Inheritance of the narrow-crowned Scots pine E 1101, "Kanerva pine"

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TIIVISTELMÄ: "KANERVAN MÄNNYN", E 1101:N, KAPEALATVAISUUDEN PERIYTYMINEN

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There is some evidence to support the hypothesis that crown form in Scots pine can be inherited either mono- or polygenically. In Finland, special attention has been given to a genotype called E 1101, "Kanerva pine". A narrow, horizontal whorl-layer structure is extremely striking in about one half of the offspring of E 1101. The offspring are characterized by a narrow crown, short and thin branches at an angle about 90° to the stem, minimal tapering and by numerous long, lateral shoots, long needles and the common occurrence of three-needled fasci-cles among the dwarf shoots. These features are connected to a high growth rate, a high harvest index and unfortunately to a tortuosity of the stem. It is suggested that this complex of characters (termed as kanerva) is determined by a single dominant gene.

In this study, several offspring of the narrow-crowned special tree E 1101, were classified into three tree form types in seven sets of progeny test data. The data included progenies of various ages having E 1101 as either *maternal* or *paternal* parent as well as open-pollinated progenies of E 1101 *second genera-tion offspring*. A segregation close to 1:1, suggested in earlier reports, was found both in the first and in the second generation progenies when wilds and intermediates were combined and compared with kanervas. The result indicates that the tree type kanerva can be due to a single dominant allele (K). Kanervas are heterozygous (Kk) for the allele and wilds are recessive homozygotes (kk) resulting 1:1 segregation in their progenies. However, there were also remark-able deviations from the expected distribution. The differences as well as the inheritance pattern are discussed.

Havaintojen mukaan männyn latvusmuoto voi periytyä joko mono- tai poly-geenisesti. Suomessa on kiinnitetty erityistä huomiota erikoispuu E 1101:een, "Kanervan mäntyyn", sillä noin puolet sen jälkeläisistä on erityisen kapealatvaisia. Puille on tyypillistä lyhyet, ohuet ja lähes 90 asteen kulmassa runkoon nähden sijaitsevat primaarioksat. Runko kapenee vain lievästi, ja puilla on runsaasti pitkiä lateraalioksia, pitkät neulaset sekä kääpiöversoissa usein kolme neulasta. Nämä ominaisuudet yhdistyvät voimakkaaseen rungon kasvuun ja korkeaan satoindeksiin, mutta myös mutkarunkoisuuteen. Ilmiön arvellaan olevan yhden geeni aiheuttama.

Tässä tutkimuksessa luokiteltiin E 1101:n ensimmäisen ja toisen polven jälkeläisiä latvuksen ja rungon ominaisuuksien perusteella kolmeen tyyppiin: kanerva, villi ja edellisten välimuoto seitsemässä jälkeläiskokeessa. Aineistossa oli mukana jälkeläistöjä, joiden emo- tai isäpuu oli E 1101 sekä sen jälkeläisten vapaapölytysjälkeläisiä (F2-polvi). Aikaisemmissa tutkimuksissa havaittu 1:1 jakautuma jälkeläistöissä saatiin myös tässä tutkimuksessa, jos välimuotopuut yhdistettiin villipuiden luokkaan. Tulos viittaa siihen, että kanerva-ominaisuus olisi yhden dominantin alleelin (K) aiheuttama; Kanerva-tyypin puut ovat

genotyypiltään heterotsygootteja (Kk) ja villityypin puut resessiivisiä homo-tsygootteja (kk). Toisaalta osa tutkituista jälkeläistöistä poikkesi huomattavasti-kin odotetusta 1:1-jakautumasta. Tutkimuksessa on pohdittu poikkeamien syitä, samoin latvusmuodon periytymismallia.

1 Introduction

Variations in branching habit are well known among coniferous and deciduous tree species throughout the world. Pendulous, fastigiate and columnar tree forms have long been used in horticulture. Inheritance of a particular, very narrow-crowned tree form can sometimes be attributable to a single, dominant gene. This has been demonstrated for a few pendulous forms of Norway spruce (Lepistö 1984). Mendelian segregation of crown forms within offspring of those trees has indicated a monogenic inheritance.

