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Influence of year of cone collection on seed weight and cotyledon number in Abies procera

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Introduction

In studies of natural variation of plant parts of wide-ranging forest species, plant samples may all be collected in 1 year or different samples may be collected in different years but treated as if there were no effects due to year of collection. Theoretically, a year effect is possible, either of environmental origin or, if progenies are being evaluated, of paternal origin. In the latter case, the paternal contribution could change from year to year due to different proportions of self-pollination or to different sources of cross pollen.

We report here results of a study of seed weight (SW) and cotyledon number (CN) in which seeds were collected from the same individual trees at four locations (two in Washington and two in Oregon) in 2 years (1967 and 1968). Effect of year on SW and CN and the relationship between the two traits were investigated. Inclusion of both SW and CN in the study of year effects provided a character predominantly of maternal origin (SW) (RICHTER, 1945, SQUILLACE, 1957) and one with a paternal contribution (CN) (SILEN *et al.*, 1965, and unpublished).

Material and Methods

Seeds were extracted by hand and filled and empty seeds were separated by X-ray. From each single tree collection (40 lots total), 10 filled seeds were taken at random. Seeds were weighed individually, and cotyledons were counted on the embryos they contained. Variation was analyzed on an individual seed basis using the analysis in *Tab.* 1.

Provenances were treated as random, having been chosen only to represent the region. Years were treated as random since they were not chosen to represent any special characteristic of year but only year-to-year variability. They did happen to include a year with heavy cone crop (1967) and one with a relatively light crop (1968). Trees were likewise random except that they had to have cones since we were working with a seed trait; seeds were random as noted above. A test was not made on provenances. Only an approximate test would have been possible *(Tab. 1)*, and in this investigation our interest was in the year effects rather than place effects.

Pooled within-seed-tree and within-provenance correlations between SW and CN were determined according to SNEDECOR and COCHRAN (1967, p. 185—88).

Results

Year effects including interactions with places and trees in places made up an estimated 45% of the variance in SW and 25% of the variance in CN *(Tab.* 2). The greatest difference between the 2 years for a single source was 0.86 cotyledons (5.94 to 6.80) in CN and 2.34 g (6.16 to 8.70) in SW. Average differences between the 2 years were 0.48 cotyledons and 1.69 g SW.

Unexplained variation (remainder) was much higher for CN than for SW. Perhaps this was due to the pollen contribution to CN variance. Coefficients of variation were 12.9 and 12.1% for SW and CN, respectively.

Average correlation coefficients (r) between SW and CN were 0.13 (pooled trees within provenances) and 0.06 (pooled seeds within trees). Correlations coefficients for the different provenances did not differ significantly, nor did correlation coefficients for the different trees within prove-

Table 1. — Sources of variation and expected mean squares used in testing (SCHULTZ, 1955).

Sources of variation	Degrees of freedom	Expected mean squares[1])
Total	psty—1	
Provenance (P)	p—1	σ^2syt (p) + Sσ^2yt (p) + STσ^2py + SYσ^2t (p) + STYσ^2p
Trees in provenances (T in P)	p (t—1)	σ^2syt (p) + Sσ^2yt (p) + SYσ^2t (p)
Years (Y)	y—1	σ^2syt (p) + Sσ^2yt (p) + STσ^2py + PSTσ^2y
Y × P	(p—1) (y—1)	σ^2syt (p) + Sσ^2yt (p) + STσ^2py
Y × T in P	p (y—1) (t—1)	σ^2syt (p) + Sσ^2yt (p)
Remainder	pty (s—1)	σ^2syt (p)

[1]) "Trees in provenances" represented by t (p) and "seeds" by s in the expected mean squares.

nances. This indicates that the relationship between SW and CN was consistent for the various sampling places and trees.

Discussion

Year-to-Year Variation in Seed Weight and Cotyledon Number

Seeds are relatively easy to obtain, transport, and store. Both SW and CN and are quick and easy to evaluate. Seed size is considered to be one of the least plastic plant characters (PALMBLAD, 1968). For these reasons they are often among the traits used in describing intraspecific variation and, in some cases, for identifying seed collections of unknown provenances. However, in this test significant year effects and year-place and year-tree interactions were all present. Year effects on SW have also been reported for European larch *(Larix decidua)* (HEIKEN and SØEGAARD, 1962), Scots pine *(Pinus silvestris)* (STROHMEYER, 1938) and soybeans *(Glycine max)* (BASNET *et al.*, 1974). An interaction of varieties with years was found in soybeans.

