tistical differences among regions, trees and cones (when applicable). However, future studies must include additional sources such as levels of variation within trees. Also needed would be more trees within stands and stands within regions, rather than more regions. The populations of Baja Verapaz and Jalapa had the maximum values for most seed, cone and needle traits. The cluster analysis, identified the population of Jalapa as being a different cluster, probably due to its geographic isolation, in addition to its association and hybridization with other species, i.e. *P. oocarpa* and *P. maximinoi* Moore, with which it is said to hybridize rather easely. The population of the Sierra de las Minas, Jalapa, followed by the population of the Communal forest of Patsajón, El Quiché, have the most uniform stands of *P. tecunumanii.* A number of traits were correlated, and they should be sorted out in future studies. Only one lateral face of stomata rows need be counted in the future, in addition to the stomata rows of the external face. Since the number of serrations on the right and left edges were highly correlated, recording on one edge is sufficient for future studies. In spite of the presence of high correlations among cone and seed characteristics, all traits should be measured until additional information is obtained which would indicate which might be dropped.

The most highly correlated characteristics were allocated to specific factors. Thus, stomata rows accounted for almost the total variance of Factor 2, while the needle serrations accounted for most of the variance of Factor 4. This meant that the weights to these factors is probably due to similar effects of the environment on each group of traits, although they may be the result of linked genes or genes with pleiotropic effects or a combination of these. High weights of the same trait on different factors, may be the result of either independent gene complexes effects, environmental effects or both combined.

The best phenotypes of the Tecun Umán pine as well as some of the best stands are threatened by woodcutters, uncontrolled forest fires and pest epidemics in most of the regions studied. It is therefore, urgent to encourage seed collections in all locations, since no provenance trial information is available. This would protect from the risk of loosing trees from other regions as has happened in region 3. This is particularly true for phenotypes which will prove to be invaluable in planting programs.

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# Genetic Variation in Resin Canal Frequency and Relationship to Terpene Production in Foliage of Pinus contorta[1]

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## 1. Abstract

Resin canal frequency was examined in needles from grafts and corresponding open-pollinated families of lodgepole pine *(Pinus contorta* Dougl.). Correlations between tree resin canal frequencies and absolute amounts of monoterpenes and three sesquiterpenes indicate that their synthesis or storage is largely compartmentalized in resin canals. In grafted trees, differences between clones in resin canal frequency were highly significant, indicating genetic control of resin canal frequency. Heritability estimates for resin canal frequency based on degree of resemblance between grafts of the same clone may have been influenced by the stabilization in grafts of position effects from the mother tree. Heritability estimates for resin canal frequency based on resemblance between open-pollinated seedlings of the same families, and correlations between progeny and mother trees, were moderate.

*Key words:* *Pinus contorta, Pinaceae,* lodgepole pine, genetics, leaf anatomy, terpenes, resin canals, biosynthesis, compartmentalization, heritability.

### Zusammenfassung

Bei *Pinus contorta* Dougl. wurde die Häufigkeit des Auftretens von Harzkanälen in den Nadeln von Pfropflingen und entsprechenden frei bestäubten Familien untersucht. Korrelationen zwischen den Häufigkeiten des Auftretens der Harzkanäle eines Baumes und den absoluten Mengen der Monoterpene und von drei Sesquiterpenen zeigen an, daß ihre Synthese oder Lagerung zum großen Teil auf die Harzkanäle verteilt ist. Bei den Pfropflingen sind die Unterschiede in der Harzkanal-Frequenz zwischen den Klonen höchst bedeutsam, insofern als dadurch auf eine

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genetische Kontrolle hingewiesen wird. Heritabilitätsschätzungen für die Harzkanal-Frequenz auf der Basis des Ähnlichkeitsgrades zwischen den Pfropflingen derselben Klone sind bei der Stabilisierung der Positionseffekte in den Pfropflingen wahrscheinlich vom Mutterbaum beeinflußt. Heritabilitätsschätzungen für die Harzkanalfrequenz auf der Basis der Ähnlichkeit zwischen frei bestäubten Sämlingspflanzen der gleichen Familie zeigen nur eine geringe Korrelation zwischen den Mutterbäumen und ihren Nachkommenschaften.

## 2. Introduction

Previous studies (WHITE 1983, WHITE and NILSSON 1983) have been directed to clarifying the biosynthetic and genetic relationship of terpenes in lodgepole pine, since these affect the value of terpenes as taxonomic characters for breeding and other purposes (VON RUDLOFF 1975).