There is some evidence supporting the hypothesis that crown form in Scots pine can be inherited either mono- or polygenically. In Finland, special attention has been given to a genotype called E 1101, "Kanerva pine". This special tree is growing in Punkaharju, southeastern Finland (lat. 61°43' N, long. 28°25' E, alt. 85 m). In 1955 it was registered by district forest officer Yrjö Kanerva because of its conspicuous, narrow crowned form. Later on, it has been much used for progeny testing. In the studies concerning the offspring of E 1101 a bimodal segregation of trees has been reported concerning certain crown characters (Kärki and Tigerstedt 1985, Mikola 1985a, Kuuluvainen et al. 1988, Velling 1988).

The results imply that deviation from the mean pattern of shoot distribution in young Scots pine occurs either towards a layered or a non-layered structure (Kuuluvainen et al. 1988). In a layered structure, the shoots form narrow horizontal whorls while a non-layered or "bushlike" structure is characterized by a rather even vertical shoot distribution (Kärki 1983, Kuuluvainen et

al. 1988, Pulkkinen et al. 1989). The pure tree form types of these two shoot patterns are also attributed, correspondingly, to ideotypic trees and wild type trees (Kärki 1983).

Both crown structure patterns are evident in the progenies of E 1101. A narrow horizontal whorl-layered structure is extremely striking and it can be demonstrated both phenotypically (Kärki 1983, Mikola 1985a, Velling 1988) and by statistical methods (Kuuluvainen et al. 1988). Because of its good match with the phenotype of E 1101, "Kanerva pine", the type is referred to as kanerva type (Velling 1988) or as kanerva.

The bimodal distribution is so drastic that Kärki and Tigerstedt (1985) suggested that the narrow-crowned habit of E 1101 is determined by a single, dominant gene. The single-gene effect probably regulates the apical dominance of tree growth and has pleiotropic effects on the crown characters (diameter, angle and number of branches) and stem tortuosity of offspring of E 1101. A segregation approaching 1:1 among open-pollinated offspring has been reported. Mikola (1985a) and Rusanen and Velling (1988) estimated that about a half of offspring of E 1101 display an extremely narrow crown, short and thin branches at angle of nearly 90° to the stem and minimal tapering. They are typically characterized by numerous long, lateral shoots, long needles and the common occurrence of three-needled fascicles among the dwarf shoots (Mikola 1985a). These features are connected to a high growth rate of the stem (Mikola 1985a, Velling 1988) and a high harvest index (Kärki 1984, Kuuluvainen et al 1988). Harvest Index (HI), introduced by Don-

ald (1962), is considered to be a complex marker trait for ideotypes (ideal tree forms for cultivation). In the case of forest trees, HI is defined as the ratio of harvested dry matter to the total dry matter computed on the basis of individual tree (Tigerstedt and Velling 1986).

The aim of this study was to analyse crown and tree type distribution in the first and the second generation offspring of E 1101 growing in seven progeny tests. The primary objective was to provide information about the assump-tion of bimodal distribution indicating a dominant single-gene effect among offspring of E 1101. The genetic model tested is following: the kanerva type trees (kanervas, Fig. 1) are a result of a dominant allele (K). Kanervas are heterozygous (Kk) for the allele, while wild type trees (wilds, Fig. 1) are recessive homozygotes (kk). Thus the crossing between kanerva and wild results 1:1 segregation (kanerva:wild) among their progenies.

2 Material and method

The results presented in this report are based on classifications made in the course of six field tests and in one test orchard (see Mikola 1985b) of Scots pine. Four field tests (160/1, 396/1, 396/2, 427/1) and the test orchard (565/2) were classified by the Finnish Forest Research Institute (FFRI). In two field tests (998/1 and 998/2) the classification work was carried out by the Foundation for Forest Tree Breeding (FFTB) (Table 1). The tests differed in age. The tests measured by FFRI were older than those measured by FFTB.

