CONE AND SEED WEIGHT RELATIONSHIPS IN DOUGLAS-FIR FROM WESTERN AND CENTRAL OREGON

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Abstract. Cone sizes and weights and seed weights were determined for 89 trees in 9 stands in the Oregon Coast Ranges, Cascade Ranges, and central Oregon. From west to east this represented a transition from mesic to xeric sites and from longer to shorter growing seasons. Differences among regions for all cone traits, and regression coefficients for change in cone and seed weights with distance from the ocean, were significant. Cone size and weight decreased, seed weight increased, and the regression coefficient of seed weight on cone weight, based on trees within regions, increased with distance from the ocean. Geographic variation in cone and seed weights was compared with variation in the phenology of cone and seed development as reported in the literature. This comparison indicated that where relatively large seeds were important to regeneration success and the growing season was short, Douglas-fir showed at least 3 changes in the timing of development as compared with milder sites. (1) The cone growth period was reduced more than the seed growth period. (2) The overlap in time of the developmental cycles of cone and seed was increased. (3) Cones and seeds grew during an increased portion of the growing season.

Key words: Adaptation: Douglas-fir; length of growing season; natural selection; Oregon; racial variation; trees.

INTRODUCTION

Seed size often increases with increasing dryness (Baker 1972), presumably because of the need on dry sites for vigorous early seedling development. In many coniferous species seed size is also found to increase with increasing cone size (Willis and Hofmann 1915, Eliason and Heit 1940, Plym Forshell 1953, Squillace 1957, Florescu et al. 1960, Dushkevitch 1961, Veracion 1964, Goggans and Posey 1968). Cone size, in turn, often increases with geographic changes that are associated with an increase in the length of the growing season, for example, decreasing latitude (Langlet 1938, Sziklai 1969) and decreasing elevation (Atay 1959, Hermann 1968).

In Oregon, on the average, elevation increases, moisture decreases, and length of the growing season decreases from the Pacific Coast to the central part of the state. This means that from west to east seed size would be expected to increase because of increasing dryness, but to decrease because of decreasing growing season length and decreasing cone size. We report here an analysis of seed size/cone size relationships in Douglas-fir (Pseudotsuga menziesii) along a transect from the Coast Ranges to central Oregon.

METHODS

Ten undamaged cones were taken at random from upper-crown cone collections from ten 50- to 100-year-old trees at 3 locations within each of the following regions: (1) Coast Ranges, (2) Cascade Ranges (upper elevation and east slopes), and (3) central Oregon (Table 1). Cone length and maximum width (measured with calipers to the nearest millimetre), dry weight (after 72 h at 80°C), and number of scales (in the part of the cone bearing round seeds) were determined for each cone. Seeds were extracted from the entire collection from each tree, separated on an air column into filled and empty seeds, and the number of filled seeds determined. Seed weight was calculated from 100-seed samples of filled seeds.

One-hundred-seed weights, numbers of filled seeds per cone, and weight of filled seeds per gram of cone (dry weight) were analyzed using a nested classification. Sources of variation were regions, seed sources within regions, and trees within seed sources. Cone traits were analyzed similarly, but included cones within trees as an additional level of sampling.

One-hundred-seed weight, cone weight, and filled-seed weight per gram of cone weight were regressed on distance from the ocean, and 100-seed weight and seed weight per gram cone weight were regressed on cone dry weight. Because variation among locations within regions was not significant, the regressions were based on regional means or on tree means within regions. Within-region regression lines were compared using analysis of covariance after testing for homogeneity of variance (Snedecor and Cochran 1967).

RESULTS

Differences between regions and between trees within regions were highly significant for all cone traits (Table 2, top). Differences between locations within regions were nonsignificant or, in the case of cone scale number, barely so and contributed only a minor component to the variation. The uniformity within regions vis-à-vis between regions suggests, at first glance, nongenetic differences between regions. However, because the sample points within regions were close together and the regions large, the results also
would be consistent with a clinal pattern of variation. Neither regions nor locations within regions differed significantly for seed weight traits.