Compartmentalization of biosynthetic pathways can produce different compounds from the same precursor in different tissues, with the result that genes controlling tissue structure and synthesis of enzymes may have epistatic interactions. CROTEAU and WINTERS (1982) have shown that the terpene 1-menthone is reduced to a different product in the epidermis than in the mesophyll of *Mentha piperita* leaves because the enzymes of the two pathways are differentially located in the two tissues. The site of terpene synthesis in *Pinus sylvestris* and *P. nigra* needles appears to be the epithelial cells lining the resin canals. These contain large numbers of plastids with little internal structure, associated with globules of lipid-like material assumed to represent resin (WALLES *et al.* 1973, CAMPBELL 1972). In *P. pineae* cortical resin canals these simplified plastids were sheathed with endoplasmic reticulum and it was suggested that the initial stages of resin production were carried out inside the plastid and subsequent stages by enzymes of the endoplasmic reticulum membranes (WOODING and NORTHCOTE 1965). Parallel cytological and biochemical observations in maritime pine *(P. pinaster)* indicated compartmentalization of terpene synthesis (BERNARD-DAGAN *et al.* 1979). The epithelial cells of the resin ducts showed progressive degeneration from the base to the tip of the needles. Absolute amounts of monoterpenes were highest in the base of the needle while sesquiterpenes were higher in the upper parts of the needle. Isotope labelling indicated terpene precursor synthesis occurred in the photosynthetically active upper parts of the needle. Further elaboration of both mono- and sesquiterpenes occured mainly at the base of the needle, though the relative activity of base versus upper parts was 66 times for monoterpenes and only 8—16 times for sesquiterpenes.

Variation in occurrence and position of needle resin canals is one of the traits that have proved useful in multivariate expressions for discriminating pine provenances and hybrids (e. g. SNYDER and HAMAKER 1978, WELLS *et al.* 1977), indicating it is variation that is under some degree of genetic control. Variation in needle resin canal frequency in lodgepole pine was described by CRITCHFIELD (1957) in plantations and wild populations, mainly from the southern part of its range. Resemblance between resin canal frequency in plantations and wild trees from the sources of the plantations was sufficient to indicate that variation in resin canal number was largely genetically controlled. Frequency of resin canals showed greater differences within geographic areas than between them, except for the Mendocino White Plains population which was distinguished by the absence of resin canals. In inland areas resin canal frequency increased with elevation and leaf width, though resin canal frequency and leaf width appeared to vary independently. Data reported by ILLINGWORTH (1971) indicate significant differences in resin canal frequency between five wild populations of lodgepole pine.

Earlier studies indicated that the foliar terpenes of lodgepole pine form three biosynthetically related groups: the monocyclic monoterpenes, the bicyclic monoterpenes, and the sesquiterpenes (WHITE 1983). Qualitative patterns of monoterpene production appeared to be under strong genetic control, mainly by additive genes acting on factors such as enzyme concentration and compartmentalization which control terpene metabolic steady state (WHITE and NILSSON 1983). This study was undertaken to determine correlations between resin canal frequency and terpene levels, and to determine the genetic variances for resin canal frequency in a lodgepole pine seed orchard and clonal archive.

## 3. Materials and Methods

### 3.1 *Plant material*

The trees sampled were part of a clonal archive and seedling seed orchard near Falun, Sweden. Scions for grafts and seed for open-pollinated families had been collected from plus trees in central British Columbia, Canada (SZIKLAI 1972). The trees sampled were 5 ramets from each of 10 clones, representing mother trees, and 19—21 seedlings from the corresponding wild open-pollinated families, progeny of the respective mother trees. Details of sampling were reported earlier (WHITE 1983, WHITE and NILSSON 1983). Samples were taken around the tree from the upper second and third whorls to minimize position and shading effects.

### 3.2 *Chemical analysis*

Absolute amounts of terpenes were analysed on a fresh weight basis in n-'pentane extracts of foliage using an internal standard. Details of extraction and analysis were reported earlier (WHITE 1983). Analytical error was ± 0.1 mg/10 g fresh weight. Average foliar dry weight of all trees was 41.3 ± 1.8% and mean dry weight did not vary significantly between families.

