Table 2. — Genotypic stability and productive quality for height.

Rank	Clone	Mean height (cm)	Tai's α	Tai's λ	Wricke's ecovalence	PQI
1	Jac. 15	140.75	-0.1607	4.8038	1 611.3522	2.4281
2	GA. 88	133.78	0.6271	1.1374	857.6878	1.9567
3	Jac. 17	123.58	-0.4918	2.2706	1 044.0938	1.2668
4	DN. 5	119.75	0.6984	0.2929	696.2642	1.0078
5	DN. 16	115.28	0.1560	0.5525	211.6058	0.7054
6	CAG. 23	115.23	0.7560	0.1232	743.4418	0.7021
7	Jac. 16	114.63	-0.9722	-0.0349	1 151.0078	0.6615
8	DN. 17	107.63	0.5764	0.0798	434.9118	0.1880
9	DN. 7	102.30	-0.1864	0.4146	179.0802	-0.1725
10	DN. 42	101.28	-1.1848	1.0733	2 079.4758	-0.2415
11	DN. 2	99.43	0.2518	0.6223	282.5998	-0.3666
12	Jac. 4	99.03	0.2224	1.0763	414.7578	-0.3936
13	D. 38	95.70	-0.1261	2.3954	807.2162	-0.6189
14	IH.78B	95.08	-0.1383	0.7141	258.3338	-0.6608
15	DN. 28	93.25	0.5013	0.6450	521.1422	-0.7846
16	C. 147	94.13	-0.4515	1.7248	817.8558	-0.7251
17	IH.45/51	88.83	-0.2633	2.4818	901.3438	-1.0835
18	CAG. 26	87.43	-0.1648	-0.0007	33.8498	-1.1782
19	DN. 30	85.58	0.6031	0.1168	485.7898	-1.3033
20	D. 89	84.35	-0.2524	0.7286	317.9082	-1.3865

Table 3. — Clones selected for various sites under option 1.

Clone	Goose Arm	Millertown Jct. Road	Robinson River	Wooddale
Jac. 15	+	+		+
GA.88	+	+	+	+
Jac. 17		+	+	+
DN.5	+			
DN.16			+	
CAG.23	+			+
Jac. 16		+	+	
DN.17				

which is 692.4859 in this case. This gives 10 clones, DN.16, DN.17, DN.7, DN.2, Jac. 4, IH.78B, DN.28, CAG.26, DN.30 and D.89. Out of these, four clones, DN.7, IH.78B, CAG.26 and D.89 qualify under Tai's method. These four clones can be recommended for environmental conditions resembling those at any of the test sites under study.

The first option identifies clones which are fast growing as well as best suited for the environmental conditions represented by the test sites specified. This method is recommended if the environmental conditions at the planting sites are known and match those represented by the test sites used in this study. The second option identifies clones which may not be the best in growth but are genotypically stable. This method is recommended for situations in which environmental conditions at the planting site are unknown or do not match those at any of the test sites planted in this study.

Conclusion

The important conclusion is that if environmental conditions of the planting sites are known to resemble those at the four test sites, *Table 3* should be used as a guideline for selection of suitable clones. Clones DN.7, IH.78B, CAG.26 and D.89 seem to be the best suited for boreal regions if the environmental conditions of the planting site are not known.

Acknowledgements

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Variation and Heritability of Wood Density and Fibre Length of Trembling Aspen in Alberta, Canada

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Abstract

Fifteen putative trembling aspen (*Populus tremuloides* Michx.) clones in north-central Alberta were sampled to examine patterns of variation and determine the heritability of wood density and fibre length among clones. Large increment cores from the southern radius at breast height of each of five to nine trees in each clone were divided into four-year sections from the pith outward. All trees sampled were at least 36 years of age. Wood density measurements were made on each four-year section, and fibre lengths were measured on every second four-year increment period.

There were significant clonal differences for both wood density and fibre length. Broad-sense heritabilities for wood density and fibre length were 0.35 and 0.43, respectively. Wood density is generally high near the pith, decreases substantially a short distance from the pith, then increases in the mature wood zone. Fibre length is short near the pith and increases markedly across the radius. There was a slight negative phenotypic correlation between

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wood density and growth rate and a slight positive phenotypic correlation between fibre length and growth rate. Genetic correlations indicated these relationships are under moderate genetic control.

Key words: Populus tremuloides (Michx.), clones, wood density, fibre length, variation, heritability.

