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Tree architecture in young Scots pine: properties, spatial distribution and relationships of components of tree architecture

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TIIVISTELMÄ: NUORTEN MÄNTYJEN LATVUKSEN ARKKITEHTUURI: LATVUSKOMPONENTTIEN OMINAISUUDET, TILAJAKAUMA JA KESKINÄISET SUHTEET

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The architecture of Scots pine (*Pinus sylvestris* L.) was studied in an eight-year-old progeny test. The measurements included characteristics of crown structure, spatial distribution of shoots and yield components. The spatial distribution of shoots showed striking between-tree differences and two extreme distribution patterns were detected. One represented a non-layered structure with a vertically relatively even shoot distribution, and the other a layered structure with a vertically highly uneven shoot distribution.

Close correlations existed between several components of tree architecture and it is suggested that changes in the phenotypic architecture in Scots pine follow an epigenetic pattern, which enables the prediction of adaptational changes in structural components. The structural characteristics related to high above-ground biomass were a long crown, high total shoot length, high number of branches per whorl and big shoots of low needle density occupying a big share of the crown volume.

Männyn (*Pinus sylvestris* L.) arkkitehtuuria tutkittiin käyttäen aineistona kahdeksanvuotiasta jälkeläiskoetta. Aineistosta mitattiin sekä latvusarkkitehtuurin ominaisuudet ja versojen tilajakauma että puiden eri osien biomassa. Versojen tilajakaumassa esiintyi huomattavaa vaihtelua. Kaksi selvästi toisistaan poikkeavaa tilajakaumamallia erottui. Toinen edusti kerroksellista rakennetta, jossa oksat olivat ryhmittyneet erittäin selvästi kiehkuroittain. Toiselle mallille oli taas ominaista pensasmainen rakenne ja versojen tasaisempi vertikaalijakauma.

Puiden välillä rakennetunnusten vaihtelussa oli voimakkaita korrelaatioita. Näyttää ilmeiseltä, että edullisissa olosuhteissa ja ilman kilpailua kasvaneiden nuorten mäntyjen rakenteen vaihtelu noudattaa epigeneettistä mallia, joka mahdollistaa puiden rakenteellisen vaihtelun ennustamisen. Suureen maapäälliseen biomassaan liittyviä rakenneominaisuuksia olivat mm. pitkä latvus, suuri versojen yhteispituus, oksien suuri määrä kiehkurassa, ja tilavuudeltaan suurien, mutta neulastiheydeltään pienien versojen suuri osuus latvuksen kokonaistilavuudesta.

Keywords: crown architecture, tree ideotype, biomass production, branching pattern.
ODC 174.7 *Pinus sylvestris* + 53 + 181.6

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1. Introduction

The amount of absorbed light and gas exchange and, consequently, growth of a tree is to a high degree determined by the spatial distribution of its above-ground structural elements (e.g. Jahnke and Lawrence 1965, Norman and Jarvis 1974, Brunig 1976, Kellomäki et al. 1984). Therefore, knowledge of tree architecture and factors regulating it is a prerequisite to detailed ecosystem-level studies related to competition, microclimate and productivity (Flower-Ellis et al. 1976).

The role of tree architecture in tree growth becomes most obvious when structural differences between progenies, families or individual trees are related to yield components (e.g. Calahan 1981, Cannell et al. 1983, Velling and Tigerstedt 1984). In particular, the structural analysis of trees could be useful when one tries to explain the differences in yield. However, little is known about the actual structural and functional features that determine growth and its partitioning (Cannell 1984, Ford 1985).

The aim of this study on Scots pine (*Pinus sylvestris* L.) is (a) to map and quantify the phenotypic tree architecture and its variation, (b) to study the relationships between components of tree architecture and (c) to study structural characteristics as related to high total above-ground biomass yield. The quality of biomass yield, i.e. the allocation of photosynthates to make up harvest indices, wood density etc. will be dealed with in the second part of this study.