### 3.3 *Microscopic analysis*

Preliminary investigations showed that resin canal frequency varied with position of twig on tree, position of needle on twig, and position of cross-section in needle (cf. WHITE, J. B. and BEALS 1953). Resin canals were more frequent in needles at the distal end of the twig, and more frequent in cross sections taken from the mid and basal parts of needles. For calculation of resin canal frequency, sections were made from the mid-portion of 1—2 needles taken 8—10 cm from the bud of 5 twigs/tree (seedlings), or 3 twigs/tree (grafts). Twenty micron cross sections were cut using a freezing stage microtome, sections were mounted in D.P.X. mountant (B.D.H., England), leaf width was measured using a light microscope equipped with an ocular micrometer, and number of resin canals was recorded.

### 3.4 *Statistical analysis*

Correlations were calculated between mean resin canal frequency of individual trees and their terpenes expressed both as absolute amounts (in mg/10 g foliage) and relative amounts (as percentage of sum of monoterpenes) in all

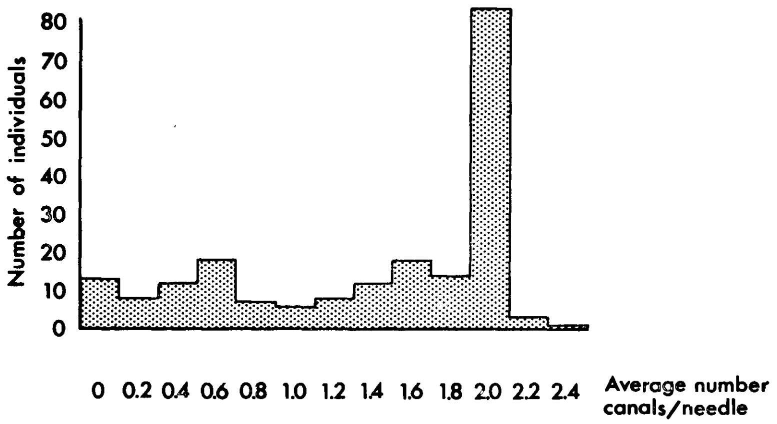

*Fig. 1.* — Frequency distribution of average number of resin canals/needle in all seedlings.

seedlings combined, all grafts combined, individual families and individual clones.

Components of between- and within-group variance were calculated for resin canal frequency in clones and families. "Broad-sense" heritability was estimated as clonal intraclass correlations and "narrow-sense" heritability both as 4 times family intraclass correlations and 2 times the coefficient of regression of progeny on maternal parent (Falconer 1981). Details of the analysis were given previously (White and Nilsson 1983).

Variances for needle width in needles with 0, 1, 2, and 3 (or more) resin canals were calculated in all trees combined, grafts of all clones combined, seedlings in all families combined, and trees in individual families and clones. The significance of differences of mean width of needles with 0, 1, 2, and 3 resin canals was tested in all clones combined and all families combined, and the correlation between resin canal frequency and needle width was calculated based on family means.

A frequency distribution was drawn for resin canal frequency in trees of all families combined, and the regressions of family means for resin canal frequency on elevation and latitude of origin of mother tree were calculated.

## 4. Results

Needles from the same tree had variable numbers of resin canals, and mean resin canal frequency in different trees varied considerably, from an average of 0 to 2.4 resin canals/needle *(Fig. 1)*. The correlation between resin canal frequency and total terpene production estimated from all individual trees was highly significant *(Table 1*, columns 11 and 12). Correlations between mean resin canal frequency

*Table 1.* — Correlations between terpene level and mean number of resin canals in needles of individual trees.