Zusammenfassung

Es wurden fünfzehn vermutliche *Populus tremuloides* Michx. Klone in Nord- Zentral-Alberta als Stichproben entnommen, um Variationsmuster zu untersuchen und die Heritabilität der Holzdichte sowie der Faserlänge zwischen den Klonen zu bestimmen. Von je 5—9 Bäumen jedes Klones wurden auf der Südseite in Brusthöhe radial dicke Bohrkerne entnommen und vom Mark auswärts in Vierjahressektionen unterteilt. Alle getesteten Bäume waren mindestens 36 Jahre alt. In jeder der Vierjahressektionen wurden Holzdichte-Messungen vorgenommen und in jeder zweiten Vierjahres-Wachstumsperiode Faserlängen-Messungen durchgeführt.

Sowohl für die Holzdichte, als auch für die Faserlänge gab es signifikante Klonunterschiede. Die Heritabilitäten im weiteren Sinne für Holzdichte und Faserlänge waren 0,35 bzw. 0,43. Die Holzdichte in der Nähe des Markes ist generell hoch, sie nimmt in kurzer Entfernung vom Mark wesentlich ab, um in der äußeren Holzzone wieder anzusteigen. Die Faserlänge in der Nähe des Markes ist gering und nimmt entlang des Radius merklich zu. Es gab eine leichte negative phänotypische Korrelation zwischen Holzdichte und Wachstumsrate und eine leichte positive phänotypische Korrelation zwischen Faserlänge und Wachstumsrate. Genetische Korrelationen zeigen, daß diese Beziehungen mäßig genetisch kontrolliert sind.

I. Introduction

It has been well established that in conifers, wood density and fibre length are anatomical characters which exhibit moderate to strong heritability (Goggans 1961, Zobel 1961). Heritability estimates for these wood properties in hardwood species are unfortunately relatively scarce. However, the increasing economic value of trembling aspen *Populus tremuloides* (Michx.), particularly in the Great Lakes-St. Lawrence Valley region of North America, has caused a number of investigators to examine the natural variation and heritability of wood density and fibre length in aspen. Van Buijtenen *et al.* (1959) estimated broad-sense heritabilities for trembling aspen in Wisconsin to be 0.17 and 0.35 for wood density and fibre length, respectively. Narrow-sense heritabilities using five year-old aspen indicated moderate to good genetic control for both wood density and fibre length (Einspahr *et al.* 1967). Similarly, moderate to high heritability values for these two wood properties have been reported in triploid clones of trembling aspen (Einspahr *et al.* 1963). Along with studies of genetic control of these wood properties, natural variation of wood density and fibre length in trembling aspen have also been well documented (Brown 1961, Brown and Valentine 1963, Einspahr and Benson 1966, Valentine 1962).

Little information is available on clonal variation of these wood characters outside of eastern North America. Conceivably, inter- and intra-clonal patterns of wood property variation should remain relatively constant within a species. However, clinal patterns are often present for a number of wood properties (Einspahr and Benson 1966, Ledig *et al.* 1975), and it is likely that large differences in wood properties may occur across a large geographic distribution. In a previous paper we reported on intra-clonal and within-tree variation of wood density (Yanchuk *et al.* 1983). In this paper we report on variation and heritability of wood density[2]) and fibre length among naturally occurring aspen clones in north-central Alberta, Canada.

II. Materials and Methods

Trembling aspen typically forms clones of many genetically identical ramets (Barnes 1966). Fifteen clones, located approximately five km north of the town of Blue Ridge in north-central Alberta

(LD-SE1/4; Sec10; TP60; R10; W5th),

were delineated on the basis of phenotypic and phenological differences as outlined by Barnes (1969). The clones occurred in two stands located approximately eight km apart. Twelve clones were sampled in one area and three clones in the other. Since the effect of sample areas was of little concern in this study, no attempt was made to include more sample areas. Sample trees were at least 36 years of age in each putative clone and were selected for stem straightness and absence of obvious decay. Ten trees were sampled in each clone. Due to an unusually high incidence of heartrot, the number of acceptable trees in each clone varied from five to nine.

Whole cores, from the pith to the bark were removed from the southern radius of each tree at breast height with a large diameter (11 mm) increment borer. To account for the variation present in the radial direction, increment cores were segmented into four-year increments or "sections" (i.e., rings 1—4, 5—8, 9—12 etc.). Measurements of width (indicative of rate of growth over a four-year period), physical distance from the pith (measured at the mid-point of each four-year section) and wood density were recorded for each section. Wood density determinations were made by the maximum moisture content method (Smith 1955).

