To conclude, the fastest-growing progeny on a given site may be expected to produce the best coppice, since the number, height and biomass of the regeneration are directly related to tree size before cutting.

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Summary

Tree growth of E. camaldulensis varied with the origin of the seed, thereby determining the amount and rate of coppice regeneration after cutting.

The number of coppice shoots, height of the tallest shoot and biomass were directly related to tree height and girth before coppice cutting.

Key words: Coppice regeneration, Eucalyptus camaldulensis, seed. provenance, progeny tests.

Zusammenfassung

Das Wachstum von Eucalyptus camaldulensis variiert mit der Samenherkunft. Sie ist auch maßgebend für Anzahl und Wuchs der Stockausschläge nach dem Hieb.

Menge des Stockausschlags, Höhe der höchsten Schößlinge und Biomasse stehen in direkter Beziehung zur Baumhöhe und zum Umfang der Ausgangsbäume.

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Genetic Differences Between American and Chinese Ailanthus Seedlings[1]

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Introduction

Ailanthus altissima Swingle was introduced to England from Nanking, China (119° E, 32° N) by d'Incarville in 1751 (Davies, 1942). From England it was introduced to North America in the late eighteenth century (Illick and Brouse, 1926; Davies, 1942). Since its introduction to the Unites States ailanthus has been used extensively as an ornamental shade tree and has become extensively naturalized. Moslemi and Bhagquat (1970) concluded that ailanthus wood properties resembled those of ash. Pulp and fiberboard characteristics have been reported by several authors (Narayanamurti and Singh, 1962; Adamik and Braun, 1957; Adamik, 1955; Vidal and Aribert, 1927 and Rawlings and Staidl, 1924).

Because of its potential use as a fiber source and because ailanthus grows on a variety of sites (Anonymus, 1956; Adamik, 1955; Richardson, 1966) it may have economic potential. No genetic investigations of ailanthus have been performed. Its method and recency of introduction into the United States leads to speculation that naturalized populations in the United States may differ genetically from orginal Chinese populations because of possible inbreeding due to a reduced gene pool, or because of adaptation to the North American environment. This study was established to test the hypothesis that ailanthus in the United States is not genetically different from Chinese populations. For this purpose a series of morphological, physiological and biochemical measurements were undertaken.

Material and Methods

In 1971 seed were collected from five mother trees at each of twelve United States sources. In 1972 the People's Republic of China sent seed from five mother trees at each of six sources located in mainland China. The Chinese

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Table 1. — United States Seed Sources used for American and Chinese Comparisons.

Source	Symbol	Long	Latitude	Altitude (ft.)
Shasta County, Cal.	CA	122^0 29’	40^0 36’	1,026
Yonkers, N. Y.	NY	73^0 50’	40^0 40’	30
Wooster, Ohio	OH	81^0 56’	40^0 48’	1,000
Morgantown, W. Va.	WV	79^0 58’	39^0 39’	1,000
Pulaski, Va.	VA	79^0 50’	37^0 15’	1,100

sources varied in location from 105^0 40’ E, 34^0 10’ N, to 123^0 30’ E, 41^0 10’ N, but location of each source was not supplied.

Data from first year height growth measurements of the 12 United States sources (Feret, unpublished data) were used to select five seed sources representative of American ailanthus seedling height growth variability *(Table 1).* These five sources were then used to compare genetic variation of American seed sources with that of Chinese seed sources· The fastest growing source (Shasta Co., California), the slowest source (Morgantown, West Virginia); and three sources intermediate in seedling height growth (Wooster, Ohio; Pulaski, Virginia; and Yonkers, New York) were chosen and are referred to as CA, WV, OH, VA and NY, respectively. Chinese seed sources are denoted by Roman numerals. Seeds from the five American sources and the six Chinese sources were germinated in July, 1972. Chinese source VI was eliminated due to poor germination. In early August twelve randomly selected seedlings from each of five parent trees within each seed source were transplanted in the greenhouse into six-inch pots containing a mixture of soil, coarse sand, and peat moss (3 : 2 : 2). Pots were arranged into twelve replications. Four harvests were made of each seed source; each harvest included three replications. In addition, 250 seedlings, randomly selected from seedlings of each country of origin, were outplanted in a replicated field trial.

The first harvest of greenhouse plants was made September 30, 1972. Shortly after the first harvest it was noted that height growth ceased and that some leaves yellowed and dropped. It was assumed that this was a photoperiodic phenomenon, and seedlings were placed in an unheated greenhouse in early November.

