Genetic Variation in Two *ex situ* Collections of the Rare *Metasequoia glyptostroboides* (Cupressaceae)

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Abstract

We report allozyme variation in 46 new single-tree seedlots of *Metasequoia glyptostroboides* collected in 1990 in Hubei and Sichuan provinces, China; and comparative growth data for 20 of the seedlots. Fourth-season heights ranged from 60 % to 119 % of plantation means at New Brunswick, New Jersey, and Newark, Ohio. Height ranks at both sites were strongly correlated; there was no family x site interaction. Family heritability was 0.72. Several phenotypic mutants (dwarf, weeping, "corkscrew") appeared among the 46 new seedlots. Frequency analysis of foliar allozymes showed that 3 of 15 loci were polymorphic in the 1990 seedlots, *vs* 2 of 15 polymorphic in the 1947 Arnold Arboretum seedlot. All measures of genetic variation calculated were higher in the 1990 seedlot. It is clear, however, that the 1947 seedlot could not have all come from one large, isolated tree (implying self-pollination) because the FE-2 locus exhibited 4 alleles.

Key words: *Metasequoia glyptostroboides* HU et CHENG, dawn redwood, provenance, progeny, allozyme, isozyme.

FDC: 232.12; 165.3; 174.7 *Metasequoia glyptostroboides*; (749); (771).

Introduction

Fossils were all that was known to the Western world of *Metasequoia glyptostroboides* HU et CHENG until 1947; the genus had been established only recently by MIKI (1941) from fossilized leaves and cones. While it formerly grew in Japan, Idaho, and the Canadian Arctic, it now is restricted to a small area in China where the provinces of Hubei, Hunan, and Sichuan join. Most of the trees grow in an area of 30 km x 20 km in Hubei (*Fig. 1*).

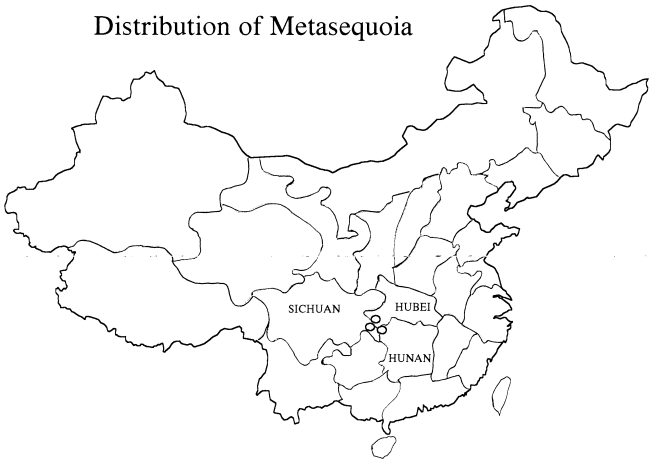

Fig. 1. – *Metasequoia* seed collection areas in the People's Republic of China. The 3 small circles show locations of groves in Sichuan, Hubei, and Hunan (1. to r.) (LI, 1994).

When this tree's existence was first realized by the Western world, there was speculation that it might become an important timber plantation species because of its fast growth and decay-resistant heartwood (LIU, CHOU and HSU, 1978). This speculation was not realized because it soon became apparent that *Metasequoia* in cultivation was heliophilic and would require much wider spacing than its shade-tolerant relative, *Sequoia sempervirens*, in spite of what CHU and COOPER (1950) had stated about its shade tolerance in the wild. In addition, the quality of its wood characteristics was questioned by LIANG (1948) and ETHINGTON (1967). However, during the half-century since its introduction to the West, it has been widely planted in the temperate zones (KUSER, 1982, 1990, 1992) and has become a useful urban forest species (GERHOLD, LACASSE and WANDELL, 1993).

