should be compared with *Pinus pinaster* and tested on leached, acid and well drained soils not on sites suitable for *Pinus radiata* (Personal communication by Dr. R. POYNTON). It was also clear that *Pinus muricata* suffered heavier mortality than *Pinus radiata* on waterlogged sites like at Witfontein.

At Bergplaas and Witfontein very strong positive correlations existed between the four and eight year measurements and selection at age four years was perfectly possible if we accept that the relative position of the provenances remains constant from the age of eight years. This was the case in provenance trials of *Pinus caribaea, Pinus elliottii* and *Pinus taeda* in South Africa (FALKENHAGEN, 1978, 1979).

It is recommended that more seed should be obtained from the Sonoma provenance. Further testing of provenances of the green variety should also be contemplated.

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Inheritance Pattern of the Flavonic Compounds in Scots Pine (Pinus sylvestris L.)

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Abstract

A genetic experiment of variation of the flavonic pattern in different crosses of *Pinus sylvestris* is presented. Variations fall in distinct categories in crosses between two clones. Some individuals show high prodelphinidin content (> 85%) and lack taxifolin; they are regared as homozygotes tt, or T^-. Clones with low prodelphinidin content and presence of taxifolin are all regarded as heterozygotes Tt, or T^+. We found no clone homozygote for TT genotype, which is probably rare in the population.

Crossing experiments between heterozygote Tt and homozygote tt clones give offsprings compatible with 50: 50 segregation, whereas crosses between two heterozygotic clones give offsprings compatible with 75: 25 segregation. Thus it is suggested that one simple locus is responsible for most of the differences seen in the flavonoid patterns in Scots pine.

Key words: inheritance flavonoid *Pinus sylvestris.*

Introduction

LARACINE (1984), LARACINE and LEBRETON (1988), reported the occurrence of two chemotypes within the Scots pine, *Pinus sylvestris:* the first contains prodelphinidin as major flavonic component of the needles. In the second chemomorph, phenyl-trihydroxylation decreases in favour of dihydroxylation of the lateral ring; prodelphinidin is rivalled by procyanidin whereas quercetin increases and taxifolin (= dihydro-quercetin) appears (see biochemical scheme). This taxifolin dimorphism has been more recently confirmed by LUNDGREN and THEANDER (1988).

Thus, the first chemomorph was called T^- (taxifolin absent) and the second T^+ (taxifolin present). In the natural range of Scots pine, covering the whole of Europe, two modes of distribution of these morphs are observed: the first is located at high elevations (over 800 m) and/or latitudes (above Polar circle); the T^--morph is largely predominant there, even exclusive in most of the cases (Alps, Pyrenees,..).

The second group of populations with taxifolin present is located at low elevations (from Eastern Europe to Southern France; Central and Southern Sweden is also covered). In these populations, the occurrence of individuals with taxifolin present represents 32% to 62%; however none of these populations differs significantly from the proportion 50%:50%.

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The purpose of this paper is to elucidate the inheritance mode of flavonic characters in *Pinus sylvestris* by the analyses of clones and their full sib progenies.

Materials and Methods

1. Crossing experiments

Clones were collected from Långtora clonal seed orchard near Enköping, Sweden. The clonal archive was established by the Department of Forest Genetics in Stockholm. Progenies were obtained from controlled crosses collected from a progeny trial in Alunda, planted in 1978, and Pustnäs, planted in 1981, both near Uppsala; Ljusfallet, planted in 1978 near Garpenberg. All these progeny trials were established by the Department of Forest Genetics in Uppsala.

2. Biochemical experiments

After spontaneous drying of mature needles, two grams of finely ground material were submitted to acidic hot treatment (HCI 2 N). After cooling, one part served for (pro) anthocyanidin analysis (see below), whereas ether extraction gives the taxifolin (and quercetin) fraction.

Spectrophotometry (O. D. at 535 nm) and HPLC (for determination of the prodelphinidin/procyanidin ratio, expressed as prodelphinidin L. D. %) were run to obtain absolute and relative values of the two (pro)anthocyanidins. T. L. C. (on polyamid) served to determine the presence/absence of taxifolin (brown spot under U. V. light).

Results of the chemical analyses are expressed as:
— relative proportion (L. D. %) and absolute content (mg/g of dried needles) of (pro)delphinidin;
— presence/absence of taxifolin.

Moreover, at the population or progeny level, the flavonic pattern was expressed by two complementary ways: the frequency (%) of the T+ morph and the mean value (with standard error) of the prodelphinidin content. Thus, by study of F1-individuals issued from each cross, we could determine the various modes of inheritance at one statistic level.

Results and Discussion

The flavonic patterns of the parental trees are summarized in *table 1*. For the inheritance study, progenies from controlled crosses with or without taxifolin are used.

Table 1. — Flavonic pattern of the parental trees.

