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Relating Pine Seed Coat Charxteristics to Speed of Germination, Geographic Variation, and Seedling Development

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Loblolly pine—Pinus taeda L.-evaluations indicate that speed of germination, which refects dormancy, is directly related to the ratio of the weight of the seed coat to total seed dy weight. Further evaluations with loblolly and ponderosa pine-P. ponderosa Dougl. ex Laws.—show significant correlations between the ratio of seed coat weight to total seed weight and ecotypic variation and seedling development. Seed dormancy was shown to vary by geographic location and to influence seedling development if stratification treatments are not optimized for conditions under which germination occurs. This finding may result in the maternal effects of the seed coat obscuring other genetically controlled growth processes early in seedling development. The effect of these early seed coat differences on seedling development can be minimized by extending the length of seed stratification. Tree Planters' Notes 48(1/2): 38-42; 1997.

The influence of seed size and weight on early seedling growth of tree species has been studied for over 50 years (Baldwin 1942; Champion 1928; Gast 1937). Righter (1945) found that, in the genus *Pinus,* the positive correlation between seed weight and seedling height was temporary and disappeared after time in the field. A more recent study with loblolly pine (*Pinus taeda* L.) has shown a statistically significant positive correlation between seed weight and tree height after 15 years (Robinson and van Buijtenen 1979). Khalil (1981) reported that seed weight in white spruce (*Picea glauca* [Moech] Voss) was positively connected with annual growth of the terminal shoot at 2 and 4 years.

Several studies have evaluated the effect of size and other seed properties on germination and early seedling development. The evidence that seed size alone is a useful criterion for predicting seedling performance continues to be conflicting (Belcher and Gresham 1974; Bamett and Duniap 1982; Wrzesniewski 1982). Other seed parameters that may be closely related to size are probably more directly related to seed and seedling performance. Dunlap and Bamett (1983) found that larger loblolly pine seeds germinated more quickly and produced larger germinants than smaller ones after 28 days. Size differences resulted from differences in the rate of germination are unique to each size class. Seedling size and possibly uniformity of growth were considered a function of germination patterns that were strongly influenced by seed size and weight. Results from a number of studies have shown that germination rates (Barnett 1979; Dunlap and Bamett 1984; McLemore 1969) and subsequent seedling growth (Bamett and McLemore 1984; Boyer and others 1985) can be manipulated in pines by means of seed stratification procedures. Seed stratification affects rates of germination of dormant seeds and, it turn, affects early seedling development. Therefore, parameters that are detrimental to or closely related to rates of germination may provide a better means of predicting early seedling performance than seed weight or size alone.

Review of Seed Coat-Germination Relationships

The relationship of the ratio of seed coat weight to total dry seed weight was evaluated in a number of southern pine species with a wide range of dormancy (Bamett 1976). This work showed that as much as 69% of the variation in speed of germination in 5 southern pine species was related to seed coat weight as a proportion of total seed dry weight. Speed of germination was expressed as days to reach peak value-the mean daily germination of the most vigorous component of the seed lot (Czabator 1962). This relationship was supported by evidence that constraint by the seed coats and megagametophytes is directly related to dormancy. Measurements of water absorption indicated that seed coats *restricted* water uptake by limiting how much the megagametophyte and embryo could expand. Loblolly pine seeds, the most dormant of the tested seeds, attained only about 36% moisture content (dry weight basis) until the seed coats cracked and germination began. In contrast, longleaf pine (*Pinus palustris* Mill.) seeds (the least dormant of the tested seeds) never completely stopped imbibition and attained 55% moisture content before germination began. Changes in size of the megagametophyte, with and without seed coats, support the theory that seed costs restrict imbibition by preventing swelling and limiting water absorption in the more dormant seeds.

Respiration also followed the trends of moisture imbibition (Barnett 1976), and the patterns appeared to result form imbibition levels rather than impermeability to oxygen. Germinability of de-coated seeds after different lengths of imbibition with seed coats intact and in atmospheres with various oxygen concentrations also supported the hypothesis that the seed coats slow germination by restricting megagametophytes and embryo expansion (Barnett 1972).