Measurements of fibre length were made from cells of each second four-year section from the pith outwards. Therefore, each tree was represented by five fibre length values (i.e., rings 1—4, 9—12, 17—20, 25—28 and 33—36). To obtain unbiased estimates of fibre length, fibre preparations and measurements were made as outlined by Taylor (1975). Fifty unbroken fibres in each four-year sample were measured using a micro-computer digitizer apparatus (Micko *et al.* 1982).

Statistical Analyses

A split-plot analysis of covariance (ANCOVA) model with "areas", "clones within areas", "trees within clones/areas" and "sections" as the sources of variation was selected as the appropriate model for the analysis. "Rate of growth" and "distance from the pith" were initially included in the model as covariates; however, "distance from the pith" was later removed because of the apparent non-linear trend of wood density and fibre length variation across the radius. Brown (1961) also found that measurements of wood density with "distance from the pith" used as a regression was not significant. To obtain a statistically balanced design, only the first 36 increments (counting from the pith outward) in each core were used.

The natural clonal growth habit of aspen facilitates the estimation of the amount of genetic control of various morphological and anatomical characters. Heritabilities,

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[2]) In this paper, wood density is taken to mean basic specific gravity (i. e., the ratio of OD wt. (g) divided by green vol. (ccm.).

their standard errors, and genetic correlations for wood density and fibre length were calculated from variance and covariance components derived from HARVEY's (1977) LSML76 computer program. Broad-sense heritability estimates were determined as follows:

$$h^2 = \frac{V(g)}{V(p)} = \frac{V(c)}{V(c) + V(t) + V(e)}$$

where; V(g) = genotypic variance
V(p) = phenotypic variance
V(c) = variance among clones
V(t) = variance among trees within clones
V(e) = error (unexplained) variance

Genetic correlations were calculated as described by FALCONER (1981, p. 285).

"Areas" was considered a fixed effect and "clones" and "trees within clones" (nested) were considered random effects. With this assumption it was also assumed that clones have a mean of zero (SEARLE 1971); therefore, for graphical purposes only, least-squares means used in figures ranking the clones based on means were obtained by considering clones as fixed effects. Means presented in figures showing wood density and fibre length variation at various age intervals across the radius at breast height are simple means.

The source of variation "trees within clones" typically is tested against the error mean square to determine if there is significant variation among trees within clones. This test, however, is improper in this split-plot design (ANDERSON and McLEAN 1974). Therefore, variation among trees within clones should be of little concern, and emphasis placed on clonal differences and heritabilities obtained for the traits examined.

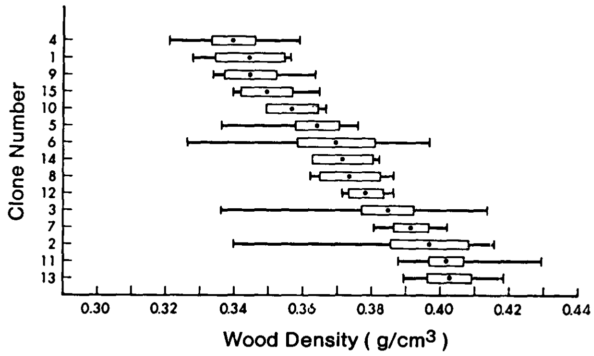

Figure 1. — Ranking of 15 aspen clones from north-central Alberta for mean wood density. Solid dots, open bars and solid lines represent least-squares means, one standard error and range within each clone, respectively.

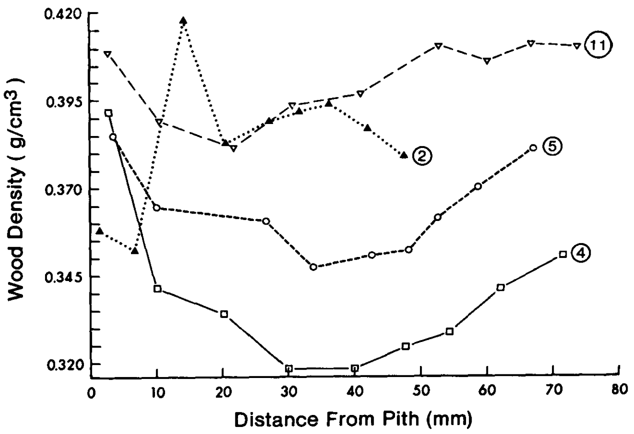

Figure 2. — Variation of wood density with distance from pith for four aspen clones from north-central Alberta. The four clones represent a high, two intermediate and a low wood density clone from the 15 sampled.

