.

Genetic variability among populations was more than twice as strong in the narrowly distributed *C. glabra* as in the more widely distributed *C. arizonica*. To be sure, the low estimates of population effects for *C. arizonica* could reflect the sampling of only a portion of the geographic distribution of the taxon (Fig. 1). However, had the Sierra de Arteaga population been included in the analysis of *C. arizonica* families, differences among populations would have been detected for only one additional variable (2nd-yr height at Silver City), and the mean intraclass correlation for population effects would have been increased to only 0.04. By comparison, 7% of the phenotypic variance in *C. glabra* was attributed to population effects.

Furthermore, relationships between family mean performance and elevation of the mother tree (Fig. 2) suggested that population differentiation in *C. arizonica* is random, while that for *C. glabra* is fitness related. In *C. glabra*, the relationships of elevation with freezing injury, survival, and response to stress not only were strong but also implied that trees from high elevations are best able to withstand severe winters. But in *C. arizonica*, a statistically significant relationship between survival and elevation had no practical meaning: significance was driven by a single data point, and the relationship was incomprehensibly negative.

Because survival of *C. arizonica* families at Silver City averaged 91.6%, one might argue that the failure to detect a cline in *C. arizonica* resulted from environmental effects that were not sufficiently severe to force expression of adaptive responses. Accepting this argument would require reconciling in *C. arizonica* the lack of correlation between fitness-related traits (e.g., freezing injury, response to stress, and survival) and elevation that were observed in *C. glabra*. For example, freezing injury averaged $\approx 33\%$ in both taxa, but the correlation of family means for injury and elevation produced a nonsignificant R^2 of 0.03 for *C. arizonica* and a significant ($P < 0.01$) value for *C. glabra* of 0.52. In *C. glabra*, the simple correlation of family means for freezing injury and survival was $r = -0.73$, while in *C. arizonica* it was $r = 0.09$.

Genetic variability within populations was abundant for all three taxa. Variances within populations were about the same for *C. arizonica* and *C. glabra*, with intraclass correlations attributing an average of $\approx 10\%$ of the phenotypic variance to family effects. As judged by the same statistic, however, the amount of genetic variation within the single population of *C. stephensonii* was nearly twice as large as that estimated for the other taxa.

The results thus demonstrate that three closely related *Cupressus* taxa exhibit high levels of genetic variability but much different genetic structures. In *C. glabra*, genetic variances among populations are high as are variances among families within populations. *C. arizonica*, however, exhibits little genetic variability among populations but abundant variability within populations. And in the single extant population of *C. stephensonii*, genetic

TABLE 6. Average intraclass correlations for the effects of populations and families within populations for fitness-related traits of nine species.

Species	Intraclass correlation		Reference
	Population effects	Family effects	
<i>Cupressus arizonica</i>	0.03	0.09	Present study
<i>C. glabra</i>	0.07	0.10	Present study
<i>C. stephensonii</i>	—	0.17	Present study
<i>Pinus contorta</i>	0.26	0.04	Rehfeldt, 1985
<i>Larix occidentalis</i>	0.20	0.08	Rehfeldt, 1992a
<i>Pseudotsuga menziesii</i>	0.11	0.07	Rehfeldt, 1978
<i>Pinus ponderosa</i>	0.07	0.11	Rehfeldt, 1992b
<i>Thuja plicata</i>	0.04	0.09	Rehfeldt, 1994
<i>Pinus monticola</i>	0.01	0.09	Rehfeldt, 1979b

variances among families within populations seems to be extremely high.

***Cupressus taxa* vs. broadly dispersed conifers**—Intraclass correlations allow for the comparison (Table 6) of the genetic structures of several wind-pollinated, coniferous species. All studies cited (1) provided estimates of genetic variances among and within populations, (2) were conducted in common gardens that used similar experimental procedures, and (3) tested similar quantitative variables. While the *Cupressus* taxa have limited geographic distributions, the other tabulated species have continuous distributions across large geographic distances (see Little, 1971). Although the studies cited differed in the geographic and ecological separation of the populations sampled, Table 6 nonetheless provides for a general comparison of the genetic structures of taxa that have much different distributions.

In broadly distributed species, the proportion of the phenotypic variance attributable to variation among populations varies widely: from almost none in *Pinus monticola* to 26% in *Pinus contorta*. The narrowly distributed *C. glabra*, however, exhibited population variance that not only was similar to that of *Pinus ponderosa* but approached the average of all species tabulated. *Cupressus arizonica*, however, like *Thuja plicata* and *Pinus monticola*, exhibited a level of population differentiation that was difficult to detect.

