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SUOMEN METSÄTIETEELLINEN SEURA
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Analysis of monoterpene variation in natural stands and plustrees of *Pinus sylvestris* in Finland

Outi Muona, Raimo Hiltunen, D. V. Shaw & Erkki Morén

TIIVISTELMÄ: MÄNNYN MONOTERPEENIKOOSTUMUKSEN ALUEELLINEN MUUNTELU SUOMESSA METSIKÖISSÄ JA PLUSPUISSA

Muona, O., Hiltunen, R., Shaw, D. V. & Morén, E. 1986. Analysis of monoterpene variation in natural stands and plustrees of *Pinus sylvestris* in Finland. Tiivistelmä: Männyn monoterpeenikoostumuksen alueellinen muuntelu Suomessa metsiköissä ja pluspuissa. Silva Fennica 20(1): 1–8.

Variation of monoterpene composition in *Pinus sylvestris* L. was studied in southern, central and northern Finland using data from both natural stands and plustrees. The natural stands were analyzed using different techniques and for fewer terpenes than the plustrees. There were large differences between areas in the proportion of 3-carene in trees from natural stands, as has been discussed by previous authors. The proportion of 3-carene is bimodally distributed and believed to be controlled by a single gene with large effect. For this reason we stratified our samples into high carene (>10 %) and low carene (<10 %) groups. Univariate analysis did not reveal any additional differences between natural populations in different zones for components other than 3-carene. In the plustrees, several components showed significant differences, but the proportion of 3-carene did not differ between areas. Multivariate discriminant analysis did not distinguish between areas for natural stands. However, for the plustrees discriminant analysis allowed us to distinguish between the zones relatively efficiently. The proportion of correct classification was greater than 64 % using the best methods. The Central zone was most distinct, and 80 % of its trees were correctly classified. Broad generalizations are not possible due to the limitations imposed by our data. Our analysis of phenotypic variation does not support the suggestion that plustrees selected from the north represent a southern type.

Männyn (*Pinus sylvestris* L.) monoterpeenikoostumuksen muuntelua Etelä-, Pohjois- ja Keski-Suomen välillä tutkittiin käyttämällä sekä luonnonmetsiköistä että pluspuuvartteista kerättyä aineistoa. Metsikköjen puut oli analysoitu eri menetelmillä ja harvempien monoterpeenien suhteen kuin pluspuut. Kuten aiemmin on todetu, alueiden välillä on metsiköissä suuria eroja 3-kareeniosuuden suhteen. 3-kareenin osuuden jakauma on kaksihuippuinen; voidaan selvästi erottaa matalakareeniset (<10 %) ja korkeakareeniset (>10 %) puut. Tästä syystä jaoimme aineistomme matalakareenisiin ja korkeakareenisiin puihin muita analyysejä varten. Eri alueiden metsiköt eivät eronneet muiden monoterpeenien kuin 3-kareenin suhteen. Pluspuissa ei ollut eroja 3-kareeniosuuksissa eri alueiden välillä, sen sijaan useiden muiden monoterpeenien osuudet vaihtelivat. Erotteluanalyysi, joka käyttää samanaikaisesti useita muuttujia, ei parantanut eri alueiden erottuvuutta metsiköiden osalta, mutta sen sijaan pluspuualueet voitiin erottaa melko tehokkaasti. Parhaillaan 64 % puista pystyttiin luokittelemaan oikeaan alueeseen monoterpeenikoostumuksen perusteella.

Key words: Geographical variation, Scots pine, monoterpenes
ODC 174.7 Pinus sylvestris+160.22

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Introduction

The relative proportions of monoterpenes in coniferous forest trees are primarily under genetic control (see e.g. Squillace 1976). Because monoterpenes are secondary gene products, they provide information on a class of markers that is rarely available in forest trees. In this report we study the variation in Scots pine monoterpene composition among individuals sampled throughout Finland.

Squillace (1976) reviewed much of the literature on monoterpenes, and suggested some very important limitations to the interpretation of monoterpene data. The most important cautions concern the necessary correlations among individual monoterpenes proportions due to statistical correlation and common biosynthetic pathways. These limitations have been further discussed by Shaw *et al.* (1982), who offer some potential methods for overcoming such limitations. In summary, previous work demonstrates that single monoterpene proportions have little meaning when considered independently of the other proportions within an individual unless the mode of inheritance is known and simple.