| | r, absolute amounts | | | | | | | | | | | | r, % of monoterpenes | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Family 9 | Family 16 | Family 19 | Family 30 | Family 39 | Family 50 | Family 59 | Family 73 | Family 76 | Family 89 | All families combined | All clones combined | All families combined | All clones combined |
| β-Phellandrene | 0.65** | 0.64** | 0.50* | 0.62** | 0.82** | 0.39 | 0.84** | 0.83** | 0.80** | 0.83** | 0.66** | 0.86** | 0.10 | 0.51** |
| α-Phellandrene | 0.60** | 0.70** | 0.41 | 0.51* | 0.79** | 0.34 | 0.74** | 0.79** | 0.83** | 0.83** | 0.63** | 0.80** | -0.01 | -0.04 |
| Sabinene | 0.66** | 0.54* | 0.42 | 0.69** | 0.75** | 0.70** | 0.89** | 0.82** | 0.73** | 0.79** | 0.68** | 0.63** | 0.28** | 0.35* |
| Myrcene | 0.56** | 0.20 | 0.51* | 0.69** | 0.87** | 0.72** | 0.74** | 0.84** | 0.84** | 0.83** | 0.65** | 0.85** | 0.07 | -0.03 |
| cis-Ocimene | 0.69** | 0.19 | 0.38 | 0.57* | 0.48* | 0.44* | 0.57** | 0.72** | 0.60** | 0.68** | 0.54** | 0.82** | 0.07 | 0.42** |
| Limonene | 0.67** | 0.72** | 0.29 | 0.67** | 0.84** | 0.72** | 0.46* | 0.78** | 0.56* | 0.69** | 0.52** | 0.55** | -0.29** | 0.01 |
| 3-Carene + 2-Hexenal | 0.35 | -0.16 | 0.10 | 0.17 | -0.12 | -0.04 | -0.28 | 0.14 | 0.48* | -0.38 | 0.06 | -0.28* | -0.46** | -0.57** |
| α-Pinene | 0.68** | 0.63** | 0.14 | 0.35 | 0.42 | 0.70** | 0.47* | 0.40 | 0.82** | 0.76** | 0.43** | 0.39** | 0.07 | -0.10 |
| β-Pinene | 0.34 | 0.24 | -0.01 | 0.22 | -0.09 | 0.59** | 0.39 | 0.26 | 0.58** | 0.41 | 0.30** | 0.32* | -0.02 | -0.08 |
| Bornyl Acetate | 0.58** | 0.32 | 0.12 | 0.18 | 0.25 | 0.48* | 0.30 | 0.45* | 0.74** | 0.13 | 0.21** | -0.13 | 0.06 | -0.21 |
| Tricyclene | 0.37 | 0.40 | 0.16 | 0.22 | 0.31 | 0.63** | 0.32 | 0.35 | 0.67** | 0.65** | 0.28** | -0.13 | 0.19** | -0.21 |
| Isoborneol | 0.23 | 0.12 | 0.13 | 0.22 | 0.57** | 0.50* | - | 0.38 | 0.62** | -0.07 | 0.22** | n.d. | 0.09 | n.d. |
| Camphene | 0.67** | 0.57** | 0.11 | 0.20 | 0.28 | 0.63** | 0.31 | 0.67** | 0.87** | 0.83** | 0.24** | 0.02 | 0.14* | -0.14 |
| Cadinenes 1 | 0.56** | 0.22 | 0.28 | 0.48* | 0.65** | 0.58** | 0.73** | 0.67** | 0.57** | 0.60** | 0.49** | 0.38** | not applicable | |
| Cadinenes 2 | 0.57** | 0.20 | 0.29 | 0.46* | 0.68** | 0.58** | 0.75** | 0.64** | 0.54* | 0.60** | 0.49** | 0.31* | -"- | -"- |
| Cadinols | 0.52* | -0.12 | 0.25 | 0.42 | 0.57** | 0.46* | 0.48* | 0.73** | 0.38 | 0.47* | 0.38** | n.d. | -"- | -"- |
| Total Monoterpenes | 0.69** | 0.65** | 0.41 | 0.66** | 0.90** | 0.83** | 0.82** | 0.83** | 0.88** | 0.84** | 0.76** | 0.87** | -"- | -"- |
| Total Terpenes | 0.69** | 0.55* | 0.42 | 0.71** | 0.88** | 0.85** | 0.80** | 0.90** | 0.85** | 0.82** | 0.75** | 0.87** | -"- | -"- |
| Average number of resin canals/needle | 1.20 | 1.63 | 1.90 | 1.49 | 1.30 | 1.42 | 1.10 | 1.43 | 1.25 | 1.30 | 1.40 | 1.14 | | |
| Number of trees | 21 | 20 | 20 | 19 | 20 | 21 | 21 | 21 | 20 | 20 | 203 | 50 | 203 | 50 |

* p = 0.05
** p = 0.01
n.d. = not determined

and terpenes, estimated from individual tree data, along with average resin canal frequencies, are given in *Table 1*. Due to the low number of samples/clone, correlations for individual clones were rarely significant and are not given. Correlations between resin canal frequency and relative amounts of terpenes were low and rarely significant in both individual families and individual clones. Correlations with relative amounts (% monoterpenes) are given for combined seedlings and grafts only.