Species in which population differentiation is pronounced (Table 6) invariably demonstrate clinal responses in association with the elevation of the seed source. It is consistent, therefore, for such clines in *C. glabra* to be strong, while those in *C. arizonica* are weak. Previous works (see Rehfeldt, 1979a) dealing with clines in genetic variation along environmental gradients have used for comparative interpretations a statistic describing the distance in elevation that must separate two means such that the difference between those means equals the least significant difference ($P = 0.2$). For *C. glabra*, this interval was ≈ 550 m (for the response to stress) while that for *C. arizonica* (survival) was ≈ 1200 m, an interval that exceeds the altitudinal distribution of the taxon in Arizona (see Fig. 2).

To be sure, the steepness of altitudinal clines describing genetic variation in fitness-related traits varies greatly even among wind-pollinated conifers inhabiting similar environmental gradients. In northern Idaho, the altitudinal

interval associated with detectable genetic differentiation is ≈ 200 m in *Pseudotsuga menziesii* var. *glauca* (Rehfeldt, 1989) and *Pinus contorta* (Rehfeldt, 1988), 420 m in *Pinus ponderosa* (Rehfeldt, 1991), 450 m in *Larix occidentalis* (Rehfeldt, 1995), and 600 m in *Thuja plicata* (Rehfeldt, 1994); and in *Pinus monticola*, clines in adaptive traits cannot be demonstrated (Rehfeldt, Hoff, and Steinhoff, 1984). Thus, the relatively flat cline of *C. arizonica* has a counterpart in *Pinus monticola*, while the steeper cline of *C. glabra* is intermediate between those of *Larix occidentalis* and *Thuja plicata*. Despite their differences, *C. arizonica* and *C. glabra* display levels of population differentiation that have counterparts among broadly dispersed conifers.

Genetic variances among families within populations of *C. arizonica* and *C. glabra* that approach 10% of the phenotypic variance also tend to be typical of the broadly dispersed species (Table 6). Atypical, however, are the large family effects displayed by *C. stephensonii*: intraclass correlations averaged 0.17, a value that was at least 1.5 times larger than those estimated for any of the other conifers.

While the case of *C. stephensonii* will be considered subsequently, it may be instructive to note that flat clines seem typical of the *Cupressaceae* (*Thuja* and *Cupressus* in the previous discussion), while genetic variability within populations tends to be high (Table 6). Indeed, allozymes suggest modest interpopulation and large intrapopulation variation in *Cupressus sempervirens* in Greece (Papageorgiou, Panetsos, and Hattermer, 1994). Because the *Cupressaceae* lack buds (Pillai, 1963), shoot extension is indeterminate (Kozłowski, 1971), while growth and morphology (Harry, 1987; Krasowski and Owens, 1991) and even the reproductive cycle (El-Kassaby, 1995) respond to current weather conditions. As a result, genetic structure may primarily reflect plasticity rather than genetic differentiation (Harry, 1987). Underlying the plastic responses, however, is considerable genetic variation (Table 6; Rehfeldt, 1994).

The case of *C. stephensonii*—It is difficult to reconcile the high genetic variances estimated for a taxon whose distribution is limited to a single locality. One explanation might be sampling errors associated with a meager sample of nine families. Another might be inbreeding, a process well known to increase genetic variances among lines at the expense of variance within lines (see Falconer, 1960). While the first of these cannot be assessed without intensive resampling, evidence implicating inbreeding can be found in Table 6: the largest intraclass correlations involved variables describing growth potential and tree form, two groups of variables well known to display large inbreeding depressions (see Sorensen and Miles, 1982). For several families to exhibit dwarfism and for one family to exhibit dwarfism and an asymmetric crown suggests inbreeding.

Verifying and understanding the effects of inbreeding in *C. stephensonii* require a thorough examination of the taxon's reproductive biology. Still, the implications of inbreeding can be addressed by assuming that (1) genetic variances in *C. stephensonii* are inflated by a factor of $1 + F$, where F is Wright's inbreeding coefficient (see Falconer, 1960) and (2) an intraclass correlation of 0.09 typ-

ifies noninbred family variances within populations of *Cupressus* (Table 6). Under these assumptions, an inbreeding coefficient of 0.88 would be required to account for the average family intraclass correlation (0.17) estimated for *C. stephensonii* [$0.17 = 0.09(1 + F)$]. To be sure, an inbreeding coefficient of $F = 0.88$ in the progenies overestimates coancestry of the parental population. However, even if all of the progenies were derived from selfing ($F = 0.5$), a large inbreeding coefficient ($F = 0.76$) would still be necessary to account for the observed variation [$0.88 = 0.5(1 + F)$]. Although such degrees of inbreeding are extraordinarily high for wind-pollinated conifers (see Sorensen, 1994), other members of the *Cupressaceae* sustain remarkably low outcrossing rates: 32% in *Thuja plicata* (El-Kassaby, Russell, and Ritland, 1994), 63% in *T. occidentalis* (Perry and Knowles, 1990), and 70% in *T. orientalis* (Xie, Dancik, and Yeh, 1991).