Parental tree	Original latitude	Taxifolin type	Proanthocyanidins (mg/g)	Prodelphin. (%)
C 3001	60°20′	T+	2,1	67 %
D 2019	59°11′	T-	2,9	91 %
D 2022	59°13′	T-	2,8	94 %
E 2001	57°44′	T-	3,5	94 %
E 2008	58°44′	T-	1,6	94 %
E 3003	58°47′	T+	1,2	57 %
E 3004	58°46′	T+	0,8	63 %
E 4006	57°50′	T-	1,8	92 %
E 4008	58°08′	T+	0,6	56 %
F 1008	57°39′	T-	2,5	95 %
F 2029	58°08′	T-	2,6	93 %
T 1013	59°50′	T+	0,6	55 %
W1022	59°55′	T+	08	67 %

Table 2. — Flavonic pattern of the offsprings issued from the 18 controlled crosses. (The figure within brackets indicates the number of individuals analysed).

No.	Controlled Crosses	Presence of taxifolin		Proanthocyanidins tot. (mg/g)	prodelphin.	LD%
	T⁻ x T⁻					
4	D2022 x E2001	0 %	(15)	4,9 ± 1,4	94 ± 1	(6)
6	D 2022 xF2029	0 %	(16)	4,1 ± 0,9	93 ± 1	(6)
28	D 2019xE2001	0 %	(15)	3,7 ± 0,8	93 ± 1	(6)
30	D 2019xF2029	0 %	(15)	4,1 ± 1,2	93 ± 1	(6)
	Total mean	0 %	(61)			
	T⁺ x T⁺					
51	E 3003xC3001	80 %	(15)	T⁺ 2,7 ± 0,8	78 ± 3	(12)
				T⁻ 4,2 ± 0,6	93 ± 1	(3)
53	E 3003xE4008	56 %	(16)	T⁺ 2,3 ± 0,6	73 ± 5	(9)
				T⁻ 3,0 ± 0,9	89 ± 5	(7)
55	E 3003xT1013	67 %	(15)	T⁺ 3,1 ± 0,6	77 ± 4	(10)
				T⁻ 5,4 ± 1,7	93 ± 1	(5)
128	E 3003xE3004	65 %	(17)	T⁺ 2,6 ± 0,5	73 ± 3	(4)
				T⁻ 4,1 ± 2,2	93 ± 1	(2)
173	E 3003xW1022	75 %	(16)	T⁺ 2,6 ± 0,6	70 ± 4	(12)
				T⁻ 5,0 ± 1,4	94 ± 1	(4)
	T⁺ x T⁻	69 ± 9%	(79)			
5	E 4008xD2022	50 %	(14)	T+ 2,4 ± 0,9	72 ± 5	(6)
				T- 3,1 ± 1,1	91 ± 1	(6)
29	E 4008xD2019	50 %	(8)	T+1,9 ± 0,9	71 ± 6	(3)
				T- 3,6 ± 1,5	92 ± 2	(3)
52	E 3003xE2001	50 %	(18)	T+ 2,7 ± 1,3	76 ± 7	(4)
				T- 5,0 ± 0,3	93 ± 1	(2)
54	E 3003xF2029	56 %	(16)	T+ 2,1 ± 0,3	76 ± 2	(5)
				T- 3,8 ± 2,3	91 ± 3	(4)
119	E 3003xE2008	60 %	(15)	T- 3,0 ± 0,7	72 ± 2	(9)
				T- 3,4 ± 1,1	93 ± 3	(6)
120	E 3003xE4006	53 %	(17)	T+ 3,1 ± 0,5	74 ± 3	(9)
				T- 4,9 ± 1,0	93 ± 1	(8)
121	E 3003xF1008	50 %	(16)	T+ 1,2 ± 0,3	61 ± 2	(8)
				T- 2,7 ± 0,5	91 ± 2	(8)
129	E 3004xE4006	61 %	(18)	T+ 2,9 ± 0,7	76 ± 2	(10)
				T- 3,6 ± 0,9	93 ± 2	(7)
130	E 3004xF1008	53 %	(19)	not determined		
	Total mean:	54 ± 4 %	(141)			

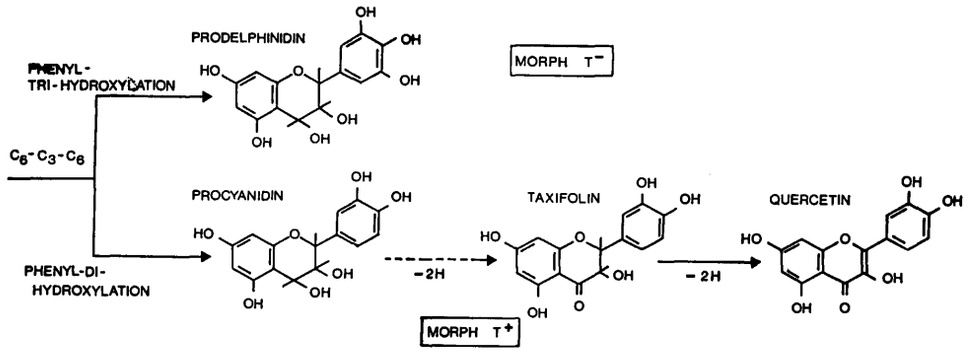
1. T⁻ x T⁻ crosses: Four different crosses originating from parents with T⁻ phenotype were investigated. All 61 progenies from these crosses appeared to have T⁻ phenotype (*Table 2*).