In 1947, the Arnold Arboretum sent money to China for seed, which was received at Jamaica Plain, Massachusetts on 5 January, 1948 and widely disseminated (WYMAN, 1970). All the large specimens, now up to 35 m tall, in the U. S. and elsewhere outside China, derive from that seed with 1 or 2 possible exceptions. WYMAN (1968), FULLING (1976), and KUSER (1982, 1990) describe how well those trees have grown. The *Metasequoia* area was visited later by CHANEY, who photographed a large, isolated tree at Modaoqi and published a leaflet with the photograph on the front page (CHANEY, 1948). Because of this and because the story of exactly how the seed collection was made had never been published, it was not known outside China whether all the 1947 seed came from that large tree (as often thought), or from several trees. In view of our finding that *Metasequoia* had substantial inbreeding depression evident in low germination rates of selfed seedlots (KUSER, 1983), whereas the 1947 seed was reported to have germinated well, we suspected that the seed had not all come from the single, isolated tree.

Our research project had 3 aims: 1) to broaden the genetic base of *Metasequoia* in cultivation, 2) to identify (and disseminate if warranted) any new or unusual phenotypes which might appear in hundreds of progeny of a rangewide sample of parents, and 3) to test the hypothesis that all the 1947 seed had come from CHANEY's large, isolated tree.

Methods

Field Tests

In November of 1990, students of Dr. LI MINGHE, professor of forestry at Central China Agricultural University, Wuhan, China, collected open-pollinated seed from 52 parent trees in Hubei, Hunan, and Sichuan provinces (*Fig. 1*). Of these, tree no. 2 was in Hunan province, lat. 29°30'N, long. 109°40'E; trees no. 47, 48, and 49 were in Sichuan, lat. 30°00'N, long. 108°10'E; and all others were in the "metasequoia valley" in Hubei, lat. 30°00' to 30°15'N, long. 108°35'E to 108°45'E. Estimated ages ranged from 30 years to 300 years, $\bar{x}$ = 125y; heights were 19 m to 51 m, $\bar{x}$ = 35 m; dbh 0.42 m to 2.4 m, $\bar{x}$ = 0.82 m; crown spread was 3.5 m to 24 m, $\bar{x}$ = 10 m; branch angle 60° to 95°, $\bar{x}$ = 76°. Cone stalk lengths were 1.0 cm to 5.7

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cm, $\bar{x}$ = 2.77 cm; cone diameters were 1.3 cm to 2.0 cm, $\bar{x}$ = 1.65 cm; cone lengths were 1.5 cm to 2.6 cm, $\bar{x}$ = 1.89. Site elevations of trees were 865 m to 1560 m, and slope aspects were S, SW, or SE for more than half of the trees. After considerable delay, these were received at Cook College, Rutgers University in late April of 1991. The seed was stored at 0 °C to 3 °C during the summer and fall, and then in the first 3 months of 1992, c. 1,400 seedlings were germinated on moist filter paper in Petri dishes in a seed germinator. Forty-eight seedlots produced germinants and 4 did not. As soon as their cotyledons were fully expanded, seedlings were planted in 10 cm (4 in.) pots in Pro-Mix BX at the research greenhouse. In June, they were moved to 7.5 l (2 gal.) containers. In September, 356 trees, then 25 cm to 1 m tall, were planted in a 0.38 ha progeny test plot on Sassafras sandy loam at Ryders Lane, New Brunswick, New Jersey. A hexagonal design (LIBBY and COCKERHAM, 1980) with 4 randomized blocks was used with 3 overlapping replicates: A (permanent), B (second thinning), and C (first thinning) so that the plantation can be thinned twice, leaving eventual spacing at 6 m between each tree and 6 equidistant neighbors. Twenty families were planted, 12 trees of each (3 of each per block) in the center of the test plot, making a total of 240 test trees. Another 26 families, of which there were too few seedlings to include them in the test, were used as A-replicate border trees, and plants of 2 families (nos. 26, 45) which had produced very few germinants were sent elsewhere. Border trees in the B and C replicates were excess plants of seedlots which had germinated well; thus they were expendable. The whole plantation included 116 border trees as well as the 240 test trees, making a total of 356 trees.