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2. Material and methods

2.1. Material

12 sample trees representing four progenies of Scots pine were analyzed. The sample trees were representatives of the Tuunaansaari test orchard, progeny trial no. 679/1 at the Punkaharju Research Station of the Finnish Forest Research Institute (61° 48′ N, 29° 17′ E, alt. 85 m a.s.l.). The effective temperature sum (5 °C threshold) of the location is approximately 1200 d.d. The trial was established 1980. The site is a fallow field of fine sandy soil which was ploughed and tilled before planting the seedlings in May 1980.

Each progeny with 5 blocks (replicates) were planted with hoe on 3×3 m squares, each consisting of 1 actual and 2 extra test seedlings, i.e. the spacing was 1.5×0.75 m. For this study four full-sib families with apparently different crown structures were selected. One family represented a crossing between plus trees from Southern Finland, the other from Central Finland and the third one from Northern Finland; the fourth was a special case as regards the father tree which was a peculiar narrow-crowned tree E 1101. For each of the four families three extra sample trees were selected, each from different blocks (Table 1). All selected trees had developed normally and were healthy.

Table 1. Sample trees and location of their parent trees of the four families selected for the study.

Sample trees	Mother × father	Locality	Longit.	Latit.	Altit.
1–3	K37	Pielisjärvi	30° 44′ E,	63° 17′ N	160 m
	K608	Tohmajärvi	30° 11′ E,	62° 10′ N	100 m
4–6	E635C	Sulkava	28° 25′ E,	61° 48′ N	90 m
	E144	Loppi	24° 20′ E,	60° 45′ N	130 m
7–9	E147	Juupajoki	24° 17′ E,	61° 55′ N	180 m
	E1101	Punkaharju	29° 18′ E,	61° 47′ N	100 m
10–12	P323	Salla	28° 8′ E,	66° 45′ N	200 m
	P2504	Kolari	23° 49′ E,	67° 3′ N	150 m

Table 2. Measured variables and their dimensions

Variable	Dimension
(1) General tree description:	
– Stem length	cm
– Stem diameter at ground level	mm
– Stem diameter at breast height (1.3 m)	mm
– Maximum crown width	cm
– Length of live whorl	cm
– Height of lowest whorl	cm
– Diameter of lowest live whorl	cm
– Number of live and dead whorls	
(2) Description of whorls:	
– Number of branches by whorls	
– Height of whorl	cm
– Orientation of branches (compass bearings)	degree
– Inclination of branches from the vertical*	degree
– Branch lengths	cm
– Branch lengths covered by needles	cm
– Branch base diameters	mm
(3) Description of shoot units:	
– Strahler bifurcation value	
– Shoot age	a
– Shoot length	cm
– Shoot diameter	cm
– Height of shoot midpoint (vertical location)	cm
– Distance of shoot midpoint from stem (horizontal location)	cm
– Shoot orientation (compass bearing)	degree
– Shoot inclination from the vertical	degree
– Shoot angle to the parent shoot	degree
(4) Others:	
– Width of annual rings	mm
– Stemwood specific gravity	g/cm³
– Needle area	cm²
– Needle dry mass	g

*) Branch inclinations were measured as the angle between the vertical and the the main direction of the branch axis (cf. Fig. 1).

2.2. Measurements

The measurements were carried out after growth cessation in August 1985. The measurements can be separated into four stages: (1) general description of trees, (2) description of whorls, (3) description of shoot units, and (4) measurement of other variables (Table 2). The median branch by base diameter was selected from each whorl as a sample branch. The basic measurement units of the branching structure were the unbifurcated shoot units, with or without needles (Fig. 1). About 500 whorls, 50 sample branches and 1400 shoot units were measured.

A stem disc from the base of the stem was taken for measurements of widths of annual rings and for calculating stem wood specific gravity. The sample branches were dried at 105 °C degrees for 24 hours, after which needles and branches were separately weighed by age classes. From each branch and age class 50 pairs of needles were sampled homogenously from different parts of the branch; the needles were weighed and their projection areas were measured.