The tests included progenies having E 1101 as either the *maternal* or *paternal* parent. The tests 998/1 and 998/2 included open-pollinated progenies of *second generation offspring* of E 1101, too. All the offspring from controlled crossings classified by FFRI had E 1101 as *paternal* parent. The field tests classified by FFTB (998/1 and 998/2) were more heterogeneous. Two controlled crosses had E 1101 as the *paternal* and five as the *maternal* parent. Among the entries there were 26 different open-pollinated progenies of E 1101 *second generation offspring*. In addition tests 160/1, 427/1, 998/1 and 998/2 each had one open-pollinated progeny of E 1101 while test 565/2 had two open-pollinated progenies.

In tests 396/1, 396/2, 427/1 and 565/2, all the trees were classified visually into one of the following groups: Kanerva type tree (kanerva), wild type tree (wild) or intermediate type tree (intermediate). The kanervas and wilds were first described by Kärki (1983). Kanervas have narrow horizontal whorl-layer structure with thin and short branches at an angle of about 90° to the stem (Fig. 1). Wilds have non-layered, "bush-like", structure with thick and long branches at small angle to the stem (Fig. 1). The class of intermediates was for trees having characteristics from both of the two ultimate classes. In tests 160/1, 998/1 and 998/2, only the kanervas were recorded, wilds and intermediates were pooled into the same group.

Fig. 1. Tree types. On the left: kanerva, on the right: wild.

Table 1. Study material. FFRI = Finnish Forest Research Institute, FFTB = Foundation for Forest Tree Breeding. For forest site types see Cajander (1909).

Test n:o	Planned by	Established	Forest site type	Number of classified families	Number of classified trees
160/1	FFRI	1960	VT+	1	50
396/1	FFRI	1972	MT	18	1553
396/2	FFRI	1972	VT	8	992
427/1	FFRI	1974	VT	1	99
565/2	FFRI	1978	CT	9	551
998/1	FFTB	1983	Field	34	1817
998/2	FFTB	1984	CT	27	1304

The goodness-of-fit test of 1:1 segregation (kanerva:wild) was made using the χ^2-test (chi-square test). The tree type classes intermediate and wild were combined for the test. If the chi-square value was below the critical value of $p = 0.05$ (df = 1, 3.841), the segregation was considered to comply with the 1:1 segregation. If it exceeded the critical value of $p = 0.001$ (10.828), the 1:1 segregation was rejected.

3 Results

In the field test data, the *mean* percentage of kanervas in progenies having E 1101 as the *maternal* parent ranged from 18 to 44 and the mean percentage of the wilds from 55 to 70 (Fig. 2). In tests 427/1 and 565/2 (test orchard) the mean percentage of intermediates ranged from 10 to 20. In test 160/1 and tests classified by FFTB (998/1 and 998/2) the wild type trees and intermediate trees were classified into the same group.

The *paternal* offspring of E 1101 (Fig. 3) followed the pattern of *maternal* offspring of E 1101. The mean percentage of kanervas in the progenies having E 1101 as their *paternal* parent ranged from 31 to 48 in the different field test data (Fig. 3). The classification carried out by FFTB (tests 998/1 and 998/2) showed a lower percentage for kanervas than that carried out by FFRI. The percentage of wilds ranged from 17 to 69. In tests in which data of intermediates were available their percentage varied between 18 and 35.

The mean percentage of kanervas was at its highest, 46, in the field test material classified by FFRI, while in the field tests assessed by FFTB it was 33. The mean percentage of wilds and intermediates in field test data classified by FFRI were 29 and 25, respectively. The pooled mean value of wilds and intermediates in field test data
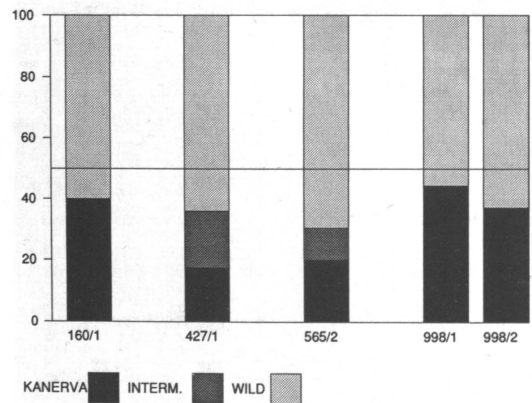