A similar lot of 360 trees was shipped to The Dawes Arboretum, Newark, Ohio for a replicate progeny test plantation. Trees there were planted on a 3.2 ha plot in a staggered rectangular design, completely randomized (no blocks), 7.62 m apart within rows, and rows 7.62 m apart, with no thinning contemplated because of the plot's adequate size. The plantation was surrounded with a single-strand electric fence and baited with peanut butter until deer learned to avoid it.

Ten seedlings of each of 10 families were sent to Holden Arboretum in Cleveland, Ohio; and lesser numbers to Scott Arboretum in Philadelphia, Pennsylvania; Morris Arboretum in Philadelphia, Pennsylvania; Callaway Gardens in Pine Mountain, Georgia; New Jersey Botanical Garden in Ringwood, New Jersey; New Jersey Forestry Services in Jackson, New Jersey; Royal Botanic Garden in Edinburgh, Scotland; Arnold Arboretum in Jamaica Plain, Massachusetts; and MICHAEL MELENDREZ in Los Lunas, New Mexico.

At the Rutgers plantation, trees were irrigated as necessary during the summers of 1993 to 1996. In April of 1993, brush blankets (Arbortec, Inc., Penticton, B. C.) were installed to protect the newly planted trees from weed competition; in May of 1994 these were replaced as necessary, and in November of 1994 they were removed because field mice living under them had girdled 2 trees the previous winter. In May 1994 and May 1995, trees were fertilized with ¼ lb. (113 g) N each (as 20-20-20), and in August 1995 and May 1996 with 1 lb. (454 g) N each (as 10-6-4, 60 % slow-release organic N). Trees were measured for height to the nearest 5 cm at the ends of their first, second, third, and fourth growing seasons (dbh and crownspread were not measured, because many trees were not large enough to provide meaningful measurements). In order to determine whether height differences among the 20 test families were significant and to rank them, an ANOVA was performed on the fourth-season data (HT = Fam + Block + Block • Fam + Error) and the families were ranked by DUNCAN's test (P = 0.05) (SAS). Family heritability and single tree heritability were calculated from variances observed at the Rutgers plantation, according to WRIGHT's (1975, p. 243) formulas (in which F, B, S, and N are, respectively, the number of females, the number of blocks per site, the number of sites, and the number of trees per plot):

$$\textit{Family heritability} = \frac{V_f}{V_e/NBS + V_{fb}/BS + V_{fs} + V_f}$$

$$\textit{Single tree heritability} = \frac{4V_f}{V_e + V_{fb} + V_{fs} + V_f}$$

We did not use the Dawes data to determine heritability, because numbers of trees per family were not as evenly balanced as at Rutgers.

Trees at The Dawes' plantation were measured for height to the nearest 5 cm at the ends of their first, second, third, and fourth growing seasons, and an ANOVA and DUNCAN's test were performed with the fourth-season data. Because The Dawes' plantation was not blocked, the model was simply HT = Fam + Error. After this, a joint ANOVA was run on heights of both plantations together; the model was HT = Fam + Fam • Site + Error.

Height data for both plantations were converted to percents of their respective plantation means, to make comparison easier. PEARSON correlation and SPEARMAN rank correlation analyses (SAS) were then performed to compare the height and rank data for the Rutgers and Dawes plantations.

Allozyme Tests: Field Collection

In June of 1995, 120 foliar samples were taken from trees in the Rutgers plantation (including at least one tree from each of the 46 remaining 1990 seedlots) for allozyme variation analysis. Foliar samples were also taken from 40 trees derived from the Arnold Arboretum 1947 seedlot. Some of these were original trees now averaging 30 m tall, others were seedlings or cuttings (now 10 m to 15 m tall) grown from trees of the 1947 seedlots, and still others were commercially grown dawn redwoods attributable to the 1947 seedlots. All trees were tagged with individual numbers, tree locations recorded in a fieldbook, and individual allozyme profiles recorded in a lab notebook.