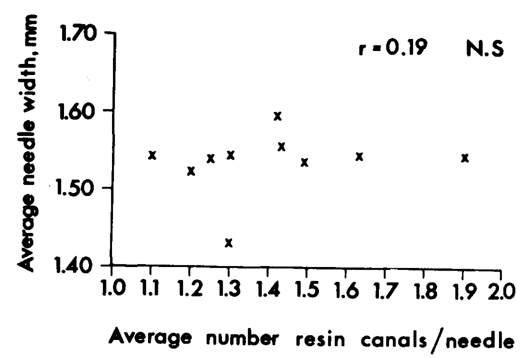

*Fig. 2.* — Relationship between average needle width of families and number of resin canals.

Correlations between mean resin canal frequency and both total terpenes and total monoterpenes were highly significant in seedlings of all families and grafts of all clones combined, and in seedlings of all individual families except 19. Correlations for absolute amounts of all individual monocyclic terpenes except 3-carene were significant in all but one or two families. Three-carene was poorly separated from an unknown, possibly 5-methyl-pent-l-en-al, and will not be discussed further. Correlations between resin canal frequency and absolute amounts of bicyclic monoterpenes were lower than those for monocyclic monoterpenes, and were significant in fewer families. Absolute amount of $\beta$-pinene was significantly correlated with resin canal frequency in only 2 families. Absolute amounts of the camphane carbon skeleton bicyclic monoterpenes were not correlated with resin canal frequency in grafts from all clones combined. Correlations for the sesquiterpenes monitored in this study were significant in most individual families as well as combined families and clones.

Estimates of the heritability of resin canal frequency and their confidence intervals are given in *Table 2*.

There was no correlation between mean needle width and resin canal frequency in individual families *(Fig. 2)*. There was a tendency for needles with higher numbers of resin canals to be wider when data for individual needles was combined irregardless of which came from the same tree. However the differences in mean width of needles with 0, 1, 2 and 3 or more resin canals were small, less than the standard deviation of width in each class.

*Table 2.* — Estimates of heritability of resin canal frequency.

| | Intraclass correlations, clones ("Broad sense") | 4 x Intraclass correlations, families ("Narrow sense") | 2 x Coefficient of regression of families on clones ("Narrow sense") |
|---|---|---|---|
| Heritability estimate | 0.69 | 0.25 | 0.31 |
| Confidence limits, p = .05 | 0.44 - 0.89 | 0.02 - 1.01 | -0.17 - 0.79 |

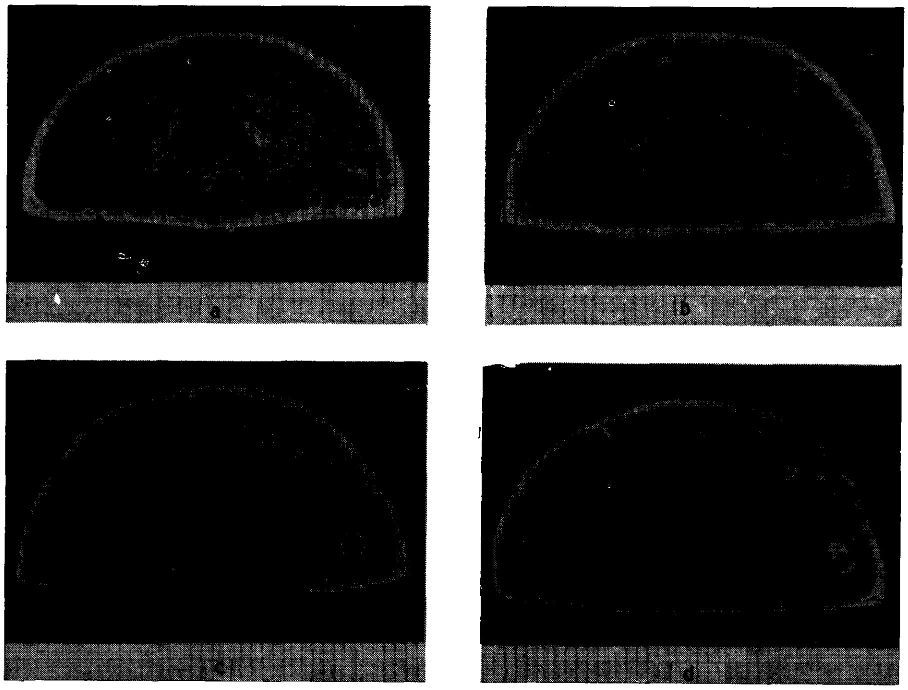

*Fig. 3.* — Needles with (a) 0, (b) 1, (c) 2 and (d) 5 resin canals.