Fig. 2. Mean percentages of tree types in *maternal* progenies of E 1101 in five progeny tests.
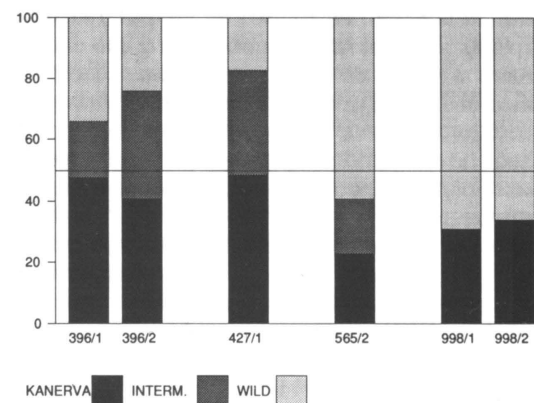

Fig. 3. Mean percentages of tree types in *paternal* progenies of E 1101 in six progeny tests.
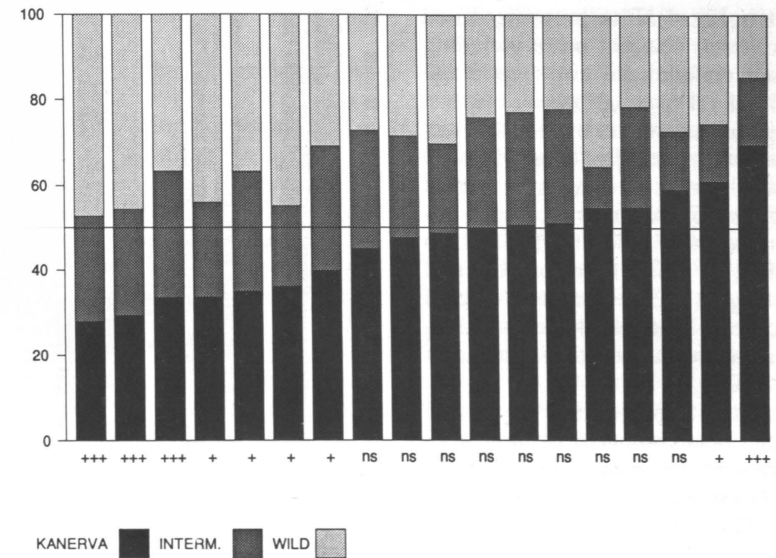

Fig. 4. Overall percentages of tree types in *paternal* progenies of E 1101. ns (non-significant) indicates that 1:1 segregation is accepted (p > 0.05), three plus signs (+++) that 1:1 segregation is rejected (p < 0.001).
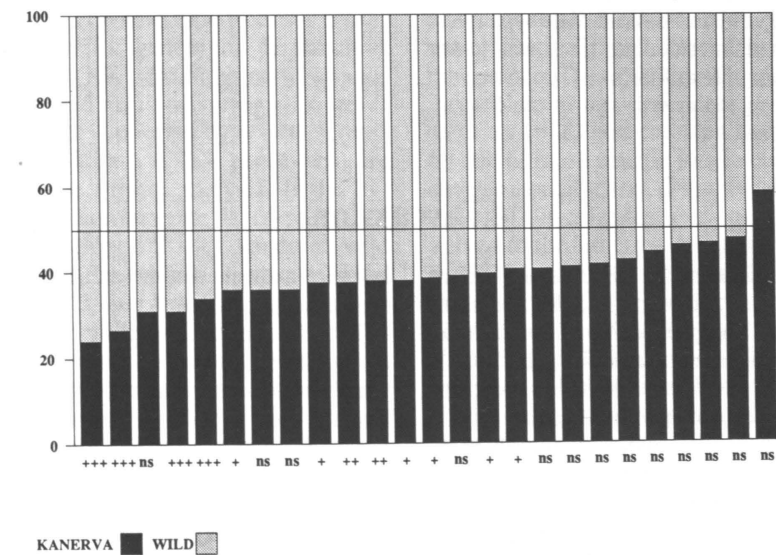

Fig. 5. Overall percentages of tree types in *maternal* progenies of the offspring of E 1101 (*second generation*). Families common in tests 998/1 and 998/2 are included (for explanations see Fig. 4).

classified by FFTB was 67. In FFRI's test orchard the corresponding percentages of Kanervas, wilds and intermediates were 23, 59 and 18.