Laboratory Procedure and Statistical Analysis

Population genetic surveys were based on horizontal starch gel electrophoresis performed on foliar samples (needles) ground in liquid nitrogen and prepared using the extraction buffer described by MITTON *et al* (1979), as modified by ECKERT (1995). Samples were subsequently evaluated for scorable allelic composition for the following allozymes: acid phosphatase (ACP-1, ACP-2), aldolase (ALD), fluorescent esterase (FE-1, FE-2), glutamate oxaloacetate transaminase (GOT), glucose-6-phosphate dehydrogenase (G-6-PDH), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH-1, MDH-2), malic enzyme (ME), 6-phosphogluconate dehydrogenase (PGD), phosphoglucoisomerase (PGI-1, PGI-2), shikimate dehydrogenase (SKD), and triose-phosphate isomerase (TPI-1, TPI-2). Buffer systems and enzyme assays followed WENDEL and WEEDEN (1989). Standard measures of genetic variation were estimated, including percent polymorphism, mean number of alleles per locus, effective number of alleles per locus, and

expected heterozygosity at the population and species level (HAMRICK and GODT, 1990). A locus was considered polymorphic if the most common allele was present at a frequency of 0.95 or less. Data from both the 1947 and 1990 seedlots were pooled to calculate species-level estimates. To obtain population-level measures, estimates were calculated for both seedlots and then averaged.

Hierarchical F-statistics analysis of genetic variation within and between the 1947 and 1990 seedlots was then performed, with estimates based on procedures outlined in WEIR (1990, pp. 152–155).

Results

Height Growth

At the Rutgers plantation, survival on 7 November 1996 was 98.5 %. There were no differences among families (only 5 trees have died: 2 were girdled by mice and 3 died during a hot, dry period when irrigation failed to reach the windward edge of the plantation). The tallest tree measured 5.36 m. Mean height was 2.50 m, and differences among families were significant ($P < 0.0001$). There was a significant block effect ($P < 0.0001$), with trees in block 4 being noticeably taller; but block x family interaction was not significant ($P < 0.0736$). Mean height of the tallest family was 1.97 times mean height of the shortest. At The Dawes' plantation, survival on 30 December 1996 was 96.9 %; mean height was 2.38 m, and the tallest tree measured 3.72 m. Mean height of the tallest family was 1.85 times mean height of the shortest. Mean heights of the 20 center-plot test families at Rutgers and the same families at The Dawes are shown in *table 1.* The PEARSON correlation coefficient between mean heights at the 2 plantations was $r = 0.90$ ($P < 0.0001$), and the SPEARMAN correlation between height ranks at the 2 plantations was $r = 0.85$ ($P < 0.0001$). The ANOVA on heights at the 2 plantations combined found that family differences were significant ($P < 0.0001$, site differences were significant ($P < 0.005$), but family x site interaction was not significant ($P < 0.99$). Family heritability as calculated from variances observed at the Rutgers plantation was 0.72 (std. error 0.23), and single tree heritability was 0.82 (std. dev. 0.05).

Table 1. – Heights (as % of plantation means) of *Metasequoia* at Rutgers plantation, New Brunswick, New Jersey and The Dawes plantation, Newark, Ohio after 4 growing seasons. Ranked by DUNCAN's test ($P = 0.05$).

Family	Height at Rutgers	n	Duncan's Rank	Height at Dawes	n	Duncan's Rank
29	119	13	A	113	27	AB
34	115	12	AB	111	13	ABC
19	112	12	AB	108	12	ABC
30	112	12	AB	108	11	ABC
40	111	12	ABC	100	12	ABC
36	110	12	ABC	107	12	ABC
33	110	12	ABC	108	10	ABC
27	109	12	ABC	117	23	A
31	108	12	ABC	98	36	ABCD
43	102	12	ABC	95	12	BCD
35	101	11	ABCD	97	11	ABCD
5	99	13	ABCD	95	12	BCD
22	99	11	ABCD	100	12	ABC
24	95	12	BCDE	105	7	ABC
32	94	12	BCDE	105	7	ABC
18	94	11	BCDE	93	12	BCD
38	89	11	CDE	91	12	CD
50	80	12	DEF	64	10	E
7	75	11	EF	79	9	DE
47	60	12	F	63	10	E
Plantation mean,cm	250			238		