FRANKLIN and GREATHOUSE (1968) reported SW's and CN's for provenances of the noble fir-California red fir *(Abies procera* REHD. and *A. magnifica* var. *magnifica*, respectively) complex extending over 11° in latitude. Average CN's ranged from 4.88 to 8.22 and 100-seed weights from 3.30 to 10.26 g based on examination of 1 year's seed collections. It was suggested that "an average count within ±0.3 cotyledons of known source would seem to be at least an acceptable comparison" for broadly identifying sources. No specific recommendations were made concerning SW.

In the present test, the four sources extended over 2° 30' latitude and 2 years of sampling were included. The average difference between the 2 years amounted to 14 and 23% (CN and SW, respectively) of the range reported for the species complex for the 1967 collection (FRANKLIN and GREATHOUSE, 1968). For the source showing the greatest yearly effect, the differences between the 2 years equaled 26 and 34% of the range reported for the species complex. It is concluded that in spite of the relative stability of the traits, the year effects are large enough to make source identification unreliable except within much wider limits than previously expected.

Estimated mean square for years was larger relative to the variance for places in the SW trait than it was in the CN trait. Coefficients of variation were about the same, indicating similar precision for similar expenditure of seeds. Consequently, CN, because it seems less sensitive to the factors causing yearly variation, may be a more useful trait for identifying noble fir sources or describing variation patterns.

Influence of Seed Weight on Cotyledon Number

CN, at least in forest trees, has been considered more as dependent of SW than as an independent trait (BUCHHOLZ, 1946, MASCHNING, 1971, STROHMEYER, 1938). However, in this test and elsewhere (HOLZER, 1966, SQUILLACE, 1966, HELLUM, 1968, esp. *Fig. 4*) it appears that when site effects are removed, little of the variation in one trait is associated with variation in the other.

Additional evidence for the independence of CN comes from inbreeding and reciprocal crosses. In several instances inbreeding has increased CN but not SW (FOWLER, 1965, SORENSEN and MILES, 1974, SORENSEN *et al.*, 1976), and conversely, seed from reciprocal crosses has differed greatly

Table 2. — Results of analyses of variance and estimated components of variance for seed weight and cotyledon numbers in noble fir. Collections made in 2 years at four places.

Source of variation	d. f.	Estimated components of variance (seed weight × 10⁴)	(percent)	Estimated components of variance (Numbers of cotyledons × 10)	(percent)
Total	399				
Provenances	3	2.24n.t.	46	2.40n.t.	25
T in P	16	0.00n.s.	0	0.03n.s.	0
Y	1	1.22*	25	0.95n.s.	10
Y × P	3	0.00n.s.	0	0.55*	6
Y × T in P	16	1.00**	20	0.84*	9
Remainder	360	0.45	9	4.54	49

** Significant at 0.01 level of probability.
* Significant at 0.05 level of probability.
n.s. Nonsignificant.
n.t. Not tested.

in SW but only slightly in CN (SILEN *et al.*, 1965 and unpublished).

An adaptive function of CN has not been established, but the unusually high photosynthetic rates of young cotyledons (KRUEGER, 1963) indicate that it could affect root and shoot growth in a like manner to seed size (BAKER, 1972). As a result, significant SW-CN correlations could occur in provenance tests, not because of a dependence of CN on SW, but because the two characters are responding to similar selection pressures.

Summary

Seed weight (SW) and cotyledon number (CN) were determined on individual seeds collected from the same trees at four locations in 2 years. Year and year-interaction effects accounted for 25% of the variation in CN and 45% of the variation in SW. Correlation between SW and CN was not significant when based on individual seeds within trees. Evidence for the adaptive importance of CN and its independence of SW is discussed.

Key words: provenance, year-provenance interaction, year-tree interaction, adaptation.

Zusammenfassung

Das Gewicht (SW) und die Kotyledonenzahl (CN) einzelner Samen von Bäumen verschiedener Herkunft wurde bei zwei Samenjahrgängen ermittelt. Der Einfluß des Erntejahres zusammen mit den Wechselwirkungen, Jahr × Herkunft, und, Jahr × Einzelbaum-innerhalb der Herkunft, erklärten 25% und 45% der Gesamtvarianz von CN bzw. SW. Die Korrelation zwischen CN und SW, bezogen auf Samen von einzelnen Bäumen, war statistisch nicht zu sichern. Die Zweckmäßigkeit SW und CN zur Bestimmung der geographischen Herkunft zu verwenden, wurde zusammen mit der Bedeutung der CN für den Wachstumserfolg von Sämlingen diskutiert.

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