The percentage of kanervas in progenies having E 1101 as the *paternal* parent varied between 30 and 70 in the field test material classified by FFRI. Eight progenies reached the level of 50 percent (Fig. 4). Nine of the 18 studied progenies complied with the segregation ratio of 1:1 (p > 0.05, ns in Fig. 4) while four failed to do so

(p < 0.001, +++ in Fig. 4). Five progenies fitted neither of the criteria. The test made including the total paternal material did not support the segregation ratio of 1:1 (p < 0.01).

The percentage of kanervas in open-pollinated progenies of *second generation offspring* of E 1101 was below 50 except for one family (figure 5). Thirteen of the 25 progenies studied complied with the segregation ratio of 1:1 (df = 1, p > 0.05, ns in Fig. 5) while four did not (p < 0.001, +++ in Fig. 5). Eight progenies fitted neither of the criteria. The test made including the total material did not support the segregation ratio of 1:1 (p < 0.01).

The classification of entries growing in two different locations was compared using progenies common for tests 396/1 and 396/2 (Fig. 6). All the progenies compared had E 1101 as the *paternal* parent. The classifications of kanervas were carried out by FFRI in a similar manner in both tests. The difference between the percentages of kanervas in the progenies was less than 10 % except for progeny E 719 D. All other progenies complied with the segregation ratio of 1:1 (p > 0.05). There was more variation in the classification of wild and intermediate type trees. The proportion of intermediate trees was lower in test 396/1 than in test 396/2.
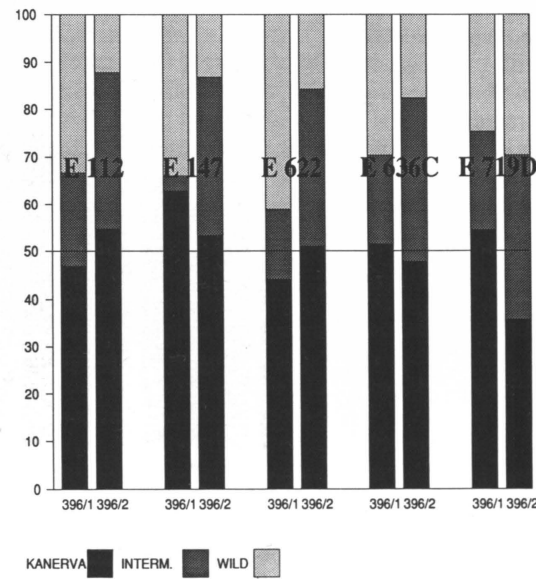

Fig. 6. Percentage of tree types in *paternal* progenies of E 1101 common in tests 396/1 and 396/2. The identification numbers of maternal trees are shown in the figure (e.g. E 112).

4 Discussion

The visual identification by FFTB and FFRI of kanervas in the progenies of E 1101 seems to be in agreement. The proportion of kanervas in the different progenies was quite obscure in older tests. If intermediates and wilds are combined, the segregation of tree type groups within the progenies of E 1101 seems to comply with the segregation ratio of 1:1 in most of the studied progenies. However, in some tests (as well as in progenies within tests) the proportions of kanervas were lower or higher than 50 percent.

The main reason for the above variation in proportions was apparently in the small sample size. The number of classified trees in the progenies varied between 43 and 144 in the tests assessed by FFRI and between 16 and 64 in the tests assessed by FFTB. Although no clear connection could be asserted to exist between sample size and the frequencies of kanervas, the effect of classification errors can be significant, because a single tree in small groups can represent several percent.