III. Results and Discussion

Wood Density

Mean wood density varied from 0.32 g/cc to over 0.40 g/cc among the fifteen clones *(Figure 1)*. In addition to the large differences among clones, there also were substantial differences in the level of within-clone variation. For example, the tree with the highest wood density measured in clone 4 was 0.36 g/cc, whereas the tree with the lowest wood density in clone 13 averaged 0.39 g/cc. Most clones exhibited narrow ranges similar to clones 4 and 13; however, large variation was present in a few cases (i.e., clones 2, 3 and 6). The cause of such large variation may have been the presence of tension wood or wet-pocket bacterial infections. A more informative approach to intra-clonal variation might consider the standard error of the means for each clone.

Inter-clonal differences for wood density were significant *(Table 1)*. The estimated variance components suggested that the effect of clones accounted for approximately

Table 1. — Least-squares analysis of covariance (ANCOVA) for wood density for 15 putative aspen clones (5—9 trees/clone) from north-central Alberta. Model includes the covariate "section width" and "section" to account for within-tree variation of wood density.

SOURCE	DF	MEAN SQUARES	F	VARIANCE COMPONENTS
Areas	1	0.017646	0.68	
Clones/A	13	0.025946	10.46**	.00038767
Trees/C/A	88	0.002480	4.93**	.00022022
Section	8	0.004205	8.34**	
S x A	8	0.001821	3.61**	
Regression X1(section width)	1	0.002492	4.95*	
Error	807	0.000503		.00050324

** significant at the 1% level.
* significant at the 5% level.
regression coefficient = b(×1) = 0.00073009
Broad Sense Heritability = 0.35 S.e. of h^2 = 0.09

Table 2. — Phenotypic and genetic correlations for rate of growth on wood density and fibre length. Phenotypic correlations were done on each of the four-year sections and genetic correlations by combining two increment periods or "sections" (i.e., sections 1 & 2, 2 & 3 etc.). Section number represents a four-year increment from the pith outward for 100 aspen trees from 15 aspen clones from north-central Alberta.

Section number	years (rings) represented	Wood Density phenotypic r(p)	Wood Density genetic r(g)	Fibre Length phenotypic r(p)	Fibre Length genetic r(g)
1	1-4	-.143		+.404**	
			-.177		
2	5-8	-.093			+.730
			-.331		
3	9-12	-.128		+.196*	
			-.445		
4	13-16	-.197*			+.595
			-.196		
5	17-20	+.007		+.207*	
			+.084		
6	21-24	+.272**			+.457
			-.299		
7	25-28	-.166		+.401**	
			-.450		
8	29-32	-.041			+.487
			-.525		
9	33-36	-.266		+.288**	
OVERALL CORRELATION		-.094*	-.479	+.311**	+.577

** significant at the 1% level.
* significant at the 5% level.

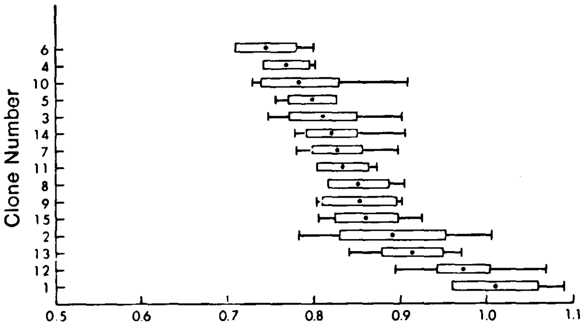

Figure 3. — Ranking of 15 aspen clones from north-central Alberta for mean fibre length. Solid dots, open bars and solid lines represent least-squares means, one standard error and range within each clone, respectively.

35 percent of the phenotypic variation of wood density. This is similar to the heritability ratios reported for wood density in aspen elsewhere (Van Buijtenen *et al.* 1959, Einspahr *et al.* 1963).

The effect of the four-year sections in the model also was significant ($P < 0.01$), indicating that great variation is present along the radius at breast height *(Table 1).* Clones 11 and 4 represent clones of high and low wood density, respectively, while clones 2 and 5 represent clones of intermediate wood density *(Figure 2).* Except for the erratic variation patterns exhibited by clone 2 (which was very atypical and probably due to a combination of incipient decay and small numbers of trees in a clone), wood density near the pith was always high, then decreased to a minimum at 30—40 mm from the pith and then increased in the "mature wood" zone. The magnitude of this decrease in wood density in the transition from juvenile to mature wood would seem to be the major contributing factor in determining the average wood density for a clone.