On February 6 the seedlings were returned to the greenhouse where they resumed rapid height growth. The second harvest was made March 17, after which nitrogen, phosphorus, and potassium were applied at the rate of 200, 20 and 690 pounds per acre respectively. The third harvest was made on May 10, and the fourth on June 5, 1973. The second, third and fourth harvests were incomplete due to random mortality from root rot which had occurred during the over-wintering period. Seedlings with more than one terminal shoot were also disregarded. Over all four harvests, a total of 194 seedlings of American origin and 186 of Chinese origin were sampled.

At each harvest, stem diameter at soil level and stem height were measured on all plants. Leaf area for each plant was obtained by removing all leaflets from each rachis and measuring leaflet area by photoplanimeter. At each harvest potting soil was washed from the roots, and the biomass of each plant separated into the following components: 1) root, 2) stem, 3) rachis, and 4) leaflet. The material was dried at 70^0 C until constant weight was achieved, and dry weights were obtained for each component of each plant. The average area per leaflet was calculated for plants included in the last two harvests. This was done by dividing total leaf area by total number of leaflets. Most terminal leaves were disregarded in these calculations because of their small area and disproportionate number of leaflets. An area of at least fifty square centimeters was arbitrarily chosen as the basis for inclusion of a terminal leaf. Calculated ratios included the dry weight present in each component (referred to as root ratio, stem ratio, rachis ratio and leaf ratio), and shoot/root ratio.

Analysis of peroxidase isoenzymes of leaf material was made utilizing experimental plants included in the field trial. Electrophoretic techniques using polyacrylamide disc gels were the same as used by Feret, 1970 for the genus *Ulmus.*

Data were analyzed through use of one-way, multiway and nested analysis of variance, regression coefficients of variable pairs, the t-test for significant differences between regression coefficients (Dixon and Massey, 1969), discriminant analysis (White and Mead, 1971) and Chi square analysis. Unless otherwise specified, analyses included data from all four harvests. Logarithmic transformations were used in analyses of all dry weight, leaf area, height and diameter measurements due to heterogeneity of variance over the four harvests. Because of homogeneity of variance, it was not necessary to transform calculated ratios.

Calculated ratios and the logarithms of the measured variables (area/leaflet was excluded) were paired in all possible combinations, and regression coefficients were obtained for all 78 pairs within each country of origin. A t-test was used to indicate significant country effects upon the regression coefficients. Except where otherwise noted, a significance level of five percent was used for all analyses.

Growth analysis data were obtained according to the following formulae (Radford, 1967):

$$\overline{\mathrm{RGR}} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$$

$$\overline{\mathrm{NAR}} = \frac{W_2 - W_1}{A_2 - A_1} \times \frac{(\log_e A_2 - \log_e A_1)}{t_2 - t_1}$$

$$\overline{\mathrm{LAR}} = 1/2\,(\mathrm{LAR}_1 + \mathrm{LAR}_2)$$

where t_1 and t_2 = time 1 and time 2
W_1 and W_2 = weights at t_1 and t_2
A_1 and A_2 = areas at t_1 and t_2
$\overline{\mathrm{RGR}}$ = mean relative growth rate from t_1 and t_2
$\overline{\mathrm{NAR}}$ = mean net assimilation rate from t_1 to t_2
$\overline{\mathrm{LAR}}$ = mean leaf area ratio from t_1 to t_2

Due to overwintering between Harvests 1 and 2, growth analysis could be performed only on the time periods between Harvests 2 and 3 and between Harvests 3 and 4. Multiple linear regressions for estimating total dry weight and leaf area at earlier times were of the form:

$$\log_{10}(\text{weight or area}) = a + b_1\log_{10}D^2 + b_2\log_{10}D^2H$$

where: D = Diameter; H = Height.

Each estimated value was adjusted through multiplication by the fraction (actual value at harvest) / (estimated value from the harvest's multiple regression equation). In this manner, those trees that are shown to be larger or smaller than the regression estimate (i. e., where a residual exists) can have their estimated weights or areas adjusted appropriately to better estimates of their values at earlier harvests. The assumption involved in this manipulation is

Table 2. — Mean values for measured and calculated variables over all harvests, by country of origin and seed source.