2. T+ x T+ crosses. Five different crosses with T+ x T⁺ phenotype with a total number of 79 offspring were studied. The progeny of these crosses segregated into T⁺ and T⁻ phenotypes (see *Table 2* and *Figure 1*) with the proportion 54T⁺/25T⁻. These segregation distributions correspond to the ratio 68:32, which does not differ statistically from the 75:25 one (χ^2 test: 1.52) but well from the one with 50:50 distribution (χ^2 test: 9.92).

3. T+ x T⁻ crosses. Nine different crosses are identified as T+ x T⁻. A total of 141 individual offsprings were investigated among these crosses (*Table 2* and *Figure 1*). Here the results of segregation appeared with a 76/65 T+/T— ratio, which is in good agreement with the 50:50 distribution (χ^2 test : 0.41), but not with the 75:25 distribution (χ^2 test : 32.36).

All χ^2-values are corrected for continuity.

The results of this study are in good agreement with a simple mode of inheritance of the flavonic pattern. All the T⁻ phenotypes must be considered as homozygotes recessive, tt. All the six T+ parents we have studied here can be regarded as heterozygotes Tt, dominant. All crosses produced biomodal distribution which is demonstrative for monogenic control of the flavonic pattern. This conclusion is similar to that previously described for monoterpenes (Yazdani et al., 1982).



Scheme T+ and T— morphs within *Pinus sylvestris*. Postulated relationship between the flavonoids.

Figure 1. — Biochemical relationships of prodelphinidin, taxifolin and quercetin synthesis in *Pinus sylvestris*.

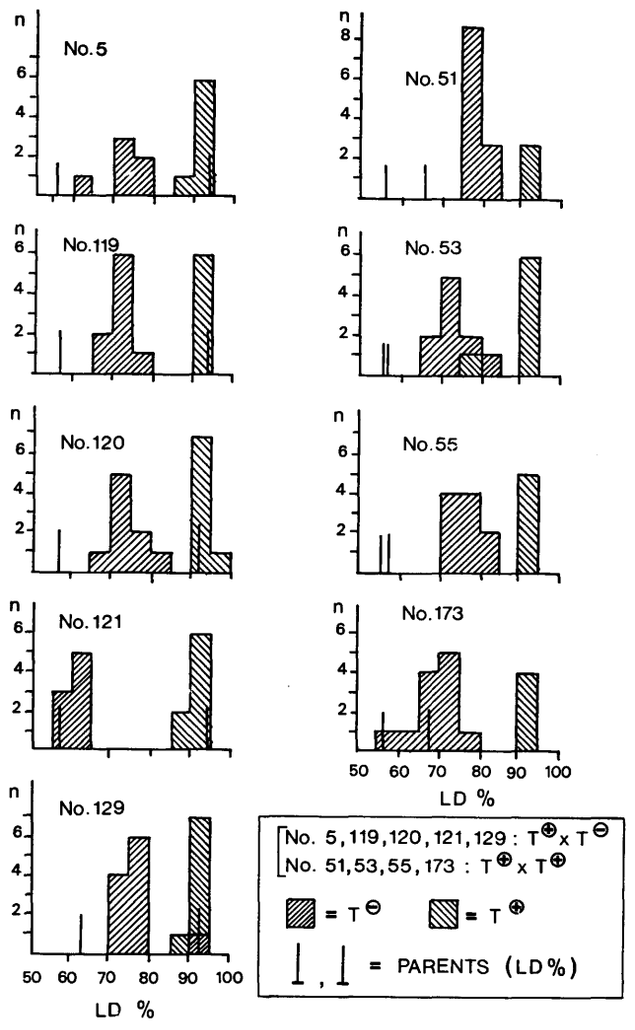


Figure 2. — Histogram of the distribution of the relative value (%) of prodelphinidin phenotypes in the progeny of the 9 controlled crosses.

However, three comments must be emphasized here:
— In the previous study with 317 individual trees (Laracine and Lebreton, 1988) and in the present study with 190 trees, only 2 individuals show inadequation between prodelphinidin and taxifolin + quercetin (negative) correlation. Thus, the "flavonic locus" considered as a whole covers at least two different genetic systems, respectively devoted to o-phenyl-hydroxylase and alcohol-dehydrogenase (see biochemical scheme).

— Neither in the present experiments, nor in nature, did we find *any* group exhaustively constituted with the T+ phenotype. This led us to believe that homozygotic TT individuals are rare in the population. One explanation of this could be perhaps the lethal characteristic of the homozygotic combination T+ T+.

— In most of the cases T+ x T+ as well as T+ x T− crosses), the mean relative content of prodelphinidin may be significantly higher in the T+ offsprings than in the T+ parents (see figure, for experiments no. 51, 53, 55, 119, 120 and 129). This deviation could be due to physiological differences (age of the offspring, mode of cultivation), but may also be related to a more general phenomenon of "chemical heterosis". An earlier study of several grafts originating from numerous clones planted in three distinct arboretums in the north, central and south of Sweden has proved the constance of the site effect on flavonic pattern.

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