

VARIATION IN NEEDLE CHARACTERS OF *PINUS RADIATA* FROM MAINLAND CALIFORNIA¹

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ABSTRACT

Three needle characters were studied in 10-year-old *Pinus radiata* D. Don trees of mainland California origin growing in Kaingaroa Forest. In all, 238 trees from 10 families within subpopulations \times 5 subpopulations within populations \times 3 populations were sampled. No differences between subpopulations within populations were detected for any of the traits, in contrast to a previous study within natural stands. The populations differed strongly in needle length, rather less in fascicle dry weight, and not significantly in weight/length ratio. The Cambria population had the longest needles and the Ano Nuevo population the shortest, although in the natural stands longer needles had been observed at Ano Nuevo than at Monterey. It appears that results from within natural stands largely reflected environmental effects.

INTRODUCTION

Forde (1964a; b; c) studied variation of branch, cone, and needle characters in natural stands of *Pinus radiata* D. Don in mainland California. She found numerous morphological differences both between the three populations at Ano Nuevo, Monterey, and Cambria, and between stands (subpopulations) within these populations, but any genetic effects were necessarily confounded with non-genetic ones. Offspring of 50% of Forde's sample trees have since been planted in common environments in New Zealand in a combined provenance-progeny trial. From this experiment, Burdon and Bannister (1970; 1973) have confirmed genetic differences between all populations, albeit in younger trees and mostly for very different characters, but have obtained no firm evidence relating to differences between subpopulations.

The study reported in this paper was immediately concerned with whether certain differences which Forde had found between populations and, more especially, between subpopulations, were actually genetic. It involved three needle characters — length, dry weight per fascicle, and dry weight/length ratio. Needle length had been studied by Forde, while weight/length was included here in lieu of Forde's direct but laborious measure of needle thickness.

¹ A more detailed but unpublished account of the work (N.Z. For. Serv., For. Res. Inst., Genet. & Tree Impr. Internal Report No. 84) is available from the author.

MATERIAL AND METHODS

The experimental stand was 10 years old from seed (9 years from planting) in Cpt 918, Kaingaroa State Forest, with effectively a fully randomised layout (Bannister, 1966). The trees potentially available for study represented 2 trees within families \times 10 wind-pollinated families within subpopulations \times 5 subpopulations within populations \times 3 populations. Of these 300 trees, 62 either died or were rejected as subdominant or unhealthy, leaving appreciable imbalance of numbers of trees per family and slight imbalance of numbers of families per subpopulation.

From each tree one fascicle was taken approximately 15 cm from the tip of each of five vigorous second-order laterals which were spread around all aspects of the free-growing crown. As soon as possible after collection all needles were oven dried, and then stored for weighing in a constant-humidity room. For each tree were obtained:

- (1) mean needle length (mm) in each complete 3-needled fascicle;
- (2) aggregate dry weight (mg) of all such fascicles;

from which were estimated:

- (1) Mean needle length (mm);
- (2) Mean weight per fascicle (mg);
- (3) Mean weight per unit of fascicle length (mg/mm).

An unbalanced fully hierarchical analysis of variance (Mahamanulu, 1963) was used and the phenotypic variance (σ_p^2) was assumed to be of the form

$$\sigma_p^2 = \sigma_p^2 + \sigma_{s:p}^2 + \sigma_{f:s}^2 + \sigma_{w:f}^2$$

where σ_p^2 = variance between populations

$\sigma_{s:p}^2$ = variance between subpopulations (localities) within populations

$\sigma_{f:s}^2$ = variance between families within subpopulations

$\sigma_{w:f}^2$ = variance between individual tree values within families.

In the case of needle length $\sigma_{w:f}^2$ could be partitioned as follows:

$$\sigma_{w:f}^2 = \sigma_{t:f}^2 + \sigma_e^2/n$$

where $\sigma_{t:f}^2$ = variance between trees within families

σ_e^2 = variance between fascicles within trees

n = harmonic mean of number of fascicles per tree

RESULTS

Populations differed strongly ($P < 0.001$) in needle length, each being clearly different from the other two (Table 1). They differed significantly ($P < 0.05$) in fascicle weight, with Cambria exceeding the others, but not in weight/length ratio. Comparing needle lengths with those observed in the natural stands, Monterey and to a lesser extent Cambria had longer needles at Kaingaroa. Hence, although Monterey had the shortest needles in California, it was intermediate in the common environment at Kaingaroa.

Differences between subpopulations within populations (Table 1) did not approach statistical significance for any of the three traits. Moreover, the subpopulation differences in needle length showed no overall tendency to parallel those observed by Forde in California, even though the seed parents constituted roughly half of each of Forde's population samples.