Illustrations of needles with variable numbers of resin canals are given in *Figure 3*. Regressions of resin canal frequency on elevation and latitude of mother tree were not significant, though there was a tendency to increased numbers of resin canals with higher elevations.

## 5. Discussion

### 5.1 *Correlation between resin canal frequency and terpene production*

The highly significant correlations between absolute amounts of terpenes and resin canal frequency provide an explanation for the variability in total terpene production in tees with similar percentage terpene patterns. Trees which produced smaller amounts of terpenes had a lower resin canal frequency, i.e. more needles with less than 2 resin canals. The correlations indicate that terpene production or storage is compartmentalized in the resin canals. The generally low correlations between resin canal frequency and relative amounts of monoterpenes indicate that this compartmentalization is relatively independent of the type of terpene produced.

Production of monocyclic monoterpenes and sesquiterpenes was highly correlated with resin canal frequency in most families. The low correlations in family 19 were due to the lack of variation in resin canal frequency in seedlings of this family (average resin canal frequency 1.96, only three seedlings with $< 2$ resin canals/needle).

Among the bicyclic monoterpenes, those with the camphane skeleton were correlated with resin canal frequency in family 50, in which 3/4 of the trees contained relatively large amounts of camphanes (White and Nilsson 1983, *Figure 2*). In families 9, 16, 73, and 76, in which no trees contained large amounts of camphanes, there were significant correlations between resin canal frequency and those camphane skeleton terpenes which were commonly measurable. The sporadic occurrence of high camphane values in the families which contained only a few high camphane trees (19, 30, 39, 59 and 89) resulted in lack of correlation between camphanes and resin canals in these families. Thus the results indicate that the synthesis or storage of camphane skeleton monoterpenes also occurs in resin canals.

Trees containing measurable $\alpha$- and $\beta$-pinene occurred relatively frequently in all families. In particular, both low and high $\beta$-pinene trees were common in all families. The two families in which the absolute amount of $\beta$-pinene was significantly correlated with resin canal frequency were the two with the largest number of trees containing high relative amounts of $\beta$-pinene. The occurence of more low $\beta$-pinene trees in other families may explain its low correlation with resin canal occurrence.

Correlations between resin canal frequency and absolute amounts of terpenes were similar in clones to those in families, though the camphanes were non-significantly negatively correlated to number of resin canals. This was because the only clone which contained large amounts of these terpenes had a low average resin canal frequency (0.6). Within the grafts of this clone all camphanes were positively correlated with resin canal frequency.

The strong correlations between resin canal frequency and total terpene production indicate that variation in resin canal frequency is the major cause of variation in total terpene production. A tree having the enzymes necessary for terpene production will not have high total terpene levels if it lacks resin canals. Thus genes controlling the terpene synthetic enzymes and those controlling resin canal morphology could act eptistatically.

### 5.2 *Heritability estimates for resin canal frequency*

Variation in resin canal frequency had both genetic and environmental components. Differences in resin canal frequency between clones were highly significant. Between clonal variance accounted for 69% of the total variance in grafts, indicating rather strong genetic control of this character. Nevertheless, variability in resin canal frequency of grafts of the same clone did occur. The number of resin canals has been shown to vary between needles of the same tree with level on the tree and exposure to sunlight in *P. rigida* (White, J. B. and Beals 1953). It is possible that mother tree position effects on resin canal frequency in the scions may have been maintained in the grafted trees. The variable terpene patterns within clone 73 (White and Nilsson 1983) might be explained by variability in resin canal frequency. Variation in terpene pattern in this clone was due to variation in the relative amount of $\beta$-pinene in different grafts. If $\beta$-pinene levels are less dependent on resin canal frequency they would not change as much as other terpenes with a change in number of resin canals. The high % $\beta$-pinene grafts had a lower average number of resin canals/needle (0.6 in high versus 1.25 in low % $\beta$-pinene grafts), but the sample is too small to draw conclusions.

