compagnent d'une forte variabilité entre moyennes de clones; ceci laisse espérer des gains génotypiques élevés par sélection,

— le classement des deux espèces de Chêne européen *(Quercus petraea* et *Quercus robur)* pour la qualité intrinsèque du bois est confirmé,

— les liaisons génotypiques entre caractères ne sont pas de nature à poser au sélectionneur des problèmes insurmontables, en ce qui concerne tout particulièrement les relations entre vigueur et propriétés du bois,

— une étude bibliographique confrontée à nos résultats nous a indiqué en premier lieu que les corrélations phénotypiques entre les principaux caractères de qualité ou de vigueur chez les *Quercus* varient sensiblement en fonction du type de matériel végétal étudié (âge, sylviculture, gamme de largeur de cerne). En ce qui concerne les trois espèces de *Quercus* étudiées *(Quercus petraea, Quercus robur* et *Quercus rubra),* il semble que dans les conditions d'une sylviculture dynamique, il n'y aurait pas d'inconvénients majeurs à rechercher une croissance maximum, le seul risque étant d'augmenter l'anisotropie de la rétractibilité du bois.

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Mode of Genetic Control of Monoterpenes in Foliage of Controlled Crosses of Pinus contorta

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1. Abstract

Monoterpenes were examined in foliage of controlled crosses of lodgepole pine *(Pinus contorta* Dougl.). Total terpene production was strongly related to resin canal frequency. Segregation of progeny into classes based on relative amounts (percentages of total monoterpenes) of β-pinene fitted both one and two locus models for genetic control. Modality in frequency distributions of relative amounts of β-phellandrene could be explained by constraint due to the method of expressing results. Modes in relative amounts of minor monoterpene constituents were due to instrumental detection limits in samples with very low total terpene production.

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Key words: Pinus contorta, Pinaceae, lodgepole pine, genetics, monoterpenes, leaf anatomy, resin canals.

Zusammenfassung

Bei Nachkommen von *Pinus contorta* Dougl. aus kontrollierter Kreuzung wurden die Nadeln auf Monoterpene untersucht. Hierbei stellte sich heraus, daß die Gesamtproduktion an Terpenen streng mit dem Vorkommen von Harzkanälen korreliert war. Die Aufteilung der Nachkommenschaft in Klassen auf der Basis der relativen Menge (in Prozenten der Gesamtproduktion) der β-Pinene paßte sowohl für ein- als auch für zwei-Locus-Modelle zur genetischen Kontrolle. Die Modalität der Auftrittshäufigkeits-Verteilung der relativen Mengen an β-Phellandrenen konnte gezwungenermaßen erklärt werden, indem die ausdrück-

lichen Resultate auf die Methode zurückgeführt wurden. Die Art und Weise, in der die in relativ geringeren Mengen auftretenden Monoterpene-Bestandteile auftraten, war auch von den Meßgrenzen der Instrumente abhängig, besonders bei Proben mit sehr geringem Terpengehalt.

2. Introduction

The mechanism of genetic control of terpenes is an important consideration when applying terpene analyses to systematic studies in conifers (VON RUDLOFF 1975). Studies of segregation ratios for relative levels of terpenes in controlled crosses of conifers have indicated major gene control for several terpenes, including 3-carene, myrcene, β-pinene, limonene, β-phellandrene, α-pinene, caryophylle, and longifolene (BARADAT *et al.* 1972, 1975; FORDE 1964; HANOVER 1966; HILTUNEN *et al.* 1975; MARPEAU *et al.* 1975, ROCKWOOD 1973; SQUILLACE 1971; SQUILLACE *et al.* 1980). Though segregation ratios fitted control by one locus, wide ranges within dominant and recessive genotypes suggested strong effects by other genes (HANOVER 1966; HILTUNEN *et al.* 1975). Different terpenes appeared to be under major gene control in different species. BARADAT *et al.* (1972) pointed out that their demonstration of monogenetic control for 3-carene in maritime pine was possible because the landaise provenance which they studied contained a single major gene segregating for 3-carene. Genetic control for limonene was more complex, apparantly involving several major genes, but they remark that it may be possible to find provenances in which the variation in levels of this terpene could also be explained by a monogenetic mechanism. HANOVER (1966) noted that the interpretation of the mechanism of control for 3-carene in western white pine could vary depending on the range of parental genotypes tested. Von RUDLOFF and REHFELDT (1980) point out that the selection of parental genotypes affects the definition of the characters tested in such segregation studies, since the differentiation point between modes in terpene levels varies in different populations. In addition, when relative data are used, the point of differentiation between modes in one terpene is affected by modes in others (GANSEL and SQUILLACE, 1976; SQUILLACE *et al.* 1980).