Source	Root (gm)	Stem (gm)	Rachis (gm)	Leaf (gm)	Total (gm)	Area (cm²)	Height (mm)	Diameter (cm)	Area per[1] Leaflet (cm²)	Root Ratio	Stem Ratio	Rachis Ratio	Leaf Ratio	Shoot/ Root
American														
CA	4.127	0.863	0.578	2.571	8.140	611.83	122.2	0.461	9.65	0.529ab[4]	0.104	0.057	0.310	0.954
NY	4.101	0.677	0.442	2.114	7.334	530.17	99.0	0.437	9.68	0.561a	0.098	0.008	0.292	0.847
OH	4.091	0.836	0.518	2.206	7.651	587.97	123.1	0.456	9.54	0.547a	0.104	0.052	0.296	0.868
VA	5.045	0.989	0.703	2.758	9.495	685.81	112.9	0.472	10.77	0.528ab	0.103	0.060	0.309	0.948
WV	3.939	0.904	0.623	2.493	7.959	604.24	107.0	0.476	10.16	0.500b	0.105	0.060	0.336	1.063
$\bar{X}$	4.270 **[2]	0.850 NS	0.571 **	2.430 **	8.122 **	603.43 **	112.6 *[3]	0.460 NS	9.98 **	0.534 **	0.103 **	0.055 NS	0.308 **	0.934 **
Chinese														
I	5.216	0.906	0.622	2.694	9.438	674.4	113.3a	0.480	7.69ab	0.571	0.095a	0.054	0.280	0.778
II	4.439	0.597	0.555	2.412	8.003	547.3	91.5b	0.426	6.89b	0.569	0.081bc	0.055	0.296	0.800
III	4.125	0.678	0.455	2.363	7.621	549.0	103.2ab	0.447	7.49b	0.565	0.089ab	0.048	0.299	0.815
IV	3.691	0.495	0.487	2.147	6.819	519.3	73.2c	0.410	7.92ab	0.552	0.078c	0.058	0.313	0.877
V	5.854	0.953	0.615	2.675	10.097	667.8	113.8ab	0.486	8.64a	0.591	0.089ab	0.049	0.270	0.716
$\bar{X}$	4.754	0.744	0.556	2.487	8.540	598.9	100.7	0.453	7.73	0.571	0.087	0.053	0.290	0.791

[1] Means calculated on basis of last 2 harvests only.

[2] ** Indicates significant differences between countries at 1% level.

[3]) * Indicates significant differences between countries at 5% level.

[4] LSD not significant at 5% level for entries followed by the same letter. Entries with no alphabetical designation were not significantly different at the .05 level.

that the fraction (actual value/estimated value) remains constant for a single seedling throughout the experiment.

Results

Experimental results are tabulated in *Tables 2—6*. The results of nested analysis of variance *(Table 2)* indicated that for the four measured dry weight variables, significant between country differences were found for all except stem dry weight. Seedlings of Chinese origin were significantly greater in total dry weight than American seedlings, possessed larger roots and carried more leaf biomass. American seed sources had a significantly larger leaflet area, were taller and carried more leaf area than the Chinese sources. Analysis of calculated ratios indicated that Chinese seedlings possessed a greater proportion of dry weight in roots than seedlings of American origin. Conversely, American sources possessed a greater proportion of their dry weight in stem and leaf tissue when compared to the Chinese seedlings. The proportion of dry matter in the leaf rachis did not significantly differ between seedling groups. Because of greater root dry matter, shoot-root ratios were significantly smaller for Chinese seedlings than American seedlings. There was no significant correlation among shoot-root ratios and total plant dry weight.

Among seed sources within countries, differences were less evident *(Table 2)*. American seed sources differed only in the proportion of total dry matter in root tissue, while among seed source differences in the Chinese seedlings were evident for height, leaflet area and stem ratio.

Analysis of the relationships between plant parts (using the t-test for significance between two regressions) demonstrated significant differences among seedlings of American and Chinese origins. Among the 78 variable pairs analysed, 23 pairs (29%) yielded a significant between country difference for regression coefficients *(Table 3)*; 5% of the between country comparisons of regression coefficients would be, on the basis of chance alone significant.

Analysis of growth data is summarized in *Table 4*. Significant difference were found among seedlings from the two countries of origin for NAR and LAR between harvests 3 and 4. No significant differences were found for among source variation within country of origin for any growth parameter estimate.