At the Rutgers plantation, clones 27-A and 34-A stand out above their next neighbors in height, crown spread, and stem diameter. One 10 cm cutting of cl. 27-A which was stuck on 29 August 1995, overwintered in a cold plastic lath-house where temperatures did not go below 0 °C, and returned to warm environment on 1 March 1996, had reached a height of 192 cm by 25 September 1996 (*Fig. 2a*). A year later, a similar cutting of cl. 27-A stuck on 16 August 1996 and grown likewise, reached 210 cm on 14 September 1997.

Several unusual variants have appeared among trees grown from the 1990 seedlots. In lot no. 3, c10 % of the seedlings have small, slightly glaucous needles. One small-needled, bluish dwarf weeping one (clone 3-B) was only 50 cm high and 65 cm wide (*Fig. 2b*) after 4 growing seasons. One of the erect small-needled ones (clone 3-C) is a border tree 2.0 m tall at the Rutgers plantation; a similar one (clone 3-A) is a 3.2 m tree in one author's lawn, and stockplants for possible horticultural introduction have been propagated from it. Seedlots nos. 3, 17, 31, 32, 33, and 35 have produced 4 % to 12 % sublethal blue/white striped mutants which did not survive long. Lot no. 32 produced an erect, drooping-branched mutant; lots nos. 23 and 29 each produced 1 "corkscrew" mutant, vigorous and fast growing but resembling corkscrew willow or curly hazel. Most plants of lot no. 47 are slow-growing and large-needled; size of short-shoots and needles varies from this extreme to very small in clone 3-B (*Fig. 2c*).

Allozymes

Frequencies of alleles in both populations are shown in *table 2*. Of the 15 scoreable loci included in this study, FE-2 and PGI-2 are polymorphic in both the 1947 and 1990 seedlots, while IDH is polymorphic in the 1990 seedlot only. Both the 1947 and 1990 populations were monomorphic at 12 loci: ACP-1, ACP-2, ALD, FE-1, GOT, MDH-1, MDH-2, PGD, PGI-1, SKD, TPI-1 and TPI-2. The 1947 population was monomorphic for IDH.

Percent polymorphic loci (P), mean number of alleles per locus (A), effective number of alleles per locus (Ae) and expected heterozygosity (He), calculated for the species and population levels, and for each population are shown in *table 3.* For each of these genetic parameters, the 1990 seedlot shows values slightly higher than those of the 1947 seedlot, and the species-level estimates are higher than the population-level estimates.

Hierarchical F-statistics analysis of genetic variation within and between the 1947 and 1990 seedlots is shown in *table 4*. The 5 loci included in the analysis show varying levels of inbreeding and differentiation among the 2 assayed populations. Positive values of F_{it} and F_{is} offer evidence of nonrandom mating of individuals relative to the total population and to their subpopulations, respectively. The value estimated for F_{st} indicates little genetic differentiation between the 1947 and 1990 seedlots, with only 21 % of the total variation found among the 2 populations.

Discussion

Our objectives to 1) broaden the genetic base of *Metasequoia* in cultivation, and 2) identify and disseminate unusual

phenotypes, and 3) test the hypothesis that all the 1947 seed had come from one, isolated tree, have been met. The presence of 4 alleles of FE2 in the 1947 population confirms our deduction that the latter seedlot did not stem from a single tree (and now that we have CHENG's story from LI (see below), we can say definitely it did not). The 1990 seedlots exhibit more genetic diversity than that of the 1947 Arnold seedlot in terms of % polymorphic loci, mean number of alleles per locus, effective number of alleles/locus, and genetic diversity index (*Table 3*).