Genetic control of terpene levels has been studied in hybrids of lodgepole pine and Jack pine *(P. banksiana)* (ZAVARIN *et al.* 1969). The results suggested terpene composition was controlled by a few major genes, though it was impossible to formulate an inheritance model.

Previous studies (WHITE and NILSSON 1983a, b) with open-pollinated families of lodgepole pine and grafts of their mother trees, indicated that relative amounts (percentages of total monoterpenes) of foliar monoterpenes are under rather strong genetic control, largely by genes with additive effects acting on factors which control their metabolic steady-state. Total production of terpenes is highly dependent on resin canal frequency, with the result that genes controlling leaf anatomy and terpene biosynthesis may interact epistatically. The present study was undertaken to examine the mechanism of genetic control of foliar monoterpenes in controlled crosses of lodgepole pine.

3. Methods and Materials

The trees sampled were three clones of lodgepole pine, progeny derived by selfing each clone, and progeny of a cross between two of the clones. The ortets from which the grafts were taken came from the Klosterheden selected Danish seed stand. The stand's exact origin is unknown, but is probably coastal Washington, U.S.A. (LARSEN 1980). Two of the parental clones (271 and 274) were represented by one graft at each of two sites (Danish Royal Veterinary and Agricultural University Plantation Krogerup, 56.6° lat., 9.3° long., and the C. E. Flensborgs Research Forest, 56.2°, 9.2°), and the third (261) by one graft at one site (Krogerup). The grafts at Krogerup were 26 years from time of grafting, and the C. E. Flensborgs Forest grafts were 18 years from time of grafting when sampled. Seedlings, (progeny), were all growing at Krogerup, and were seven-years-old from time of sowing when sampled. Ten second degree lateral twigs were collected around the tree from the upper second and third branch whorls, (1982 growth), in mid-December 1982 or early January 1983. Individual tree samples were placed in plastic bags, these in further heavy weight plastic bags, and samples were stored in an ice-packed polythene cooler at $\leq -5^0$ C until analyzed (6—12 weeks).

Monoterpenes were analysed in n-pentane extracts of 10 g (fresh weight) foliage/tree by gas chromatography, and absolute amounts of monoterpenes were determined by reference to p-cymene (1-isopropyl-4-methyl-benzene), used as an internal standard. All grafts were also extracted without added p-cymene, to check for the absence of natural p-cymene. Details of the method were published previously (WHITE 1983). Identities of all peaks were confirmed using G.C./mass spectrometry. 3-Carene was poorly separated from an unknown, possibly 5-methyl-pent-2-en-1-al. The non-terpenoid hex-2-en-1-al discussed previously (WHITE 1983) was identified as a peak immediately following β-phellandrene. Foliar dry weight of all trees was determined after drying separate 10 g samples for 24 hrs at 90—95° C in a forced draught oven. The means and ranges of monoterpenes frequently above the limit of detection in foliage of all seedlings are given in *Table 1.* In addition, small amounts of tricyclene occurred in a few samples, and peaks corresponding to cadinene and cadinol isomers occurred in most samples but were not quantified. A trace amount of a peak corresponding to p-cymene occurred in one graft and was non-detectable in the others. Mean foliar dry weight of all seedlings was 34.3 $\pm$ 0.09 % and did not vary significantly between families.