Discriminant analysis using logarithmic transformation of measured variables over all harvests confirmed the results obtained by analysis of variance. A D-square value of 0.983 with an associated F value of 11.45 was significant at the 0.01 level indicating a significant difference between the two seedling populations.

Distribution of genetic variance (expressed as a percent of the total experimental variance observed) among seed sources within country of origin and among mother trees within seed sources varied by country *(Table 5)*. Using a multiway analysis of variance for each country within each harvest and averaging results over all four harvests and over all measured variables, the results indicate that genetic variation is nearly equally distributed among and within seed sources of Chinese origin. In contrast, American genetic variability appears to be disproportionally distributed. Approximately 7% of the observed variation could be attributed to seed source variation while almost 14% of the observed variability could be ascribed to individual mother tree variability. The percent variability accounted for by seed source and mother tree together was not significantly different for seedlings originating from the two countries (21% for Chinese seedlings and 23% for American).

The results of polyacrylamide disc electrophoresis are presented in *Table 6*. Fifteen peroxidase isoenzymes were located in gels of leaf homogenates. The average number of isoenzyme per individual was 7.9 for trees from the American seed sources, and 7.5 for those of Chinese origin.

Table 3. — A list of variable pairs showing significant country effects upon regression coefficients.

X	Y	X	Y
rachis weight	stem weight	root ratio	rachis weight
leaf area	root weight	root ratio	leaf weight
leaf area	stem weight	root ratio	rachis ratio
leaf area	total weight	stem ratio	rachis ratio
leaf area	height	rachis ratio	root weight
leaf area	root ratio	rachis ratio	total weight
leaf area	shoot/root ratio	rachis ratio	stem ratio
height	leaf area	leaf ratio	rachis ratio
height	diameter	leaf ratio	shoot/root ratio
height	stem ratio	shoot/root ratio	leaf weight
height	rachis ratio	shoot/root ratio	rachis ratio
height	leaf ratio		

Table 4. — Growth Parameter Estimates on American and Chinese Seedlings.

		RGR (gm/gm week^{-1})	NAR (gm/cm^2/wk)	LAR (cm^2/gm)
Period 2—3	American	.2715	.00318	84.35
	Chinese	.2696	.00336	81.95
Period 3—4	American	.2585	.00362[1])	76.08
			*	— * —
	Chinese	.2664	.00392	71.19

[1]) * Difference significant at five percent level.
— * — Difference significant at ten percent level.
RGR = Relative growth rate; NAR = Net assimilation rate;
LAR = Leaf area ratio.

This difference was not statistically significant. Isoenzymes 1, 12 and 13 were found in all trees while isoenzymes 4, 10, 11 and 14 demonstrated significantly different frequencies between the American and Chinese populations. All other peroxidase isoenzymes varied but did not differ in frequency of occurrence between the two populations. These results suggest that there are at least some significant genetic differences at the molecular level.

Discussion

The results of this experiment indicate that *Ailanthus altissima* in the United States is genetically variable but is also genetically different from the Chinese ailanthus used in this experiment. Seedlings from the two countries differed for seven of nine measured characteristics and for four of five measurements of biomass distribution. In addition, estimates of NAR and LAR indicate that the seedlings may also differ in terms of their photosynthetic efficiency and leaf area ratios. Similarly, evidency that (between country) differences exist for the relationships among plant parts *(Table 3)* further suggests that genetic differences between the two seedling populations are real.

Table 5. — Percentages of Total Variance Due to Seed Source and Mother Tree, Averaged Over all Four Harvests.

Variable	Seed Source		Mother Tree	
	American	Chinese	American	Chinese
Root weight	2.00	3.26	20.61	10.46
Stem weight	8.73	15.56	10.55	11.97
Rachis weight	8.77	10.40	9.91	11.10
Leaf weight	7.78	2.88	9.87	20.37
Total weight	5.71	5.70	9.60	6.96
Leaf area	3.59	6.40	13.70	16.32
Height	16.16	26.44	14.58	11.89
Diameter	4.01	14.09	22.23	9.90
$\bar{\bar{x}}$	7.09	10.59	13.88	12.37

Analysis of dry weight variables, height and diameter provides evidence that American ailanthus does not suffer from inbreeding depression, nor is there a significant difference in total genetic variation between American and Chinese seedlings.