The total seed weight is determined by the seed coat, megagametophyte, and embryo. As the weight of the seed coat increases, the proportional weights of the embryos of total weight decreases (table 1). For 5 southern pines—longleaf, Sonderegger (*P.* × *sondereggeri* H. H. Chapm.), shortleaf (I? *echinata* Mill.), slash (*P. elliottii* Engelm.), and loblolly-the correlation coefficient was -0.930 (Barnett 1976). The same relationship for 5 different ecotypes of ponderosa pine (*P.* ponderosa Dougl. ex Laws.) was computed from Anantachote's data (1980) to be -0.015. Because the two parameters (weights of seed coats and embryos) are closely related, seed coats were used in the present evaluations because they were easier to measure.

The close correlation between speed of germination and the ratio of the seed coat to total seed weight provides a means of rapidly estimating relative seed dormancy. The technique may more reliably estimate innate or true dormancy than seed germination tests, particularly in lots of stored seeds. Secondary dormancy can be induced in pine seeds by unfavorable conditions during processing and storage (McLemore and Bamett 1966, 1968) and by adverse light and temperature regimes (McLemore and Hansbrough 1970; McLemore 1966), and secondary dormancy may mask the innate dormancy of seeds.

Relating Seed Coats to Ecotypic Variation

Progeny tests with many coniferous species show that 60 to, 90% of the variation in seedling size is closely related to maternal factors (Perry 1976). The seed characteristics of pines and other gymnosperms are largely derived from female tissue because only the embryo contains genes from the pollen or male parent. Thus, it should be expected that seed coat properties are related to seedling performance. The early expression of these maternal traits may affect the measurement of other genetic responses.

Loblolly pine seed lots from across the range of the species were evaluated to assess the variation in seed properties. Seed weight was unrelated to either latitude or longitude of the source (table 2). However, seed coat weight-expressed as ratio of seed coat weight to total seed weight-was positively correlated to latitude and negatively correlated to longitude. If seed coat thickness is directly related to dormancy or speed of germination, the degree of dormancy in loblolly seeds should increase in the northern and eastern portion of the range and should decrease in the southern and western portion of the range. Thorbjomsen (1961) evaluated loblolly pine seed coat thickness and found thin seed coats in the western part of the range and thicker ones in the eastern part of the range.

Anantachote (1980) also evaluated ponderosa pine seedling development for a wide range of seed parameters and ecotypic selections; however, he did not attempt to relate the ratio of seed coat or embryo weight to total seed weight to geographic distribution or seedling development. A reevaluation of these ponderosa pine data shows a relationship very similar to that of loblolly pine. Percentages of the seed coat weight to total seed weight range from 39 to 53.2 and are negatively related to embryo weight (table 3). Correlations of seed coat weight as a proportion of total weight, with locations within each ecotype of ponderosa pine, provided some interesting relationships (table 4). The proportion of the seed coat was significantly related to longitude and elevation of the seed source (-0.96 and 0.89, respectively). No relationship was found with latitude of the source. However, when the product of latitude and elevation was evaluated, a positive correlation coefficient of 0.94 was obtained. Thus, seed dormancy was greater at the higher elevations in the interior portion of the range (figure 1). The coastal sources were less dormant.

Table 1-Proportions *of the seed parts to total dry weight and* corresponding *germination data for the southern* pine *seeds (adapted from Burnett 1976)*

	Proportion of seed parts (%)			Germination data		
Species	**Seed** coat	Gametophyte	Embryo	Total germination (%)	Germination value	Peak day
Longleaf	29.2	60.2	10.6	91	44.6	6.0
Sonderegger	35.1	56.5	9.4	97	43.4	7.4
Shortleaf	35.0	55.6	9.2	92	22.0	10.0
Slash	43.5	49.9	6.6	94	25.2	9.6
Loblolly	56.4	37.4	6.2	96	24.1	12.5

Table 2-*Relation* of ***geographic*** seed source of half-sib families of *loblolly pine to seed* weight *and proportion* of the seed coat to total ***dry weight***

	Location of seed source			
County & state	Lat.	Long.	Avg. seed weight* (mg)	Proportion of seed coat to total seed weight† (%)
Cherokee, TX	31” 21’	94” 40	32	54
Grant, AR	34” 25	92” 20	25	57
Lawrence, AL	34° 30	87° 20	36	60
Jackson, NC	35” 15	83” 05	30	62
Hertford, NC	36” 25	77° 50	26	63

* No statistically significant relationship was found between seed source and seed weight.