After we had completed the allozyme analysis and rejected the idea that the 1947 seed came from one, isolated tree, we sent an early draft of this paper to Dr. LI (who had collected our 1990 seedlots) to review. He replied on 14 February, 1996, with some new information substantiating our conclusion, as follows (boldface italics ours): in the winter of 1941, on his way to Sichuan from Hubei, Professor GAN noticed a big unknown tree. Because it bore no leaves, he did not collect specimens. In 1942, GAN asked a teacher named YAN to collect for him, but YAN never did; however, he suggested to WANG in 1944 when the latter was going to Sichuan from Hubei, that he change his way so that he could see this big tree. WANG found the tree and misidentified it as *Glyptostrobus pensilis* K. KOCH. In the summer of 1945, WANG showed WU a branch and 2 cones. WU took the branch and cones to Dr. CHENG. Because the leaves and cone scales were opposite (rather than alternate as in *Sequoia, Taxodium, Glyptostrobus*), CHENG reasoned that this must be a new genus. In February and May of 1946, CHENG sent XE to the area to collect catkins and conelets (micro- and macrosporangiate strobili), then young cones. CHENG then sent these specimens to Dr. HU and asked him to check the literature; HU found MIKI's 1941 paper, and realized that he had live specimens of a tree believed to have been extinct for 20,000,000 years. CHENG then sent HUA to search the area in the fall of 1947. HUA found more than 1,000 *Metasequoia* there, and among them about 100 big ones. *From these trees, he collected*

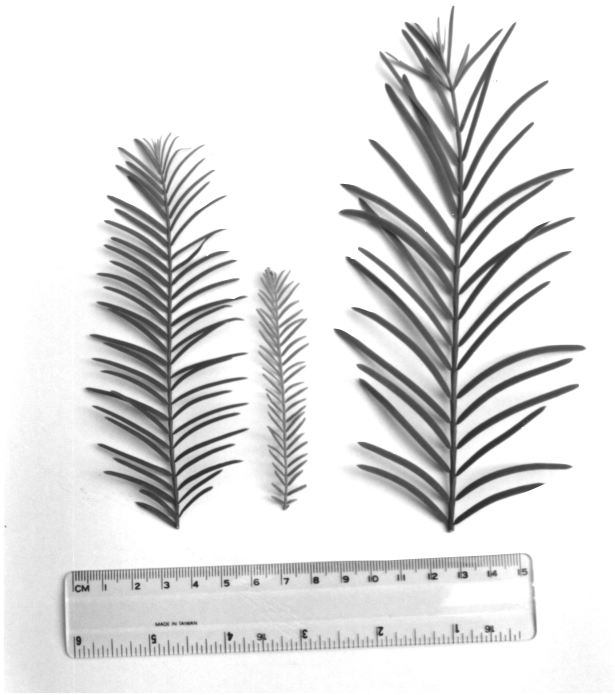

Fig. 2. – a) 13-month-old steckling of clone 27A, 192 cm tall. b) Dwarf *Metasequoia glyptostroboides* clone 3B, 50 cm tall and 65 cm wide after 4 growing seasons, with meter stick at bottom for scale. c) Comparative needle size of (l. to r.) clones 23A (normal), 3B (weeping dwarf), and 47B.

seeds which were disseminated to many countries. CHENG told this story in a paper dated 25 March, 1948, which he never published. LI (who had been CHENG's student) had kept a copy of the paper, and relayed us this account corroborating our conclusion.

Because the 1990 sample includes clones with alleles not seen in the 1947 sample, introducing those clones into cultivation, as well as clones exhibiting vigorous growth or with unusual phenotypes, will expand the genetic and phenotypic variability of *Metasequoia* grown outside of China. Due to its slightly greater genetic variability, the 1990 population may provide a better source from which to select a wide range of forms of *Metasequoia* for different uses. The species is used successfully as a street tree in Paramus and Maplewood, New

Table 2. – Allelic frequencies for *Metasequoia glyptostroboides* in the 1947 and 1990 seedlots. N = number of individuals assayed.