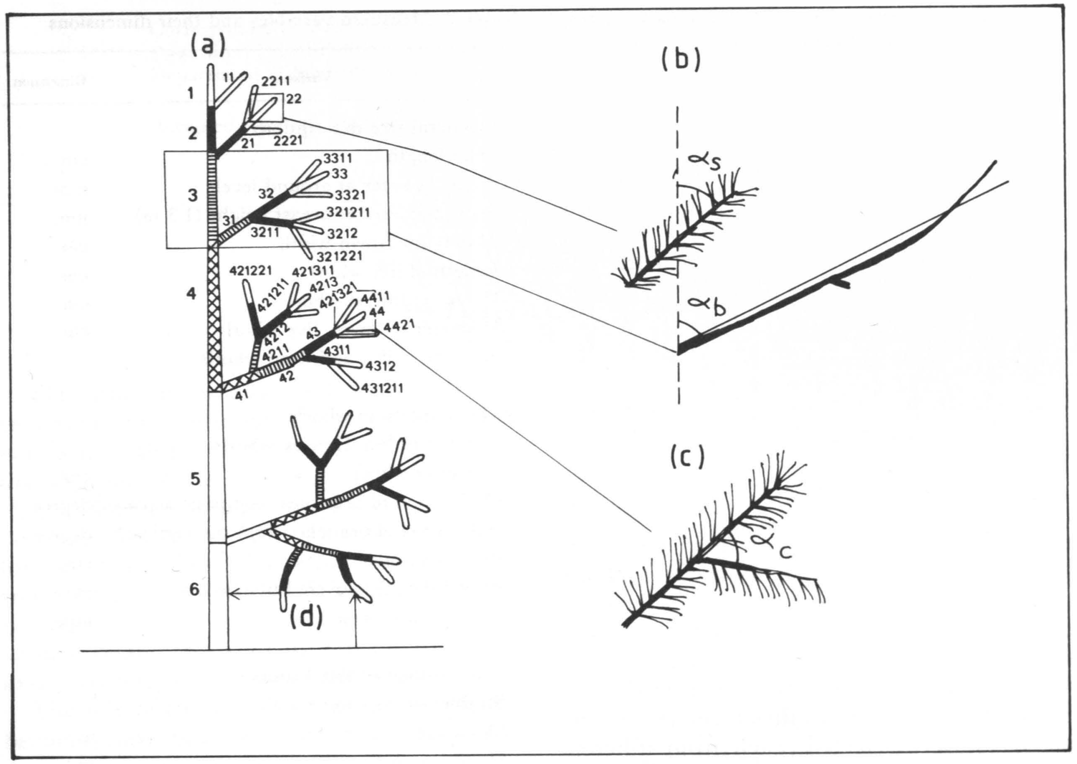

Fig. 1. (a) The numeration system used to describe the branch structure of the trees, (b) measurement of shoot (α_s) and branch inclinations (α_b), (c) measurement of shoot angle to its parent shoot (α_c), (d) measurement of shoot location as the distance from the ground level and from the stem to the midpoint of shoot length.

2.3. Preliminary calculations

Stem dry mass was calculated using the specific wood gravity measured from the sample disc. The wood density was multiplied by stem volume, which was derived by assuming that the lower portion of the stem up to 1.3 m height was as a cut cone and the rest of the stem as a cone.

The needle efficiency of stemwood production for years 1984 and 1985 was derived as the ratio of the stem volume or dry mass increment to the total needle mass or surface area of that year. The specific needle area was determined for each tree, whorl and age class up to the third year. After summing the needle areas of different age classes by branches the needle areas of whorls and trees were obtained by multiplication. The shoot needle mass density was calculated in different whorls and age classes by dividing the shoot needle dry mass by the shoot volume estimated as a cylinder.

2.4. Techniques of analysis

Tree architecture was characterized by means and their variances for the characteristics and spatial distribution for components of tree structure. For example, to characterize the distributions of shoots by whorls the means and variances of horizontal and vertical coordinates of shoots (see Table 2) were calculated for each whorl within each tree. The ratio between vertical and horizontal variances was used to quantify the whorlwise patterns of shoot distribution. Only needle bearing shoots were included.