† Correlation coefficients between latitude and longitude and proportion of the coat to total seed weight were 0.94 and -0.98. respectively. Data are based on 3 replications of 50 seeds each

Ta*°*le 3—***Relationship*** of *geographic seed source* of *half-sib ponderosa pine* ***families*** *to seed characteristics and seedling* ***development (developed*** *from Anantachofe* ***1980)***

	Location of ecotypfc source			Proportion of total weight† (%)		Seedling development‡ (cm)			
						Primary root length		Shoot length	
Ecotype*	Lat.	Long.	Elev. (m)	Seed coat	Embryo	2 moe.	9 mos.	2 mos.	9 mos.
A-California	35” 5	120” 2	1,524	41.5	8.5	69.8	86.0	7.8	15.5
S-No. plateau	44° 8	118” 5’	1,348	39.0	7.5	70.0	81.8	8.6	14.2
C-So. interior	36” 0’	113° 0’	2,134	47.0	6.0	85.5	86.9	4.5	11.5
D-Cen. interior	37” 2	105’7	2,165	53.2	4.0	84.7	84.0	4.8	9.0
E-No. interior	44° 5	105° 5	1,913	51.0	5.4	65.5	74.7	4.6	8.3

* The 5 ecotypes of ponderosa pine (Wells 1963) and the location of the sample stands:
A = California, B = Idaho and Oregon, C = Arizona, D = Colorado & New Mexico, and E = South Dakota & Wyoming.

† Seed characteristics were determined by measuring 5 randomly selected stands from each of 16 half-sib families. *The number of family selections in each ecotype were* A, 2; B, 2; C, 3; D, 4; and E, 5.

‡ *Seedling characteristics were determined by measuring 2 plants from each family in each of 3 groups of boxes grown under greenhouse conditions.*

Table 4—***Correlation coefficient*** relating ***proportion*** of ***ponderosa*** *pine seedcoafs of total seed* ***weight,*** *geographic location, and seedling development (from Anantachote* ***1980)***

Variables correlated with proportion of seed coat of total seed weight	Correlation coefficient*
Proportion of embryo of total weight	-0.915
Latitude of ecotypfc sources	- 0.267
Longitude of ecotypic sources	-0.959
Elevation of ecotypfc sources	0.692
Latitude times elevation	0.938
Primary root length (2 months)	-0.957
Primary root length (9 months)	-0.314
Shoot length (2 months)	-0.796
Shoot length (9 months)	-0.938

* *A value of ±0.878 is necessary for statistical significance at the 0.05 level.*

Relating Seed Coats to Seedling Development

Anantachote (1980) provides the best data relating the ratio of the seed coat to total seed weight to seedling development. He determined the growth of the primary root system of ponderosa pine seedlings grown in glass-sided boxes in **a** greenhouse environment. Root elongation was measured at 2 and 9 months (table 3). At 2 months, root length was negatively related to the ratio of the seed coat weight to total weight (r = - 0.957) (table 4). However, at 9 months, no significant correlation was obtained. The same associations were determined with shoot length at 2 and 9 months. Correlation coefficients of - 0.796 and - 0.935 were found, relating shoot length at 2 and 9 months to the ratio of the seed coat of total seed weight (table **4).**