The objective of our paper is a complete analysis of two data sets that were previously analyzed concentrating on a single, simply inherited monoterpene constituent. One of the data sets is from natural stands, with older methods, the other from plustree grafts with newer methods. We compare patterns of variation of many monoterpenes between natural stands and plustrees. We use multivariate statistical methods that allow the investigation of variation in the entire complement of monoterpenes. We compare the results of multivariate analysis on these correlated relative monoterpene proportions to the results obtained with univariate methods.

Material and Methods

Origin of Material

One of our data sets consisted of samples from random natural stands, another from selected grafts of plustrees in a seed orchard in southern Finland. There were 18 natural stand populations with 317 trees in total. Mean relative monoterpene proportions for all these 18 natural populations were first presented by Hiltunen, Juvonen and Tigerstedt (1975). For the purpose of our study the natural stand populations were assigned to three source zones: southern Finland (south of 62°N); central Finland (between 62°N and 64°N Latitude); northern Finland (north of 64°N Latitude). Such divisions correspond to the zoning used by the Finnish Forest Research Institute and were made to achieve correspondence between natural stand data and the plustree data set, which follows. Natural population samples consisted of 6 to 25 trees per population. The collection localities are shown on Fig. 1.

The second data set consisted of plus-trees selected from the three zones: 48 from southern Finland, 48 from central Finland, and 50 from northern Finland (See Chung 1981 for a detailed description). All plustree samples were obtained from grafts growing at a single location, Punkaharju Tree Breeding Station. Thus there is less environmental variation than in the data from natural stands. The original location of all included plustrees are shown in Fig. 1, as well as the growing location of the grafts.

Analysis of Monoterpenes

The methods of analyzing monoterpene composition for the material from natural stands have been described by Juvonen and Hiltunen (1972). Oils from natural stands were analysed using gas chromatography apparatus of older kind (Perkin-Elmer model PE-11) equipped with a stainless steel column. Ten monoterpene components could be analyzed. The precision of measurement varied between the components. Hiltunen (1976) obtained coefficients of variation based on repeated analysis of single clones ranging from 0.009 for 3-carene to 0.59 for α-terpinene. We included only the most reliably measured monoterpenes in our analysis: α-pinene, camphene, β-pinene, 3-carene, limonene, β-phellandrene and terpinolene, all of which had coefficients of variation less than 0.10.

Biochemical methods for the plustree data have been described in detail by Chung (1981). The most important differences between these and the earlier analytical methods are involved in the gas chromatography techniques. Plustrees were analysed using a high resolution gas chromatography technique. The instrument (Carlo Erba 2300A) was equipped with an all glass injection system and a high resolution glass capillary column. Altogether 18 components could be identified. Improved methods of biochemical analysis resulted in substantially more precise proportions than estimated for natural stand samples. We used eleven monoterpenes for statistical comparisons: tricyclene, α-pinene, camphene, β-pinene, sabinene, 3-carene, myrcene, limonene, β-phellandrene, γ-terpinene, and terpinolene. All included monoterpenes were quite reliably measured. In repeated analyses of a single clone, the coefficients of variation, were highest for tricyclene (0.10) and γ-terpinene (0.07), the remaining coefficients were less than 0.05.

Because of the different analytical techniques and the different numbers of terpenes distinguished, only general comparisons are possible between the two data sets.

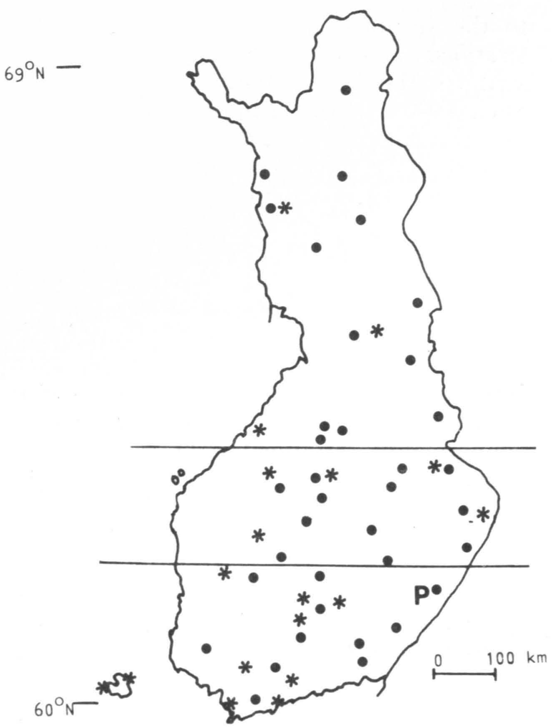

Fig. 1. Locations of natural stands (asterisks), origins of plustree clones (dots), and growing location of the grafts (P = Punkaharju).