Family differences within populations were in no case statistically significant

TABLE 1—Means (averages of individual tree values) for needle characters by populations and subpopulations

| Character | Population | Subpopulation | | | | | Population mean | |
|-----------------|------------|---------------|-----|-----|-----|-----|-----------------|-------------|
| | | 1 | 2 | 3 | 4 | 5 | Kaingaroa | California* |
| needle | Ano Nuevo | 128 | 130 | 127 | 129 | 125 | 127.7 | 127.2 |
| length (mm) | Monterey | 134 | 135 | 140 | 133 | 132 | 134.8 | 118.1 |
| (C>M>A) | Cambria | 152 | 147 | 146 | 146 | 141 | 146.0 | 136.8 |
| fascicle | Ano Nuevo | 97 | 97 | 100 | 107 | 93 | 98.5 | — |
| dry weight (mg) | Monterey | 103 | 100 | 104 | 94 | 96 | 99.6 | — |
| (C>A,M) | Cambria | 111 | 114 | 115 | 118 | 98 | 110.9 | — |
| weight/length | Ano Nuevo | 75 | 74 | 78 | 82 | 74 | 76.4 | 0.797† |
| ratio of | Monterey | 77 | 74 | 75 | 70 | 72 | 73.6 | 0.751† |
| fascicle | Cambria | 73 | 78 | 79 | 80 | 69 | 75.7 | 0.852† |

(mg/mm × 10²)

* Forde (1964c)

† needle thickness (mm)

($P > 0.05$), although with no more than two individuals per family this does not preclude appreciable heritabilities.

Needle length showed the least tree-to-tree variability of the traits investigated (Table 2) and was somewhat less variable in this study than in Forde's. Weight/length ratio was much more variable at the tree-to-tree level than needle thickness was in Forde's study, but it should be noted that the former character is effectively two-

TABLE 2—Coefficients of variation (%) between trees within subpopulations

| Study | Nature of Coefficient | Character | | | |
|---------------|---|---------------|-----------------|---------------|------------------|
| | | Needle length | Fascicle weight | Weight/length | Needle thickness |
| Present study | $(\sigma_{w:f}^2 + \sigma_{f:s}^2) / \bar{X}$ | 10.2 | 22.3 | 16.0 | — |
| | $(\sigma_{t:f}^2 + \sigma_{f:s}^2) / \bar{X}^*$ | 8.7 | — | — | — |
| Forde (1964b) | $(\sigma_{t:s}^2 + \sigma_e^2/10) / \bar{X}$ | 12.3 | — | — | 7.1 |

\bar{X} denotes mean of all individual tree values for trait in question

* This coefficient excludes estimated sampling error for individual trees.

dimensional rather than one-dimensional. All three traits were positively intercorrelated within populations (Table 3). Weight/length ratio was correlated more strongly with weight than length was, reflecting the greater variability of weight.

TABLE 3—Within-population correlations between characters, disregarding family and subpopulation classification

| | Population | | | | | |
|---------------|------------|---------|----------|---------|---------|---------|
| | Ano Nuevo | | Monterey | | Cambria | |
| | Length | Weight | Length | Weight | Length | Weight |
| weight | 0.82*** | | 0.77*** | | 0.69*** | |
| weight/length | 0.57*** | 0.93*** | 0.41*** | 0.89*** | 0.29* | 0.90*** |

* denotes significant ($P < 0.05$)

*** denotes very highly significant ($P < 0.001$)

DISCUSSION

This study indicates that there is negligible genetic differentiation in needle length, fascicle dry weight, and fascicle weight/length between localities within the mainland California populations. It therefore appears that the pronounced locality differences which Forde observed for needle length were essentially environmental. But any such conclusion regarding Forde's results for needle thickness must be tentative, since the use of weight/length ratio as an index of thickness assumes a constant ratio of dry matter to needle volume. Some departures from such an assumption are inevitable.

The existence of between-population differences in needle length was confirmed, as was the fact that the Cambria population shows the longest needles. However, there was an important disparity with Forde's results; in this study the Monterey population had longer needles than the Ano Nuevo population, instead of vice versa. Moreover, Forde found significantly thicker needles at Cambria, which does not accord with the lack of population differences for weight/length ratio in this study. The different population rankings between the two studies can be attributed to environmental effects in California. Unlike the Ano Nuevo population, the Monterey and Cambria populations had shorter needles in California than at Kaingaroa, and this is probably an effect of the considerably lower rainfall at Monterey and Cambria than at Ano Nuevo (Forde, 1966).

These results illustrate some of the limitations of field studies within natural stands for elucidating the infraspecific taxonomy and population genetics of forest trees.

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