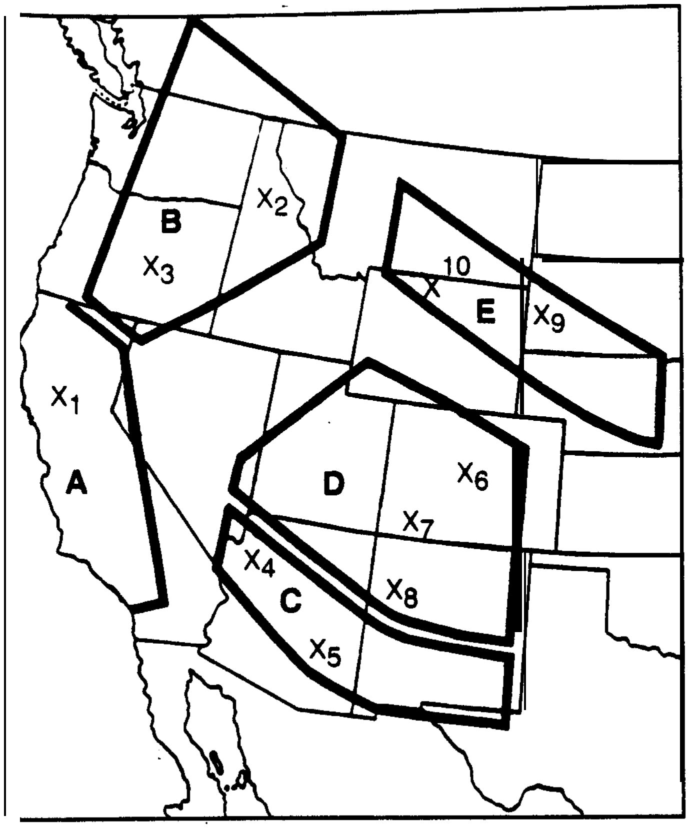

Figure 1—*The 5 ecotypes of ponderosa pine* (Wells 1963) *and the location of the sample stands. A =* California *(sample stand 1), B = north plateau (sample stands 2 and 3), C = southern* interior (Sam*ple stands 4 and 5), D = central interior (sample stands 6, 7, and 8), E =* northern interior *(sample stands 9 and 10) (adapted from Anantnckote 1980).*

These data may indicate that seeds that are less dormant and germinate faster also begin root and shoot development sooner. However, the data are not sufficiently well documented to determine if speed of germination was definitely related to seedling growth.

Discussion

Although significant correlations do not necessarily reflect causal relationships, when evaluated with other biological sound data, they are important indicators of biological responses. Earlier research has established that dormancy or speed of germination in southern pines is related to embryo constraint by the seed coat and megagametophyte (Bamett 1972, 1976; Carpita and others 1983). This relationship probably holds for other pine species. Recent research has also shown that larger loblolly pine seeds produce larger seedlings primarily because they germinate more promptly (Dunlap and Bamett 1983).

Stratification of seeds usually results in faster germination, which is why stratified seeds usually produce larger plants that unstratified ones. When stratified and unstratified seeds germinate on the same date, stratification has no affect on development (Bamett and McLemore 1984). A few days difference in time of germination may significantly affect seedling development (Boyer and others 1985). Therefore, it is easy to understand how differences in seed dormancy may affect seedling development. Short periods of stratification may seem to eliminate these differences in rate of germination when evaluations are made under standard laboratory conditions. However, when germination occurs in the field or on nursery beds where conditions are less than optimum, the rate of germination is markedly reduced, and seedlings from late germinating seeds tend to produce inferior quality plants because of competition from previously established seedlings (McLemore 1969; Dunlap and Bamett 1984).

Seed dormancy in loblolly and ponderosa pine varies ecotypically with northern and eastern sources, and higher elevations have greater dormancy. This variation may also occur with other pine species. Particularly with ponderosa pine, a species that has a wide range of geographic diversity (Wright 1976), this variation in dormancy probably reflects the differences in precipitation, temperature, and day-length at the seed source. These trends probably reflect natural selection; that is, if seeds germinate too early, they may be killed by frost and, if too late, by competition for light and moisture from earlier seedlings (Campbell and Ritland 1982). The response of seeds to environmental cues during dormancy should tend to maximize fitness of optimizing the timing of germination (Levins 1969).

Maternal factors such as seed coat properties that influence the speed of germination can obscure the nature of genetic control of subsequent growth processes (Perry 1976). Less than 15% of the weight of a conifer seed is in the embryo, which is the only portion with a genetic component from the male parent. In nature, stratification is usually optimized as a result of natural conditions, but in nursery production, the genetic component from the male parent may be obscured when researchers do not optimize the stratification needs of the seed lot. Seed dormany varies by geographic location or ecotype, and stratification procedures should be designed to meet the needs of each ecotype. These stratification needs should be determined under the stress conditions that relate to nursery bed conditions where seeds are to be sown. However, the stratification period can be extended to minimize the effect of the seed coat on initial seedling development.

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