Statistical Methods

We used the relative proportions of monoterpenes as variables. For the natural stands, we had seven components and a remainder; for the plustrees, eleven components and a remainder. The remainder includes imprecisely determined and unidentified terpenes; it is not included in further analyses (as a result, relative proportions in Tables 2 and 3 do not add to 100 %). As mentioned in the introduction, the relative proportions of monoterpenes are not independent variables. Reporting of monoterpene quantities as relative proportions of a total introduces a negative correlation among variables, while the sharing of common biosynthetic pathways introduces a positive correlation. Shaw et al. (1982) used multivariate statistics designed to remove the effects of the above correlations and to provide meaningful independent variables for statistical testing, Because such statistical methods are designed for use on normally distributed variables, their application to simply inherited secondary gene products (which are often bimodal in their distribution) may prove invalid. The most obvious case of bimodality in our material is 3-carene (Hiltunen 1975, Hiltunen, Tigerstedt, Juvonen and Pohjola 1975). Because of the bimodality of 3-carene, it is the one constituent in our data set that has been extensively studied. To avoid the problems caused by non-normal distribution of 3-carene proportions, we stratified our samples into two groups: trees containing less than or equal to 10 percent 3-carene and trees containing more than 10 % 3-carene. All data were further treated with an arcsine square-root transformation to enchance normality of the proportion data. All computations were made with the BMDP statistical programs (Dixon 1981).

We studied georgraphical variation of individual monoterpene proportions using one-way analysis of variance among the three zones. We also looked for clinal variation in the monoterpene composition by regression analysis of each component against latitude.

Stepwise discriminant analysis was applied to the stratified data sets and to the unstratified data as a second method for describing the differentiation among zones. Such analysis forms a linear function of the independent portion of the original variables that best discriminates among zones (see Morrison 1967) and eliminates problems induced by correlations among monoterpene constituents. We tested the efficiency of classification by the discriminant function with a jackknifing technique (Lachenbruch and Mickey 1968), thus avoiding circularity of reasoning. Discriminant functions for all variables include the valuable information provided by 3-carene, but are subject to some nonnormality. Stratified data sets will be closer to normal in their distribution but contain less information.

Results snd discussion

The proportions of trees with high and low 3-carene content in different zones for natural stands and plustrees are given in Table 1. The proportion of the high carene type in natural stands was smaller in northern Finland ($\chi^2_{(2)} = 60.9$ $P<0.001$), but there was no such difference among zones for the plustrees ($\chi^2_{(2)} = 2.0$ $P>0.05$). A comparison of the plustrees and natural stands within zones showed that there was no difference in the proportion of high carene trees in the northern and central zones, but the proportion of high carene trees was significantly higher among natural stands in the south than in the plustrees ($\chi^2 = 14.8$ $P<0.001$).

There was no evidence for clinal variation within stratified high carene and low carene groups in the natural stands (Table 2). No significant variation was present among zones for any of the components tested. Our analysis of regression against latitude showed that only camphene within the low carene group had a signifcant regression, with higher proportion of camphene in the south than in the north. The significant regression for camphene accounted for only 16 % of the total variation. Aside from the cline in 3-carene there was little geographical variation in monoterpene composition among natural stands.

We observed more differences among zones for plustrees than for the natural stands (Table 3). None of the major components varied among the zones, but the proportion of myrcene, limonene and β-phellandrene varied in both the high carene and low carene groups. In the low carene group, we also found significant among-zone differences for α-pinene, camphene, sabinene and 3-carene. Because central Finland was usually distinct from the north and south, the regression analysis was significant in only a few cases. Among the high carene trees, tricyclene and α-pinene had significant regressions on latitude, and among the low carene trees, myrcene and terpinolene had significant, regressions. These values should be interpreted with caution, in each case the regression accounted for less than 10 % of the total variation.

The pattern of differentiation among zones resulting from univariate analysis depended on the terpene components examined and on the kind of sample analyzed (plustree vs. natural stand). Zones were well differentiated by 3-carene for natural stand samples, but not for plustree samples (Tigerstedt et al. 1979). Other components, such as β-phellandrene and limonene, differed significantly among zones for plus-tree samples, but not for natural stand samples. A likely explanation for this latter observation is that there was better resolution due to improved methods of analysis and a more uniform environment for plustrees. Both factors have reduced the environmental variance, enabling us to detect the differences. However, it is possible that, as for 3-carene, real differences exist between natural stand and plustree samples. Our data do not allow discrimination between these alternatives.