Locus	Allele	Overall N = 159	1947 Seedlot N = 40	1990 Seedlot N = 119
ACP-1	2	1.000	1.000	1.000
ACP-2	2	1.000	1.000	1.000
ALD	2	1.000	1.000	1.000
FE-1	2	0.997	1.000	0.996
	3	0.003	0.000	0.004
FE-2	1	0.016	0.031	0.013
	2	0.412	0.250	0.447
	3	0.407	0.375	0.413
	4	0.165	0.344	0.127
GOT	2	1.000	1.000	1.000
IDH	1	0.003	0.000	0.004
	2	0.915	0.975	0.895
	3	0.079	0.025	0.097
	4	0.003	0.000	0.004
MDH-1	2	1.000	1.000	1.00
MDH-2	2	1.000	1.000	1.00
PGD	2	1.000	1.000	1.00
PGI-1	2	1.000	1.000	1.00
PGI-2	1	0.036	0.000	0.049
	2	0.451	0.487	0.438
	3	0.513	0.513	0.513
SKD	2	0.994	0.987	0.996
	3	0.006	0.013	0.004
TPI-1	2	1.000	1.000	1.000
TPI-2	2	1.000	1.000	1.000

Table 3. – Measures of genetic diversity for *Metasequoia glyptostroboides* at the species and population levels and for each seedlot. P = percent polymorphic loci, A = mean number of alleles/locus, A_e = effective number of alleles/locus, and H_e = genetic diversity index.

	P	A	A_e	H_e
Species	20.0	1.70	1.10	0.089
Population	16.7	1.55	1.09	0.087
1947	13.3	1.40	1.09	0.083
1990	20.0	1.70	1.10	0.091

Table 4. – Hierarchical F-statistics analysis of genetic variation within and between the 1947 and 1990 seedlots of *Metasequoia glyptostroboides*. Estimates are based on procedures outlined in WEIR (1990), pp. 152 to 155.

Locus	F_{IT}	F_{ST}	F_{IS}
IDH	0.231	0.024	0.212
PGI 2	0.191	0.011	0.182
SKD	0.063	0.063	0.000
FE 1	0.005	0.000	0.005
FE 2	0.480	0.136	0.397
cumulative jacknife estimate	0.658	0.213	0.527
std. dev. of jacknife estimate	0.047	0.009	0.026

Jersey; it is listed in New Jersey's street tree manual (NJSTF, 1990), in KUSER's 1992 list of exotic trees in that state, and in the widely used Street Tree Factsheets (GERHOLD, LACASSE and WANDELL, 1993).

Currently in cultivation from the 1990 collection are variants of *Metasequoia* with the following features: 1) normal, upright, straight, fast-growing, 2) "curly", like curly hazel, 3) dwarf, weeping, (original plant now at Morris Arboretum, Philadelphia, Pennsylvania), 4) upright, fine-needled (now under evaluation at a commercial nursery), and 5) slow-growing, often forking, with large needles which are coppery at shoot tips.

The seedlings produced from certain of the 1990 seedlots (29, 34, 19, and 30) outperformed those of other seedlots at both the Rutgers and Dawes plantations, while seedlings of lots no. 50, 7 and 47 fell well below the plantation mean at both locations. If height can be considered a reasonable measure of vigor, and we believe it can unless accompanied by any deleterious characteristics, then seedlings from the fastest-growing families should be targeted for horticultural propagation. The slow growth and tendencies to fork and be plagiotropic noted in progeny of tree no. 47 are surprising, because the parent tree is one of the taller trees sampled (44 m). It is possible that tree no. 47 is isolated, and its offspring have resulted from self-fertilization. This tree was the only one from Sichuan province to provide enough seedlings for testing in the replicated blocks at the plantations. Two other seedlings from Sichuan province (1 each from trees no 48. and 49), which were used as border trees in the plantations, do not appear unusual. It is unfortunate that we were unable to include progeny of other seedlots from Sichuan in the plantation trials.