The high wood density near the pith of most of the clones may indicate that an inherent growth pattern influences the types of cells produced. Brown (1961) also found high wood density near the pith of aspen stems. Possible reasons for this high wood density, such as cell composition and tension wood organization, could only be clarified by detailed anatomical study similar to that done by Isebrands (1972) for eastern cottonwood.

The covariate, section width (X1-*Table 1*), accounting for the variation in growth rate over a four-year period, suggested that a weak positive correlation existed for rate of growth and wood density. However, the overall regression coefficient (b = .000730) in *Table 1* does not account

Table 3. — Least-squares analysis of covariance for fibre length for 15 aspen clones (5—9 trees/clone) from north-central Alberta. Model includes the covariate "section width" and "sections" to account for within-tree variation of fibre length.

SOURCE	DF	MEAN SQUARES	F	VARIANCE COMPONENTS
Areas	1	0.306795	2.22	
Clones/A	13	0.138217	13.41**	.00442823
Trees/C/A	73	0.010311	2.23**	.00114078
Section	4	1.475830	318.55**	
Section x Areas	4	0.013564	2.93*	
Regression X1(section width)	1	0.081561	17.60**	
Error	343	0.004633		.00463301

** significant at the 1% level.
* significant at the 5% level.
regression coefficient = b(X 1) = 0.0063183
Broad Sense Heritability = 0.43 S.e. of h^2 = 0.11

for the known differences exhibited between juvenile and mature wood. Statistical comparisons between growth rate and wood density from various locations in a tree may lead to incorrect conclusions about this relationship. Therefore, each group of four-year sections, representing a specific increment period in the trees from all 15 clones was analyzed separately using correlation analysis. All but two of the sections from 100 trees showed slight negative correlations between wood density and rate of growth *(Table 2)*. These phenotypic correlations correspond to those reported earlier for *Populus* (Kennedy 1968, Kennedy and Smith 1959, Smith and Rumma 1971). While the statistical significance of the correlations is relatively weak in most cases, the overall trend of a negative relationship between rate of growth and wood density is evident *(Table 2)*. Genetic correlations for wood density and growth rate, however, indicate that this negative relationship has a substantial genetic basis *(Table 2)*. This suggests that the selection of faster growing clones would inherently reduce wood density.

Fibre Length

Mean fibre lengths for the 15 clones also showed a substantial range of variation *(Figure 3)*. Clone 1 had a mean fibre length of 0.97 mm, whereas clone 6 had a mean fibre length of 0.67 mm. The range of variation within clones for fibre length is comparable to that observed for wood density. Again, the best method of analyzing within-clone variation might consider the standard errors of the means for each clone (the open bars in *Figure 3* represent one standard error on each side of the mean).

As was the case for wood density, there were significant differences among clones for fibre length *(Table 3)*. The effect of clones accounted for 43 percent of the phenotypic variation (as calculated from the variance components given in *Table 3)*. This heritability for fibre length is within the range of heritabilities reported for fibre length in trembling aspen (Einspahr *et al.* 1963, Van Buijtenen *et al.* 1959).

The source of variation "sections" was very significant ($P < 0.01$) in the analysis *(Table 3)*, indicating that there were large differences in fibre length across the radius. Fibre length was initially quite short near the pith, steadily increased, and then leveled off approximately 40—50 mm from the pith *(Figure 4)*. Again the clones chosen represented a high, intermediate and low range of differences in average fibre length. Clones which had long fibres in the first four years also had long fibres at later ages. This may have practical applications, since it would permit selection of clones with long fibres at an early age.

For the five, four-year sections, there was a slight positive correlation between fibre length and rate of growth *(Table 2)*. This positive relationship between rate of growth and fibre length corresponds to that typically reported for *Populus* (Kennedy 1957, Spurr and Hyvarinen 1954). The phenotypic correlations between rate of growth and fibre length were somewhat stronger than those found between growth rate and wood density. The genetic correlations were also more postive than the phenotypic correlations. suggesting that selection of fast growing clones would inherently select for longer fibres as well.

General

Because the trees were of varying age, it would be unlikely that similar four-year increments originated under similar environmental conditions. This undoubtedly influenced both variance components in the denominator of the heritability calculation (i.e., variance of trees within clones and error). Assuming that a majority of similar four-year sections arose under different conditions, it seems reasonable to suggest that the heritabilities reported here are conservative estimates, simply because more environmental variation likely was present during the formation of the wood examined.