Resin canal frequency was examined in cross-sections from the middle part of needles of each twig, as described previously (WHITE and NILSSON 1983b). The correlation between resin canal frequency and absolute amount of β-pinene was determined in family 38, the only family in which sufficient trees contained needles with resin canals that such a calculation was possible.

Table 1. — Means and ranges of monoterpenes frequently above the limit of detection.

Monoterpene	absolute amount, mg/10g		% of total monoterpenes	
	Mean	Range	Mean	Range
α-Pinene	0.30	0 - 2.25	7.3	0 - 15.7
Camphene	0.01	0 - 0.09	0.1	0 - 0.6
ß-Pinene	1.60	0 - 12.88	18.5	0 - 60.3
Sabinene	0.03	0 - 0.17	1.1	0 - 28.5
3-Carene + unknown	0.01	0 - 0.04	0.5	0 - 21.0
Myrcene	0.07	0 - 0.49	0.8	0 - 3.3
α-Phellandrene	0.02	0 - 0.17	0.3	0 - 1.8
Limonene	0.09	0 - 0.29	0.4	0 - 11.4
ß-Phellandrene	1.15	0.07 - 5.57	53.9	22.2 - 100
cis-Ocimene	0.09	0 - 1.07	1.0	0 - 5.4
Terpinolene	< 0.01	0 - 0.07	< 0.1	0 - 0.7

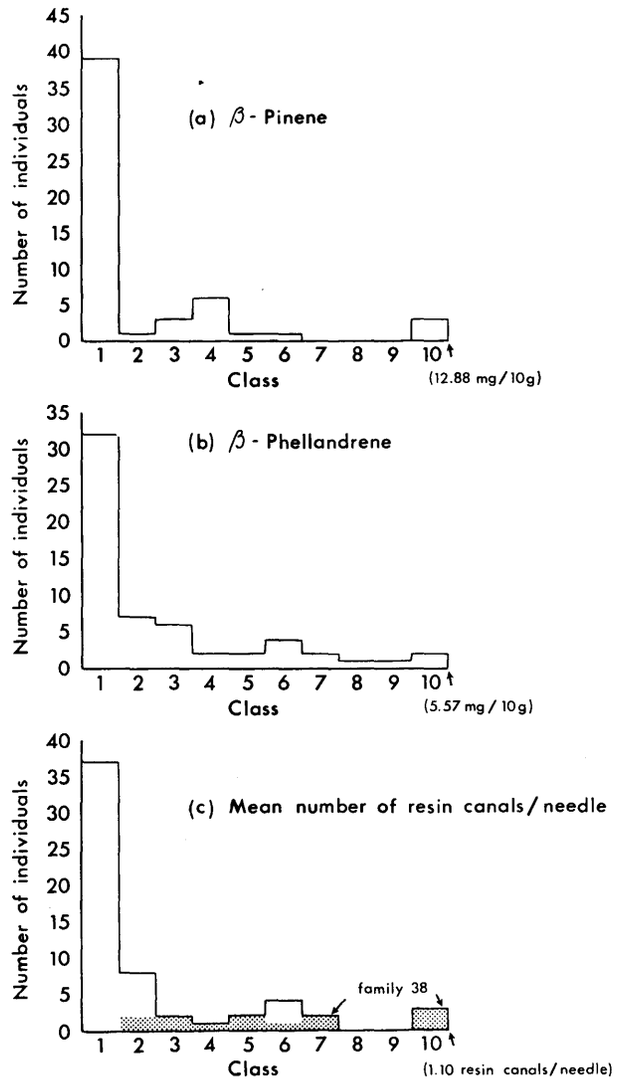

Figure 1. — Frequency distributions of (a) absolute amount of β-pinene, (b) absolute amount of β-phellandrene, and (c) resin canal incidence in all seedlings. Shaded area-trees in family 38.

Frequency distributions were drawn for absolute and relative (% of total monoterpenes) amounts of monoterpenes after dividing the range over all samples into ten equal classes. χ^2-tests of fit of the segregation of relative amounts of β-pinene to ratios appropriate to one and two locus genetic control were performed.