Reports dealing with *C. stephensonii* on file with the Cleveland National Forest, Alpine, CA (J. L. Reveal, cited previously; G. A. Scheid and P. H. Zedler, unpublished, Ecological studies of Cuyamaca cypress, Cuyamaca State Park, San Diego County: population status and management) show that: (1) the population consists of ≈ 800 individuals dispersed across 207 ha in six spatially isolated subpopulations, (2) fire has swept through the population three times during the last century, and (3) a fire in 1950 reduced the population to ≈ 12 individuals. Because the closed cones of *C. stephensonii* (Table 1) typically open after fire, the current population most assuredly is not derived from the intermating of only 12 individuals. However, the opportunity for intense inbreeding is provided by repeated fires in spatially disjunct subpopulations of a taxon described by Wolf (1948) as having (1) delayed sexual maturity, and (2) a limited capacity of seed dispersal (nearly wingless seeds). One is led toward the conclusion, therefore, that much of the genetic variability in *C. stephensonii* may be stored between a few inbred lines.

Conservation biology—The *C. arizonica* complex belongs to a geoflora whose current distribution is only a remnant of a widespread Pliocene flora (Axelrod, 1958). Yet, taxa in this complex apparently have retained as much genetic variability within populations as have broadly dispersed conifers. Both *C. arizonica* and *C. glabra*, moreover, exhibit genetic structures that have counterparts among their broadly dispersed cohorts. Genetic structure alone, therefore, does not reflect the limited geographic distributions of the *Cupressus* taxa.

Rather than reflecting depauperate genetic variability, the limited distributions of these taxa must simply result from a lack of genetic variability appropriate for adjusting to alternative habitats and competitive regimes. Perpetuation, therefore, seems dependent on habitat availability and adjusting to change on tracking the favorable environment. Adverse effects of a changing climate would then result from (1) changes beyond the plastic capability of the physiologic system, or (2) changes so rapid as to preclude migration. Several autecological characteristics (see Wolf, 1948) thus place taxa of the *C. arizonica* complex in precarious positions: a nearly wingless seed that inhibits migration; reproduction that is fire dependent in an age when wildfires are suppressed; de-

layed sexual maturity that demands migrant populations to occupy a site for a prolonged period before abundant reproduction can be expected; and habitat demands that conflict with human demands for ranching, housing, and recreation.

Because of this, perpetuation undoubtedly will require human intervention, particularly in the face of rapid climate shifts (see Wigley and Raper, 1992). The two primary human roles most likely will be to assist migration by maintaining the appropriate habitat and providing the genotypes appropriate to those habitats. As demanded by the genetic structures, the first of these roles would be appropriate for all taxa, while the second would particularly appropriate for *C. glabra*.

If inbred, *C. stephensonii* presents intriguing managerial challenges. It is difficult to accept high inbreeding coefficients in a wind-pollinated taxon that apparently exhibits pronounced inbreeding depressions. Perpetuation of this taxon, therefore, seems dependent on a strategy that involves (1) crossing of inbred lines to redistribute genetic variability, and (2) planting such individuals in both the natural population and in ex situ reserves.

Evolutionary genetics—The current results support neither population genetic theory (see Mitton, 1995) nor generalities derived from the allozyme literature (Hamrick and Godt, 1989; Hamrick, Godt, and Sherman-Broyles, 1992), all of which predict genetic structure to be directly related to geographic distribution and population size.

C. stephensonii, *C. arizonica*, and *C. glabra* have either small or minute distributions in comparison to other conifers of western North America. Yet the genetic structures of *C. arizonica* and *C. glabra* have counterparts among the broadly distributed conifers. In addition, the narrow endemic *C. glabra* exhibits more variability among populations and the same amount within populations as the more broadly distributed *C. arizonica*. And finally, *C. stephensonii* exhibits a genetic structure that has no documented counterpart: a wind-pollinated taxon that may exist as a few inbred lines within a single population. Obviously, the genetic structure of these taxa could not have been predicted from their geographic distributions.

C. glabra and *C. arizonica* also differed demographically: four of the five *C. glabra* populations that were sampled occupied large tracts of land, while all *C. arizonica* populations except that at Chase Creek (Fig. 1) were small and linearly distributed in canyons. Contrary to the expectations, however, the results showed that genetic variances in fitness-related traits were as large within the large populations of *C. glabra* as in the small populations of *C. arizonica*. It seems reasonable that the linear arrangement of individuals within populations may have counterbalanced population size in enhancing genetic variability within populations.

The present studies thus join a growing body of literature supporting Karron's (1991) view that genetic structure, first and foremost, reflects the uncertain, chance events that are interspersed throughout evolutionary history. Geographic distributions and population demographics are indirectly the result of these events, are directly dependent on genetic structure, but are not neces-

sarily predictors of either. This study of closely related *Cupressus* taxa illustrates that designed experimentation provides the only reliable means of understanding the allocation of genetic variability among and within populations.

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