Cone size, by all criteria, decreased as distance from the ocean increased, while 100-seed weight increased and weight of filled seeds per gram cone dry weight fluctuated irregularly. Regression coefficients testing the response of cone weight and seed weight to distance from the ocean were both significant \((p < .05)\), and estimated with each 100-km increase in distance from the ocean at latitude 45°N an increase in 100-seed weight of .05g and a decrease in cone weight of .97g.

The regression coefficient of seed weight on cone weight using region means was not significant. Regression coefficients based on trees within regions were positive, being steepest for central Oregon and flattest for the Coast Ranges. The coefficients differed significantly among themselves \((p < .05)\) (Fig. 1).

Cones from the 3 regions did not differ in number of sound seeds per cone nor in weight of filled seeds produced per gram dry weight of cone. When the latter trait was regressed against cone weight using region means and values for trees within region, the calculated \(b\)-values were not significant, but in all cases the weight of seeds per gram of cone weight decreased with increasing cone weight.

**Discussion**

Changes in seed and cone weights followed the expected trends. Seed weight increased from west to east with increasing dryness of the site and cone weight increased with increasing moisture and increasing length of growing season. Within a region (i.e., within areas of similar moisture conditions and growing season length) the expected positive relationship between seed weight and cone weight was observed. However, between regions the seed weight/cone weight relationship was not positive. When regeneration and growing...
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conditions required it, the species was able to produce relatively large seeds in relatively small cones and in a relatively short growing season. Information in the literature on reproductive growth and phenology of Douglas-fir indicates that this has been accomplished primarily by adjusting the timing of seed and cone development within the growing season, and probably to a lesser extent by differences in rates and durations of seed growth.

Growth rates of Douglas-fir embryos have been recorded at 180 and 915 m in the Oregon Coast Ranges (Wheeler 1967). Temperature-development rate relationships were remarkably similar at the 2 elevations, as were the average temperatures during embryo growth (Wheeler 1967, p. 61). Average temperatures (Johnsgard 1963) for representative stations in the 3 regions we sampled during the expected periods of embryo growth (June and July in the Coast Ranges, July and August in the Cascades and central Oregon) were 15.9, 16.1, and 16.2°C, respectively. If the temperature-growth relationship observed by Wheeler (1967) is general, then the occurrence of seeds of similar size would imply that the seed growth periods were also of similar length. The fact that seed weight did increase by ~10% from west to east indicates that seed growth rates or growing season lengths may have varied somewhat between localities. Nevertheless, the observations suggest considerable uniformity in rate and duration of seed development.

However, cone development periods and vegetative phenology have been observed to differ greatly, both in length (Table 1) and with respect to each other. At low elevations in western Oregon, Douglas-fir pollen flight is about mid-April, cones reach maximum dry weight in early August, and seed shed starts in early September (Ching and Ching 1962); at upper elevations in the Cascades, pollen shed does not occur until mid-May to early June and seed fall starts in mid-September to early October (personal observations). At low elevations, vegetative bud flush occurs 6–7 weeks after floral bud flush (Sorensen and Campbell 1971). At high elevation the separation is 3–4 weeks (personal observations). At low elevation, cambial growth is still strong at the time of seed shed. At high elevation it is over by the time of seed fall (Emmingham 1977).

Taken together, these observations indicate that where relatively large seeds are advantageous and the growing season relatively short, Douglas-fir has been able to adapt primarily because the length and the timing of vegetative, cone, and seed growth periods could vary independently. We propose specifically that under the conditions of increasing dryness and shortness of growing season, (1) the cone growth period has decreased more than the seed growth period, (2) the overlap in time of growth of cone and seed has increased, and (3) the proportion of the growing season used for cone and seed growth has increased.

As a result of the first response, variation in the length of growing season, even of the cone growth period, need not be accompanied by comparable variation in individual seed weight. As a result of the second and third responses, seeds and cones develop in common environmental conditions for a larger portion of the growing season on sites with short seasons than on sites with long seasons. Consequently, seed size should be more closely related to the cone size where the growing season is short.

The third response also suggests that if the growing season is short, the time available for late summer seed and cone maturation may be much shortened. For example, collecting Douglas-Fir cones 2 weeks before natural cone opening may give cones and seeds which are much more immature on sites with short seasons than on sites with long seasons.

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