The analysis of variance was further used to quantify the existing between-tree differences in the vertical and horizontal distribution of shoots. The degree of shoot clustering into whorls was described with the F-test value, representing the ratio of the between-whorl variance of shoot location to the within-whorl variance of shoot location. Vertical shoot location was determined as the distance from the ground and horizontal location as the distance from the stem (Table 2).

Correlation techniques were used to find out which structural features were connected and especially which characteristics were related to high biomass.

Because of the limited sample size the determination of heritabilities of tree characteristics was beyond the scope of the study. However, a crucial point for the analysis of the material was how the progenies should be taken into account, i.e. how similar the trees in a progeny are in relation to other progenies. To determine this the analysis of variance was used. The results showed that there were no significant differences between progeny means in any of the studied characteristics. Consequently, the material was pooled and analyzed as a single sample.

3. Results

3.1. Description of crown architecture

3.1.1. Total dry mass and dimensions of trees

The mean tree total above-ground dry mass was 3.26 kg, which was distributed into needle, branch and stem mass with the average proportions of 29.3, 28.4 and 42.3 %, respectively (Figs. 2 and 3). The crown shape ratio (crown length/crown width) varied from 1.1 to 1.6. The mean difference between tree height and crown length was 14 %, indicating that no substantial dying off of branches from below had occurred. In general, the study material was highly heterogenous and differences were greatest in biomasses and total shoot lengths (Table 3).

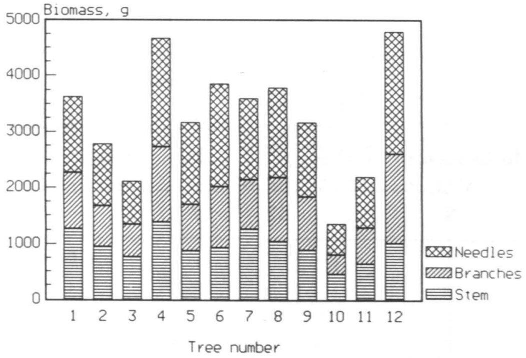

Fig. 2. Total, stem, branch and needle dry masses of the sample trees.

3.1.2. Branch structure

Total shoot lengths

The average sum of shoot length per tree was 110 m, which is more than 40 times the mean tree height. Differences in the total shoot length between the trees were much greater than differences in the tree and crown dimensions, and comparable to the variation in branch and needle dry mass (Table 3). This reflects considerable differences in the branching structure of the sample trees.

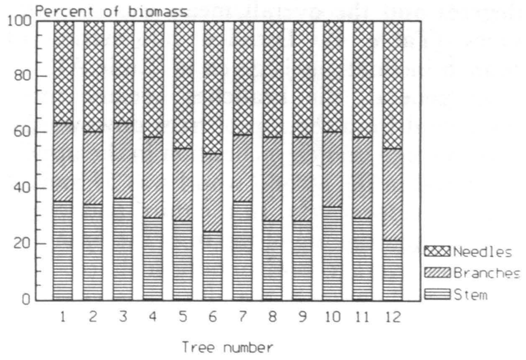

Fig. 3. The relative proportions of stem, branch and needle dry masses from total above ground dry mass in the sample trees.

Table 3. Mean dry masses and dimensions of the trees. D(max-min) = 100 × ((max.– min.)/max.)

Characteristic	Mean	s.d.	min.	max.	D(max-min), %
Total dry mass, g	3255	1024.2	1348	4788	71.8
Stem dry mass, g	952	265.2	446	1378	67.6
Branch dry mass, g	925	341.1	363	1598	77.3
Needle dry mass, g	1376	488.0	539	2183	75.3
Tree height, cm	273	33.4	208	330	37.0
Crown length, cm	235	33.4	165	300	45.0
Crown width, cm	170	17.2	132	198	33.3
Crown ratio	1.4	.14	1.1	1.6	31.3
Number of braches in whorl	9.4	1.3	6.4	10.8	40.7
Total shoot length, m	110.6	36.2	46.7	175.5	73.3

Table 4. Mean branch inclinations in whorls measured from the vertical, variances and number of measurements.