The effect of the sampling can also be promoted by other causes. The low proportion of kanervas found in some cases may be due to the fact that the tree types are manifested gradually as trees age. The tree types could not be seen fully in the youngest part of the study material because of the small size of the trees. To take an example: the field tests classified by FFTB were 8 years old and showed remarkably smaller proportions of kanervas than the older tests classified by FFRI. Similarly, poor growing conditions together with close spacing can affect penetration by tree types. This can be the cause for the low number of kanervas in test 565/2 (test orchard with close spacing) growing on very poor sandy soil. Young age and poor soil probably interact to reduce penetration by tree types. The experience has been that trees under 1.5 m height are very difficult to classify as to their crown form. It can be done only in extreme cases.

Pollen contamination during the artificial crossing may have reduced the number of kanervas in the offspring; e.g. according to documents on tests 998/1 and 998/2, the time between isolation and pollination had been quite short (only 2–3 days) thus allowing contamination by open pollination. This, together with young age, can explain the low number of kanervas in some open-pollinated families of *second generation offspring* of E 1101 in these two tests (Fig. 2).

However, in several studied progenies the segregation approaching 1:1 was found in progenies of *second generation offspring* of E 1101 as well. This and results of earlier studies (Velling 1988) indicate that the inheritance of tree form types may be due to the monogenic effect suggested by Kärki and Tigerstedt (1985). The segregations found among the *second generation offspring* indicate that the allele involved is dominant (K) and maybe lethal or closely linked to a lethal allele when a homozygote (KK genotype). In heterozygote state with normal allele it causes the tree form typical of "Kanerva pine" (kanerva, Kk genotype). The wild type trees are recessive homozygotes (kk genotype). If kanervas were homozygotes (KK), crossings between kanerva type and wild should result offspring all kanerva type, which was not supported by results. Crossings between two kanervas (Kk genotypes) are needed to facilitate further analysis. If the hypothesis of lethal homozygote is correct, then the segregation ratio of 2:1 of kanerva: wild should be found in the progenies, otherwise the segregation ratio 3:1 (see Yazdani and Lebreton 1991).

There was no evidence of maternal (cytoplasmic) effects. The proportions of kanervas were not essentially different whether E 1101 was a maternal or a paternal parent. However, the conclusions concerning the maternal effect must be rather prudent, because the number of maternal progenies studied was limited or consisted mainly of open-pollinated progenies.

The two other groups, wild and intermediate, were quite heterogeneous. The results of classification in these groups possibly were influenced by subjective scoring on the part of the classifiers. The proportions of intermediates varied from 10 to 35 percents in different data sets analysed. It seemed that the variation in the proportion of intermediates affected on the proportion of wilds rather than that of kanervas indicating that the discrimination of intermediates is subjective and is made on the expense of wilds. However, on combining the intermediates of test 565/2 (test orchard) with the kanervas, the distribution conformed well with those obtained in tests 998/1 and 998/2 by FFTB. It is possible that the intermediates of test 565/2 were a weak manifestation of kanervas. In tests 998/1 and 998/2 those trees were classified as kanervas. The results indicate that the intermediates are a buffer group, which, at young ages, consists of weak kanervas and later, when kanervas features are fully manifested, of wilds having common features with kanervas. However, for supporting this hypothesis, the tests should be re-measured using a common scoring system and its analysis is needed.

It may be worth to make efforts to search for the existence of the kanerva gene by using DNA techniques. The genetic background of intermediates needs close study, because, if it is different from wilds or kanervas, it can introduce more complex modes of inheritance and several alternative gene models. There is evidence in human and animal genetics that many genetic traits do not exhibit fully penetrant, Mendelian mode of inheritance. These include Mendelian traits with incomplete or age-dependent penetrance (Cepica et al. 1988) and complex traits determined by one of more genetic loci in combination with environmental effect (Ploughman and Boehnke 1989). Thus a further analysis of genotypes involved to the kanerva-trait is needed. A suitable method applied can be a linkage map construction with molecular markers and estimation of phenotypes based on field performance testing. According to Bradshaw and Foster (1992) genetic maps with a high density of markers have been used to locate discrete Mendelian components of quantitatively inherited traits in few crop plants. A similar approach can be used in trees to map economically important quantitative trait loci, such as kanerva trait (Tigerstedt and Velling 1986).

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