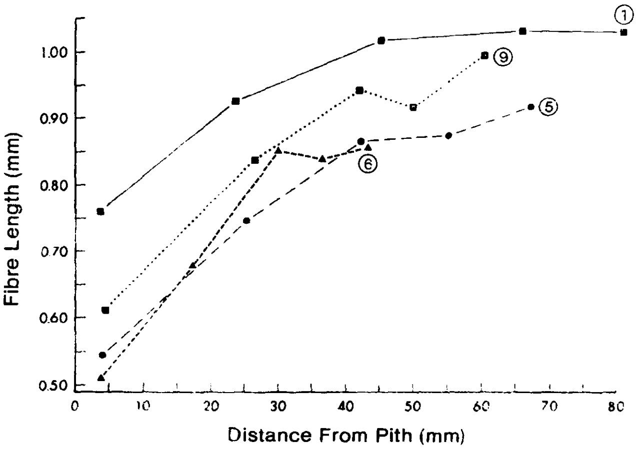

Figure 4. — Variation of fibre length with distance from pith for four aspen clones in north-central Alberta. The four clones represent a long, two intermediate and a short fibre length clone from the 15 sampled.

The inclusion of the four-year sections as a source of variation (for both wood density and fibre length) also substantially reduced the error variance, thereby decreasing the overall phenotypic variance component [V(p)]. This has the effect of increasing the heritability value obtained; however, the variance component for "trees within clones" [V(t)], was partitioned out and added to the total phenotypic variance [V(p)]. Although this may not alter the final heritability estimate, it does increase the reliability of the heritability because within-clone and among-clone variances were partitioned into separate components.

Namkoong and Squillace (1968) indicated that estimating heritabilities from clonal material in this manner may force the inclusion of special genetic and non-genetic effects which make each experiment quite separate and site-specific. These special effects are probably due to lack of replication among clones and unequal growing spaces and age for all ramets in a clone (Barnes 1966). Therefore, the heritabilities estimated here are only applicable to the two stands sampled. However, it is likely that similar results would be obtained for both wood characters in other areas or stands of aspen in its native range.

The clonal differences and heritabilities of fibre length and wood density reported here generally confirm reports of these traits of aspen in other parts of its native range and confirm the moderate strength of wood density and fibre length heritabilities. The magnitude of the relationship between growth rate and wood density or fibre length is relatively important and suggests that wood density needs to be considered in tree improvement programs of aspen. As mentioned by Kennedy (1968), the selection of clones of both fast growth and high wood density may overcome any negative effect this relationship may have.

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Foliar terpene heritability in Pinus contorta[2]

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1. Abstract

Terpenes were analyzed in ten clones and ten corresponding open-pollinated families of lodgepole pine *(Pinus contorta* Dougl.). Statistical descriptions of the genetic properties of this sample indicate strong genetic control of monoterpene levels by multiple genes acting on the factors which control terpene metabolic steady-state.

Heritabilities are discussed in regard to grafting effects, the use of different bases for chemical data, and the distribution of data based on amounts of secondary plant products.

Key words: Pinus contorta, Pinaceae, Lodgepole pine, genetics, terpenes, heritability.

Zusammenfassung

An 10 Pfropfklonen und 10 korrespondierenden, frei abgeblühten Familien von *Pinus contorta* Dougl. wurden Terpen-Analysen durchgeführt. Nach statistischer Auswertung ergab sich eine strenge genetische Kontrolle auf den Monoterpen-Levels durch multiple Genaktivität bei den Faktoren, welche metabolisch den Terpen-Gleichgewichtszustand kontrollieren.

Unter Berücksichtigung der Auswirkungen, welche aus der Pfropfung resultieren, werden die Heritabilitäten hinsichtlich verschiedener Grundlagen für die chemischen Daten und die Verteilung der Daten auf der Basis einer Wertung als sekundäre Pflanzenprodukte diskutiert.

2. Introduction

Terpene composition has been used as a taxonomic character to study geographic variation within populations of lodgepole pine (von Rudloff and Nyland 1978, Pauly and von Rudloff 1971), introgression between lodgepole and Jack pine *(P. banksiana)* (Mirov 1956), and to identify sources of lodgepole plantations (Forrest 1980, 1981). The assessment of the taxonomic weight to be given to a terpene depends on how it is genetically controlled, but the genetics of terpene production in conifers is generally inadequately known (Hunt and von Rudloff 1977).

Suggestions that levels of individual terpenes may be

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