	Whorl number				
	1	2	3	4	5
Inclination,x̄	57.0	74.2	89.6	93.5	81.9
VAR	629.5	297.8	217.3	94.0	133.7
N	12	12	12	12	5

Branch inclinations and orientations

The mean branch inclination per tree measured from vertical varied from 71.8 to 87.2 degrees and the overall mean was 77.3 degrees (Table 4). Detailed information of branch inclinations is given in Table A1.

In general, the branches became more horizontal from the top of trees downwards. The average branch inclination in the uppermost and in the second whorl was 57 and 74 degrees, respectively. In the third and fourth whorls from the top of the trees the branches were on average horizontally inclined. The branch inclination of the fifth whorl could be measured only in five trees and there again a more vertical mean inclination value of 82 degrees was detected. The within-whorl variance of branch inclination decreased from the top of the tree downwards (Table 4).

The average trend of more horizontal mean branch inclinations from uppermost to lower whorls was not, however, without exceptions (cf. trees 1, 3 and 5, Table A1) and considerable between-tree variation existed in the values of mean branch inclinations, the variances of which also showed about two-fold differences. The within-whorl variance of branch inclination was greater in the upper two whorls than in the lower ones.

The distribution of branch orientations (compass bearings) into 30 degree sectors was calculated for all trees. No significant differences in the numbers of branches in the sectors were detected, i.e. the orientation of branches was uniform.

3.1.3. Shoot inclinations

Also the shoots in whorls became more horizontally inclined from the uppermost whorl downwards. In the uppermost whorl the shoots had an overall mean inclination of 51.3 degrees and in the 2nd, 3rd and 4th whorls 71.8, 78.2 and 87.6 degrees, respectively (see Table A2). The mean shoot inclination in the 5th whorl (in five trees) was 84.4 degrees, i.e. the shoots of the fifth whorl were more vertically inclined than in the 4th whorl. The differences in within-tree variances were not as great as in the case of branch inclinations. In only two trees (1 and 7) the variance of shoot inclinations in a whorl was clearly decreasing from the uppermost whorl to the lower whorls.

When shoots were separated into first year shoots and older shoots, it appeared that in a particular tree the first year shoots were more vertically inclined than older shoots (Table A3). The mean shoot inclination of the first year shoots ranged from 67.2 to 94.5 degrees, while the corresponding range of values in old shoots was from 82.4 to 98.3. The mean shoot inclination did not correlate with tree size.

3.2. Vertical distribution of needle mass and shoot cylinder volume

The vertical distributions of needle mass and shoot volume, all sample trees included, were two-peaked. However, the comparison to treewise distributions (Fig. 4) reveals that this 'mean tree' approach is inappropriate when describing the architecture of young Scots pine trees with the typical whorl structure.

The description of the vertical distribution of needle mass and shoot volume in 10 cm vertical clips revealed considerable differences in the vertical distribution patterns. In general the concentration of needle mass and