As discussed in the methods section, multivariate methods are useful for providing comparisons when the correlation structure among variables is complicated. In our study we were concerned that significant variation among zones for several varables might be due to either positive biological or negative statistical correlation. As a critical test, discriminant functions were developed to test whether multiple variables provided better discrimination among source zones than did single variables. We performed four different classifications for each data set (Table 4): using only 3-carene content (which is then univariate analysis), using all variables for the total material, using all variables for the low carene group, and likewise for the high

Table 1. Numbers and proportions (%) of trees with high (>10 %) and low (<10 %) 3-carene content in northern, central and southern Finland in natural stands and among plustrees.

		Natural stands			Plustrees		
		High	Low		High	Low	
South	Trees	140	16	156	32	16	48
	%	90	10		67	33	
Central	Trees	80	21	101	33	15	48
	%	79	21		69	31	
North	Trees	24	36	60	28	22	50
	%	40	60		56	44	

Table 2. Proportions (%) of different monoterpenes (and standard deviations) in natural stands in southern, central and northern Finland, in trees with high (>10 %) and low (<10 %) 3-carene content, and results on analysis of variance (F-test for between zone differences) and regression analysis on latitude (b* = standardized regression coefficient). Significance of ANOVA and regression analysis are indicated by asterisks (* = P<0.05, ** = P<0.001, *** = P<0.001).

	High 3-carene					Low 3-carene				
	South	Central	North	F	b*	South	Central	North	F	b*
α-pinene	47.6	45.5	49.9	1.17	.03	75.0	74.8	74.1	0.11	−.13
	13.1	12.8	12.4			8.6	8.0	7.2		
camphene	5.2	4.9	5.4	0.99	.03	7.4	7.7	9.2	2.34	.40***
	1.8	1.7	1.4			1.9	3.0	3.5		
β-pinene	3.8	3.7	3.5	0.08	−.06	5.4	5.7	5.4	0.21	.06
	2.1	1.5	0.8			3.3	2.4	2.4		
3-carene	33.9	35.5	32.7	0.83	−.02	3.6	3.5	3.0	0.90	−.09
	10.6	11.2	11.1			1.4	1.5	0.8		
limonene	1.3	1.3	1.3	0.01	−.01	2.1	2.0	2.3	1.44	.08
	0.7	0.8	0.7			1.0	1.3	0.9		
β-phellandrene	1.4	1.1	1.1	1.18	−.12	1.6	1.6	1.7	0.20	.04
	2.4	0.6	0.8			1.1	1.1	0.8		
terpinolene	3.3	3.6	3.0	2.00	−.00	0.9	0.8	0.7	0.51	.02
	1.7	1.3	1.0			1.3	0.7	0.3		
Number of trees	140	80	24			16	21	36		

Table 3. Proportions (%) of different monoterpenes (and standard deviations) in southern, central and northern Finland, in plustrees with high (> 10 %) and low (< 10 %) 3-carene content, and results of analysis of variance (F-test for between zone differences) and regression analysis on latitude (b* = standardized regression coefficient). Significance of ANOVA and regression analysis are indicated by asterisks (* = P<0.05, ** = P<0.01, *** = P<0.001).

	High					Low				
	South	Central	North	F	b*	South	Central	North	F	b*
Tricyclene	1.5	1.5	1.2	2.9	−.24*	2.4	1.7	1.8	3.66*	−.15
	.8	.6	.4			1.1	.8	.7		
α-pinene	49.4	51.5	54.8	1.5	.24*	75.0	75.6	79.1	2.25	.26
	13.5	11.2	12.2			5.8	7.8	5.9		
camphene	4.5	4.6	4.1	0.76	−.11	7.7	4.9	5.6	7.85***	−.23
	1.5	1.8	1.2			2.3	2.0	2.0		
β-pinene	2.3	2.7	2.9	0.85	.07	4.2	3.1	3.5	2.21	−.14
	1.0	1.4	3.1			1.5	1.5	1.6		
sabinene	.9	1.0	.9	1.34	−.09	.3	.5	.3	7.68***	−.20
	.3	.3	.3			.1	.2	.2		
3-carene	28.2	25.7	25.8	0.68	−.13	.7	2.6	.6	14.34***	−.24
	10.1	8.6	8.6			.4	2.5	.7		
myrcene	1.9	2.5	1.8	14.50***	−.19	2.2	2.5	1.6	7.42**	−.33*
	.6	.6	.5			.8	.9	.6		
limonene	2.7	1.2	1.6	6.31**	−.15	2.3	1.5	2.4	3.30*	.12
	3.5	.4	.8			1.2	.8	1.2		
β-phellandrene	.5	.9	.5	15.30***	−.16	.5	.8	.5	9.27***	−.14
	.2	.3	.5			.2	.4	.2		
γ-terpinene	1.1	1.3	1.2	0.08	−.03	1.4	2.0	1.6	0.83	−.07
	.7	1.0	.9			1.1	1.6	.9		
terpinolene	2.8	2.6	2.4	0.76	−.18	.7	.5	.4	2.93	−.29*
	1.0	1.3	.7			.4	.3	.3		
Number of trees	32	33	28			16	15	22		