4. Results

The frequency distribution in seedlings for absolute amounts of the two major monoterpenes, β-pinene and β-phellandrene, and the distribution of resin canal incidence, are given in *Fig. 1.* All the trees examined had averages of less than 2 resin canals/needle, and many had no resin canals in any of the needles sectioned. Most of the trees with higher mean numbers of resin canals occurred in family 38. The class with the lowest mean number of resin canals was very large, as was the lowest class in the frequency distribution for absolute amount of each monoterpene. Absolute amount of α-pinene had a frequency distribution similar to that for β-pinene, and absolute amounts of all other monoterpenes had distributions similar to β-phellandrene, though the lowest class was generally larger. The correlation coefficient for mean number of resin canals/needle and absolute content of β-pinene in trees in family 38 was 0.821, significant at $p \leqq 0.001$.

Frequency distributions for relative amounts of representative monoterpenes, as percentages of total monoterpenes, along with levels of β-pinene in the parental clones, are given in *Fig. 2.* β-Pinene occurred in two discreet classes; trees contained either less than 12 % or more than 30 % β-pinene. In addition the lowest class was disjunctly separated into trees with no detectable β-pinene and trees with > 2 % β-pinene, and the upper class was roughly bimodal. The distinct modality in the lower class is not apparent in *Fig. 2* as the 1/10th of total β-pinene (6 %) class intervals are too broad to show a mode differentiated at 2%. α-Pinene had a large low mode, and an upper distribution that was roughly bimodal. In all trees in the lowest mode, α-pinene was below detection limits, while all the trees in the lower of the upper modes were trees with low levels of β-pinene. Relative amounts of β-phellandrene were broadly bi-modally distributed, and all trees in the upper classes contained low levels of β-pinene. Limonene, which occurred at relatively high levels, was non-modally distributed. Myrcene, one of the minor monoterpene constituents, had a very large low class, in which no trees contained detectable myrcene, and a non-modally distributed upper class.

Table 2 shows χ^2-tests of fit of the segregation of progeny in different families to models for genetic control of relative β-pinene levels, assuming one and two locus control. In the one locus model, the progeny are classified as „high" or "low", corresponding to the two discreet groups (< 12 % or > 30 %), shown in *Fig. 2.* In the two locus model, progeny are further classified into very low, medium low, medium high, and very high groups (not detectable, 2—12 %, 30—56 %, 56—60 %) corresponding to the two distinct groups in the low class and the mode in the upper group. The single locus model assumes two alleles, with an allele for high β-pinene levels dominant to that for low levels. The two locus model assumes one locus with a major effect on β-Pinene levels, having a dominant allele giving very high β-pinene levels when homozygous, or medium high levels if heterozygous in combination with a dominant allele at a second locus. The second locus is assumed to have a dominant allele with a smaller effect, giving medium high levels when present with one dominant allele at the first locus, and medium low levels if homozygous and present with the homozygous recessive allele at the first locus. The segregation ratios do not deviate significantly from those expected using either model.

5. Discussion

5.1. Resin canals and absolute amounts of monoterpenes

The low resin canal frequency in the trees examined supports the assignment of the Klosterheden selected Danish seed stand to coastal U.S.A. Critchfield (1957) reported populations with mean numbers of resin canals/needle of 1.0, 0.9, and 0.4 from coastal Washington and Oregon.

The low mean number of resin canals in many samples explains their relatively low total monoterpene content, and the frequency distribution of resin canal occurrence explains the frequency distribution of absolute amounts of monoterpenes *(Fig. 1).* The results are consistent with the compartmentation of terpene synthesis or storage in resin canals (White and Nilsson, 1983b). The highly significant correlation between absolute amount of β-pinene and resin canal occurrence in family 38 indicates that β-pinene

Table 2. — Fit of segregation ratios for relative amounts of β-pinene to one and two locus models of genetic control.