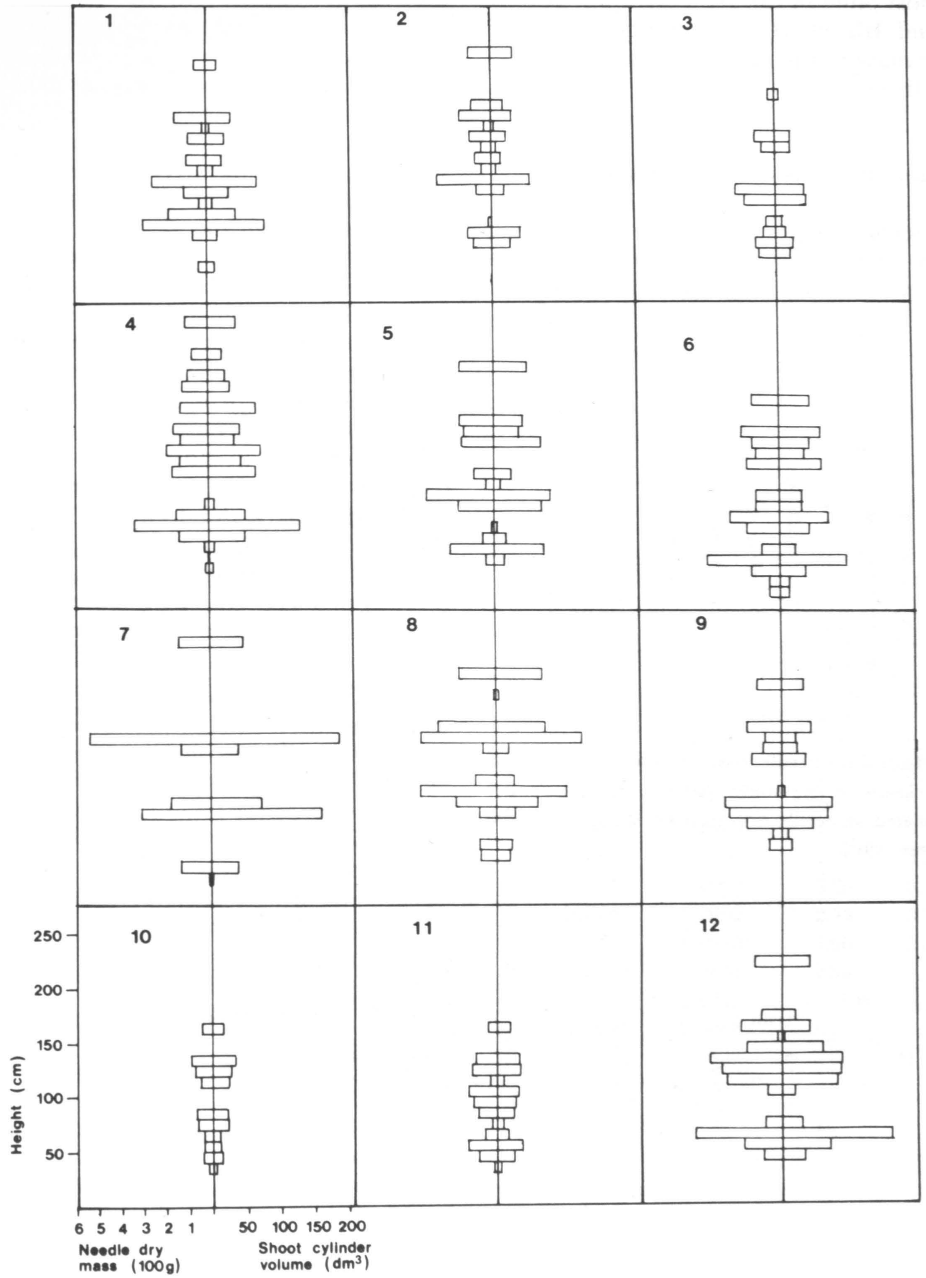

Fig. 4. Vertical distribution of needle dry mass and shoot volume in 10 cm horizontal clips by trees.

shoot volume into whorls was evident, although great between-tree differences existed. For example, tree 7 had a very distinct vertical clustering of needle mass and shoot volume into whorls, while in trees 10 and 11 this distinction was much less pronounced. The highest proportion of the total needle mass was most often in the 3rd whorl, but also the 2nd and 4th whorl had the highest share of needle mass in the case of tree and two trees, respectively.

3.3. Needle mass density of shoots

In general, the mean shoot needle mass density (needle dry mass/shoot volume estimated as a cylinder, g/cm^3) increased from older to younger shoot age classes within whorls of the same age and from the top of the tree downwards within shoot age classes (Fig. 5). However, the 5th whorl with measurements from only five trees did not follow this pattern strictly. For example, the 5th whorl had lower densities than the 4th whorl in 2nd and 4th age classes (see also Table A4).