carene group. In the discriminant analysis, we specified F-to-enter to correspond to significance at the 0.05 level and tolerance at 0.01, i.e. the uncorrelated portion of variability contributed by a constituent must be significant. For the natural stands, it was evident that practically the only useful information was provided by 3-carene. In the stratified samples our variables did not produce a classification at all (as expected from Table 2, where there were no significant F-values). When 3-carene alone was used, we obtained 50 % correct classification. Note that in this case the southern and northern zones were quite distinct, whereas the central zone was intermediate and could not be correctly classified. When all variables were used, camphene in addition to 3-carene was included in the classification function. However, this did not improve the resolution. Discrimination among zones based on 3-carene was not powerful. With three zones one would expect 33 % correct classification by chance.

Discrimination among zones based on classification of plustrees was more powerful than for natural stands. Recalling that there were no differences among zones in the frequency of high and low carene trees, it is not surprising that 3-carene used alone produced no classification for the total material. When all variables were used to classify all cases, we obtained 61 % corect classification. The best single variable, β-phellandrene, gave 28 % correct classification when used alone. In the high carene group, the best single variable was also for β-phellandrene, and it alone resulted in 54 % correct classification. Adding the other variables improved the classification to 65 % correct. Similarly, in the low carene group, the best single variable was 3-carene, which used by itself resulted in 53 % correct classification. Using all variables resulted in a classification function which gave correct results for 64 % of the cases. In all cases, using multiple variables produced more reliable results than any single variable. Further, stratification into high and low 3-carene groups improved classification.

Table 4. Proportion of correctly classified trees by discriminant function analysis using different sets of variables for classification in natural stands and plustrees of *Pinus sylvestris*.

Classification method	Percentage of correct classification				Variables included in discriminant function
	South	Central	North	Total	
Natural stands					
3-carene only, all cases	63	21	63	50	3-carene
All variables, all cases	57	21	60	46	3-carene, camphene
All variables, high carene group	no classification				
All variables, low carene group	no classification				
Plustrees					
3-carene only, all cases	no classification				
All variables, all cases	63	84	58	61	β-phellandrene, limonene, terpinolene camphene, sabinene, myrcene
All variables, high carene group	50	85	57	65	β-phellandrene, limonene, 3-carene sabinene, tricylene
All variables, low carene group	63	80	55	64	3-carene, camphene, limonene, β-phellandrene, terpinolene

The most important result of our multivariate analysis was that zones of origin are well discriminated by several monoterpene constituents, using plustrees. Improved discrimination by inclusion of several constituents indicates independent contribution by the constituents; univariate significance could occur at several constituents due to biological or statistical associations (Squillace 1976). We cannot say with confidence that natural stand samples would yield a substantially different pattern when analyzed with similar biochemical methods. Our results indicate that a reanalysis of natural stand patterns, using more advanced techniques is needed. Clear geographical differentiation with respect to several terpenes has been found in other species, e.g. *Pinus taeda* (Squillace and Wells 1981).

The pattern described for 3-carene should not be substantially altered by changes in method. Differences between plustrees and natural stand samples for 3-carene are not reflected in other constituents. Previous authors have suggested that the higher proportion of high carene trees in the north in plustrees is due to favoring of southern features in the selection of plustrees (Tigerstedt et al. 1979, Chung 1981). These analyses were based on estimating the allelic frequencies at the 3-carene locus. However, in our analysis, which is based on phenotypes, the proportion of high carene trees did not differ between natural stands and plustrees in the north. Instead, the proportion of high carene trees in the south was much lower in the plustrees than in the natural stands. This does not support the suggestion that plustrees are more representative of a southern type. Clearly, the comparison of natural stands and plustrees requires further study.

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