The following explanations are proposed:

1. d'Incarville sent a large number of seeds with a broad genetic base to the Royal Society of London. When ailanthus was exported to America, a good sample of the English gene pool was used. In addition, concomitant and unrecorded introductions may also have served to increase the gene pool in American populations. Thus, American ailanthus is as genetically variable as Chinese ailanthus and inbreeding depression has not occurred.
2. There have been both natural and artificial pressures placed on American ailanthus populations. Though possibly initially narrow-based, the ailanthus genotype has undergone favorable mutations and/or recombinations and perhaps has responded to artificial and natural selection pressures favoring the more rapidly growing, aesthetically pleasing genotypes.

The effects of mutation and/or recombination within populations of American ailanthus can not be discounted. The species has greatly expanded its population size and has become extensively naturalized within a relatively short time period. This would be expected to provide a favorable *milieu* for the survival of mutant alleles or new recombinations. Consequently, if inbreeding depression occurred shortly following importation to America, the effects of such inbreeding may have been diminished in a few generations by artificial and natural selection of favorable mutations and genetic recombinations.

Table 6. — Frequency of presence and absence for each of 15 leaflet peroxidase isoenzymes observed in American and Chinese populations and Chi square analysis of differences.

Isoenzyme	Country of Origin				Chi Square
	American (N = 194)		Chinese (N = 205)		
	Present	Absent	Present	Absent	
1	194	0	205	0	—
2	50	144	40	165	2.24 N.S.[a]
3	165	39	177	28	0.14 N.S.
4	36	158	16	189	10.14 **[b]
5	20	174	12	193	2.68 N.S.
6	77	117	73	132	0.71 N.S.
7	132	72	132	73	0.59 N.S.
8	120	74	117	88	0.95 N.S.
9	55	139	55	150	0.12 N.S.
10	15	179	6	199	4.62 *[c]
11	109	85	149	56	11.87 **
12	194	0	205	0	—
13	194	0	205	0	—
14	161	33	150	55	5.59 *
15	17	177	10	195	2.38 N.S.
Avg. bands/ individual	7.9		7.5		

a) Not significant different at the 95% level.
b) Significantly different at the 99% level.
c) Significantly different at the 95% level.

Because ailanthus has been used extensively in the United States as an ornamental, it appears possible that nurserymen, by the selection of aesthetically pleasing specimens for ornamental use, may have caused differences in the American and Chinese populations. For example, selection for height (i.e. the "healthiest seedlings") most probably occurred. Similarly, trees with a large leaf surface area may have been selected because of their aesthetic value while trees with relatively small root systems may have been easier to transport and transplant. Changes in other less obvious characteristics may have occurred by either random drift or because of genetic correlations with the above mentioned morphological characteristics. Recent relaxation of selection pressures has apparently not obviated this effect.

The alteration of the genetic variance in American populations, from a 1 : 1 ratio of seed source : mother tree within seed source (as present in Chinese populations) to a 1 : 2 ratio, may be explained by consideration of the effects domestication might have had on patterns of genetic variability. In Chinese populations, it can be argued that natural selection has been a relatively undisturbed process and that a nearly equal distribution of genetic variance among seed source and mother trees within seed source is an outcome of selection pressures at both the population and inidividual tree levels. In contrast, in the United States selection at the individual tree level coupled with transportation of individual trees from one location to another by nurserymen may have diluted any natural selection which may have occurred at the seed source (population) level and enhanced (on a relative basis) differences among individual mother trees.

Summary

By use of comparison of regression coefficients, analysis of variance, discriminant analysis and isoenzyme analysis, American ailanthus seedlings were found to be distinctly different from seedlings of Chinese seed sources. Over four harvests of seedlings from both countries, eleven of fourteen variables studied showed significant country differences. Thus, under the assumption that representative gene pools were used for experimentation significant alteration of genetic content has occurred in the introduction and naturalization of ailanthus in the United States.

Although total dry weight of American seedlings was less than that of Chinese seedlings, height and diameter and leaflet size indicated that inbreeding depression does not exist within American ailanthus. American seedlings were as genetically variable as Chinese seedlings. Consequently, two explanations are possible. First, no significant reduction of gene pool occurred when the species was introduced into the United States and second, mutation and recombination may have been factors involved in increasing genetic variance within the American populations if the initial gene pool was small. American seed sources were less diverse than Chinese seed sources while variance of individual trees within seed sources was greater. Thus, American ailanthus has undergone shifts in the distribution of genetic variance among seed sources and individual trees since its introduction two centuries ago.

Key words: Ailanthus altissima, domestication, genetic differentiation.

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