The overall mean shoot needle mass density was $.35 \times 10^{-2}$ g/cm^3 and the treewise mean varied from 0.27 (tree 7) to 0.41×10^{-2} g/cm^3 (tree 9). The mean needle densities of the first year shoots and older shoots were .37 and .31 x 10^{-2} g/cm^3, respectively. However, when examined treewise no clear pattern in the mean needle densities of shoots of different age existed: in nine trees the mean needle density of first year shoots was from 3 to 50 % greater than in older shoots, whereas in three trees the mean density of older shoots was from 6 to 10 % higher than in the youngest shoots. The mean densities in first year shoots in the different trees varied from 0.26 to 0.50 x 10^{-2} g/cm^3 and in older shoots from 0.24 to 0.35×10^{-2} g/cm^3. Thus, the range of variation in density was wider in young than in old shoots. (Table A4).

Trees 1 and 7 provide a striking example of the large differences in absolute values and distribution of shoot needle mass density (Fig. 6). In spite of the fact that the trees have almost the same height and total needle mass (282 cm, 305 cm and 1944 g, 1465 g for trees 1 and 7, respectively) the shoot needle mass density of tree 1 was 32.5 % higher than that of tree 7.

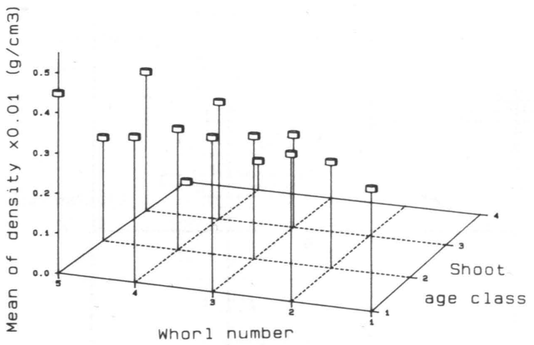

Fig. 5. Mean shoot needle mass densities by whorls and age classes in the study material. Needle density calculated as needle dry mass (× 0.01g) per shoot volume (cm^3).

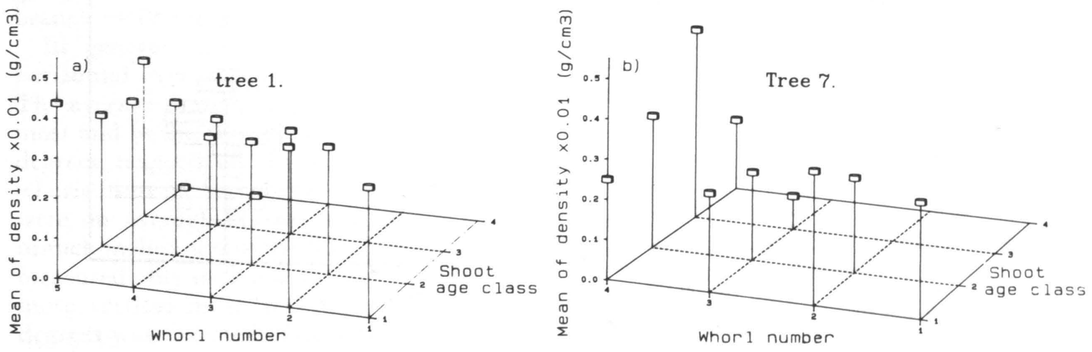

Fig. 6. Mean shoot needle mass densities by whorls and age classes of trees 1 and 7.