As discussed previously (White and Nilsson 1983), incorrect labelling of ramets in clone 73 cannot be eliminated as the source of variation within the clone, but seems unlikely. If ramets had been incorrectly substituted for those of another clone they would likely have had much higher total terpenes and resin canal frequency. Of the clones examined, only one other, clone 9, had such low total terpenes or average number of resin canals as clone 73. It is also unlikely that environmental variation or shading effects caused differences within the clone as the grafts were planted in clonal rows on one uniform block, 5 × 5 m apart, and were not large ($<$ 4 m). Examination of the grafts did not reveal morphological variation or abnormalities within the clone.

The heritability estimates for resin canal frequency are likely over-estimates, since environmental variation was minimal in the plantation studied. "Narrow sense heritability" estimates are subject to the experimental constraints due to structure of progeny and parent populations (open-pollinated progeny not necessarily half-sibs, pollen populations not necessarily the same), and differences in age of parents and progeny which were discussed earlier (White and Nilsson 1983). The stands from which the parent trees were selected all occur in a relatively limited part of the range of lodgepole pine. All parent trees except two came from the sub-boreal forest tree seed region of B.C.; trees 50 and 59 came from boreal region (Dobbs *et al.* 1976). Seedlots from this part of the range have not differed greatly in provenance trials in Sweden (Lindgren *et al.* 1980, Lindgren 1983), and the pollen populations may be similar, with the possible exception of family 50. The average resin canal frequency in grafts was lower than in seedlings, possibly an expression of a more "mature" physiological state in grafts. In *P. rigida* (White, J. B. and Beals 1953) resin canal frequency was greatest in needles produced by trees at the age when rapid secondary-wood growth occurs. The seedlings in this study were growing very rapidly compared to the grafts.

### 5.3 *Relationship between needle width and resin canal incidence, and frequency distribution of resin canal incidence*

Differences between mean widths of needles with 0, 1, 2, and 3 or more resin canals were small, less than the standard deviation of needle width in each class. Mean needle width of a family was not correlated with its mean resin canal frequency. This confirms Critchfield's observation that the relationship between resin canal frequency and needle width does not appear to be an obligate one in lodgepole pine, and indicates that genetic control of resin canal number is independent of that of needle width.

The frequency distribution of resin canal incidence in seedlings had a large mode at 2.0 resin canals/needle *(Fig. 1)*. As was noted, resin canal number is a countable character. In over 1,100 sections there was no evidence of partial resin canal development (e.g. *Figure 3)*. Critchfield (1957) noted that one reason for departure from normality in frequency distributions for resin canal incidence is the tendency toward symmetry in the occurrence of resin canals. A needle is most likely to have either 2 or 0 resin canals. This tendency was evident in this study. Of the needles from seedlings which were examined, 622 had 2 resin canals, 218 had 0, only 156 had 1, and 6 had 3. Of needles from grafts, 64 had 2 resin canals and 49 had 0, while only 28 had 1, 5 had 3, and 1 had 5 resin canals. This tendency to symmetry in resin canal occurence likely contributed to the broad confidence limits for heritability estimates. The frequency distribution of resin canal incidence explains much of the change in terpene distributions in the seedlings caused by scale transformation from absolute to % data (White and Nilsson 1983, *Figures 1* and *2)*. Resin canal distribution is a consideration in genetic studies dealing with characters such as "high" and "low" terpene levels. Resin canal distribution within a tree should be considered when sampling for terpene analysis.

### 5.4 *Concluding remarks*

Highly significant correlations between resin canal frequency and absolute amounts of most terpenes indicate that terpene production or storage is compartmentalized in resin canals, and their frequency largely determines the total amount of terpenes in lodgepole pine needles. Heritability estimates based on degree of resemblance of grafts of the same clone, open-pollinated seedlings of the same family, and correlations between open-pollinated progeny and mother trees, indicated that resin canal frequency is under moderate genetic control. Mother tree position effects on resin canal frequency of scions may give rise to differences in resin canal frequency in grafts taken from the same tree, resulting in variation in terpene production.

## 6. Acknowledgements

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# A plan for breeding radiata pine

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## Summary

A plan is proposed for improving radiata pine *(Pinus radiata* D. Don) in South Australia. Features of the plan which may be new are: (1) Low cost gene conservation areas which contain the pooled progeny of all parents in the first-generation breeding population. (2) A two-stage selection scheme, where four individuals are selected from each family in the breeding population *(stage-1)* and then progeny tested using open-pollinated seed *(stage-2)*, before finally deciding which two individuals from each family are best for future breeding. (3) An index which employs estimates of GCA to pair potential parents so that more superior families may be generated from single-pair matings.

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