		One Locus Model							Two Locus Model						
Family	Cross	Geno type	Pheno-type	Exp.	Obs.	χ^2	df	P	Cross	Geno type	Pheno-type	Exp.	Obs.	χ^2	df	P
50 Clone 274 x S	Aa x S high x S	Aa	high	9	7	1.78	1	0.25-0.10 NS	AaBb x S medium high x S	AABB	very high	3.00	2	2.44	3	0.50-0.25 NS
		Aa	high							AABb	high					
										AaBB	medium high	4.50	5			
										AaBb	high					
		aa	low	3	5					Aabb	medium low	2.25	1			
										aaBB						
										aaBb	very low	2.25	4			
										aabb						
38 Clone 271 x S	Aa x S high x S	AA	high	9.75	12	2.077	1	0.25-0.10 NS	AaBB x S medium high x S	AABB	very high	3.25	4	2.08	2	0.5 -0.25 NS
		Aa	high							AaBB	medium high	6.5	8			
		aa	low	3.25	1					aaBB	medium low	3.25	1			
35 Clone 261 x S	aa x S low x S	aa	low	15	15	0	1	0.999 NS	aaBb x S very low xS	aaBB	medium low	3.75	5	0.56	1	0.75-0.50 NS
										aaBb	very low	11.25	10			
										aabb						
87 Clone 261 x 274	aa x Aa low x high	Aa	high	9.5	12	1.316	1	0.50-0.25 NS	aaBb x AaBb very low x medium high	AaBB	medium high	7.125	12	5.85	2	0.10-0.05 NS
		aa	low	9.5	7					AaBb						
										Aabb	medium low	4.75	4			
										aaBB						
										aaBb	very low	7.125	3			
										aabb						

is also compartmentalized in resin canals in these trees. Lack of correlation between absolute amount of β-pinene and resin canals in the previous study may have been due to its sporadic occurence as a major terpene in the families examined.

5.2 Relative (percentage) monoterpene patterns

The frequency distribution of relatively amounts of β-pinene, with two discreet modes showing further bi-modality, *(Fig. 2a)* suggested major, and possible modifying, gene effects on this character. The bi-modality of the lower mode was not solely a result of resin canal occurrence; many trees with 0 resin canal incidence contained β-pinene, while some trees with resin canals did not. In contrast, the low mode in α-pinene, myrcene and other minor monoterpenes was probably due to trees with low resin canal frequency. For these monoterpenes the low mode contained exclusively trees with non-detectable levels of the monoterpenes in question, and with 0 resin canals/needle. In such trees, the total monoterpene production was so low that production of minor monoterpenes at the same relative levels as those in trees with resin canals would amount to less than 0.01 mg/10 g, the limit of detection (cf. *Table 1).* Bi-modality in the upper range for % α-pinene *(Fig. 2b)* was possibly related to its biosynthetic correlation with β-pinene (White 1983). Trees in this range with lower α-pinene levels were also trees with lower β-pinene levels. One exceptional tree contained relatively high levels of α-pinene, and low levels of β-pinene and β-phellandrene. Forrest (1980, 1981) reported rare monoterpene patterns with high levels of α-pinene, not associated with high levels of the camphanes, in cortical resin of lodgepole pine. Major gene effects on relative amounts of α-pinene may also occur in some populations.

The broad modality in the frequency distribution of relative amounts of β-phellandrene *(Fig. 2c)* could be explained by constraint caused by expressing results as percentages. β-Phellandrene was a major monoterpene in all samples, while in some trees β-pinene occurred at equal or higher levels. Consequently, modality in β-pinene levels caused modality in relative amounts of β-phellandrene; those trees with high levels of β-pinene contained less β-phellandrene when results were expressed as percentage of total monoterpenes.

Relative amounts of limonene were non-modally distributed *(Fig. 2d),* and modality in the distribution of the minor monoterpenes, e.g. myrcene *(Fig. 2e)* could be explained by their dropping below detection limits in trees lacking resin canals.

Segregation of progeny in the crosses examined fitted both one and two gene models of genetic control. In view of the wide range of dominant phenotypes, and the segregation of recessive phenotypes into two disjunct classes, it is likely that at least two major genes were segregating in these crosses. It is possible that more genes are involved or that other models for two locus control are more appropriate. However, the number of progeny was too small to allow plotting of frequency distributions with sufficiently small intervals to characterize further modes or test the validity of alternate models. The results demonstrate that segregation of progeny into classes appropriate to a one locus model of genetic control does not exclude the possibility of two (or more) locus control, and that the interpretation of the mechanism of genetic control depends on how the segregation classes are defined.