Our estimated single tree heritability of 0.82 for height growth in *Metasequoia* is high compared to estimates of 0.10 to 0.44 for other conifers (ZOBEL and TALBERT, 1984), although higher values have been estimated for the magnoliophyte, *Liriodendron tulipifera*. Our high estimate may be due to the limited number of families providing sufficient germinants for the test, and to the availability of only one plantation divided into replicated blocks containing equal numbers of each family. WRIGHT (1976) states that calculation of heritability from a single plantation is apt to result in overestimate; and ZOBEL and TALBERT (1984) caution that heritability is not estimated without error, and values obtained are only a relative indication of genetic control and should not be regarded as invariant.

Comparing genetic diversity values estimated for *Metasequoia* with those estimated for other coniferous species and for conifers in general (YEH and O'MALLEY, 1980; HAMRICK, 1989; MORAN and ADAMS, 1989; PERRY, KNOWLES and YEH, 1990; DIEBEL and FERET, 1991; GIANNINI, MORGANTE and VENDRAMIN, 1991; YING and MORGENSTERN, 1991) shows low to average genetic diversity for *Metasequoia*, with relatively high measures of inbreeding and genetic differentiation. *Metasequoia* was more widespread than now until quite recently, evidenced by buried trunks of *Metasequoia* found at Wuhan (520 km east of the present range) in 1992 after having been under the earth for 11,000 years (LI, pers. comm.). CHU and COOPER (1950) wrote that the remaining native trees grow in a closed basin with no easy river route into it. Consequently, this basin had been the last in the area to be developed for agriculture (about 200 years ago). When considering the relatively high measures of inbreeding and genetic differentiation estimated for the 1947 and 1990 populations of *Metasequoia,* it must be noted that these populations are separated temporally, rather than spatially, which is the more common use of F-statistics. Despite the somewhat unusual circumstances surrounding the collection of the 1947 seedlot, the 2 collections contain nearly 80 % of the genetic variation measured in this species. An interesting study for the future is an analysis of the level and distribution of genetic variation among the subpopulations of *Metasequoia* remaining in China. We were unable to do that analysis here because we had no trees from Hunan and too few from Sichuan to compare with trees from the larger population in Hubei.

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Age-age Correlations in, and Relationships between Basic Density and Growth in *Eucalyptus nitens*

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Abstract

Pith to bark density was measured on cores cut from 588 7-year-old *Eucalyptus nitens* trees. Heritability of ring density averaged 0.37 and was consistently higher than the heritability of earlywood or latewood density. Earlywood, latewood, and ring densities were highly genetically correlated. Age-age correlations for ring density declined with increasing age difference, and were moderately described by LAMBETH's (1980) relationship with log of age ratio. Disk and core densities were calculated as weighted averages of ring densities. Age-age correlations for disks and cores were higher and better described by LAMBETH's relationship than ring density correlations. Age-age correlations for growth assessed at 20 months, 4 years and 7 years were not well described by LAMBETH's relationship. Height, diameter, and volume were well correlated at age 7 years ($r_g > 0.9$), as were disk density, core density, outer-ring density and Pilodyn penetration ($r_g > 0.9$). Density showed a weak negative genetic relationship with diameter at age 7 years ($r_g = -0.2$).

Key words: Eucalyptus nitens, basic density, growth, age-age correlations, heritability, genetic correlation.

FDC: 811.4; 812.31; 561.24; 232.1; 181.65; 165.3; 176.1 *Eucalyptus nitens*; (945).

Introduction

Knowledge of the changes in heritability of traits, and correlations between these traits assessed at different ages, are necessary for determination of efficiencies of early selection (KANG, 1985). Determining trends in heritability and age-age correlations is relatively simple for growth traits, requiring only patience and repeated assessment. While there are many reported age-age correlations for growth in conifers (e. g. LAMBETH, 1980; MCKEAND, 1988; RIEMENSCHNEIDER, 1988; KING and BURDON, 1991; MATHESON *et al.*, 1994) there are few for *Eucalyptus* L'HÉR species (VAN WYK, 1990; BORRALHO *et al.*, 1992b).

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