In the trees examined, the number of genes strongly affecting β-pinene levels appears to be small, but it is possible that in other populations more genes may be involved in the control of relative amounts of β-pinene, or that other monoterpenes, (e.g. α-pinene), may be effected by fewer major genes. As stated by Baradet *et al.* (1975), "the mode

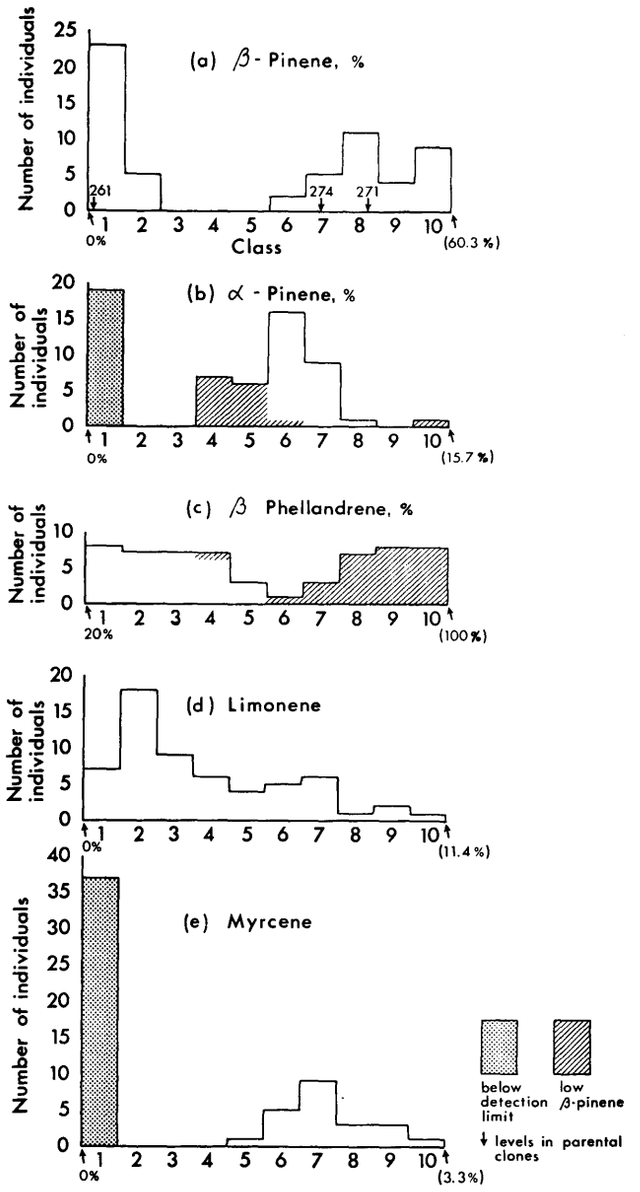

Figure 2. — Frequency distributions of relative amounts of representative monoterpenes. Arrows above the base-line in (a) show levels of β-pinene in the parental clones. Shaded areas — trees with that monoterpene below detection limits; hatched areas — trees with low levels of β-pinene.

of heredity of the same terpene can vary not only between different species but also between different geographic origins of the same species: one concludes that simple genetic determinism occurs in cases in which the number of major genes segregating is reduced." Segregation data limited in range of parental genotypes and number of progeny per cross do not allow speculation about other gene action controlling terpene production in other populations (cf. HANOVER 1966).

While monoterpene levels controlled by major genes may provide useful genetic markers in specific populations after appropriate large scale controlled progeny testing, (e.g. in a seed orchard), the mechanism of genetic control would require further testing before using the same marker in other populations. Differences in monoterpenes under strong additive gene control could provide useful information about degree of genetic differentiation of populations since differences would be based on differences of a larger part of the genome.

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