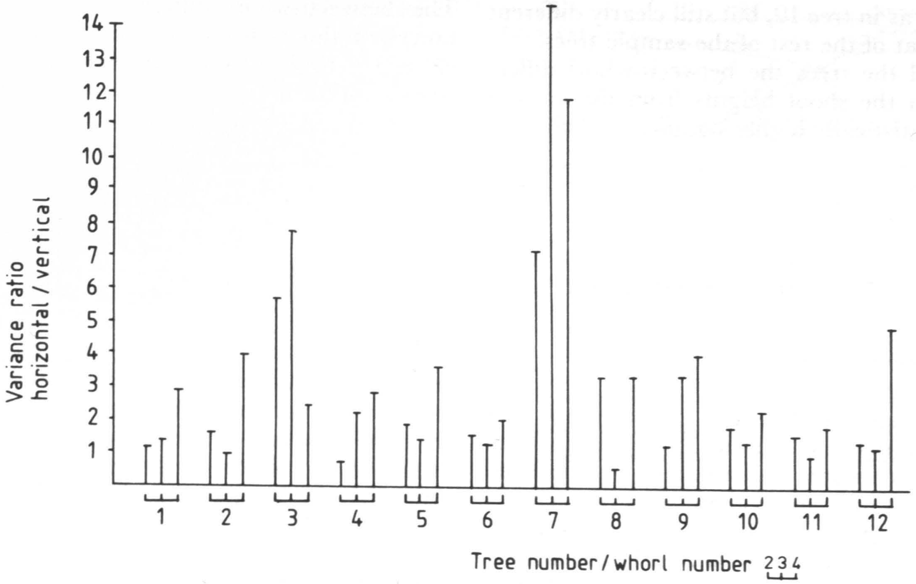

Fig. 7. The ratio of the variance of horizontal shoot distance from stem to the variance of vertical distance from ground level by shoots in the sample trees.

3.4. Spatial distribution of shoots

3.4.1. Vertical and horizontal within-whorl distribution

Considerable between-tree differences in the whorlwise needle distribution patterns were observed. A large ratio between the variances of horizontal and vertical within-whorl needle distribution (trees 3 and 7) indicated clear grouping of shoots into horizontal whorl-layers, while a small variance ratio (e.g. trees 6 and 11) indicated a more even vertical shoot distribution (Fig. 7).

3.4.2. Degree of clustering of shoots

Table 5. The analysis of variance of the vertical and horizontal shoot location data

Tree	Vertical distribution		Horizontal distribution	
	F-value	Prob.	F-value	Prob.
1	668.53	0.0000	5.78	0.0002
2	666.28	0.0000	6.13	0.0010
3	446.92	0.0000	13.75	0.0001
4	490.22	0.0000	4.75	0.0014
5	624.83	0.0000	1.50	0.2120
6	471.27	0.0000	2.26	0.0661
7	2811.06	0.0000	2.58	0.0631
8	348.69	0.0000	5.86	0.0010
9	317.65	0.0001	2.84	0.0446
10	94.07	0.0001	27.58	0.0001
11	336.27	0.0000	8.19	0.0001
12	716.45	0.0000	6.84	0.0003

The F-test results of the analysis of spatial shoot distribution indicated that three individual trees, i.e. trees 3, 7 and 10, deviated clearly from the rest of the sample trees in their pattern of shoot distribution (Table 5). Tree 7 had a high F-value for vertical shoot locations but a relatively low F-value for horizontal shoot locations. This indicated a high crown shape ratio and very distinct vertical clustering of shoots into horizontal whorl-layers. The opposite pattern was characteristic of tree 10 having a low vertical and a high horizontal F-value indicating a low crown shape ratio and even vertical shoot distribution, with no distinct whorl structures. In tree 3 this pattern of shoot distribution was not as distinct as in tree 10, but still clearly different from that of the rest of the sample trees.

In all the trees the between-whorl differences in the shoot heights from the ground were statistically highly significant (Table 5). The between-whorl differences in the distances of shoots from the stem were not as clear, i.e. in 7 trees highly significant, in 2 trees significant, in 2 trees barely significant and in one tree insignificant.

4. Correlations of crown architecture

Crown characteristics

The more narrow the crown shape the bigger were the shoots and the bigger share of the crown volume was occupied by the shoot volume. This was evident since the crown shape ratio was positively correlated with the mean shoot volume (r = .584 *) and crown shoot volume density (total shoot volume/crown volume) (r = 709 **). However, the mean needle mass density of shoots (needle dry mass/shoot volume) was smaller in narrow crowns (r = −.612 *). These relations imply that trees with a high crown shape ratio had a more even within-crown spatial distribution of needles than broad-crowned trees.

Branch, shoot and needle characteristics

Trees with horizontally inclined branches were characterized by big shoots, i.e. the mean branch inclination measured from the vertical was positively correlated with a high mean shoot volume (r=614 *).

These were also trees with many branches per whorl and characterized by big shoots occupying a large share of the total crown volume. This was since the mean number of branches per whorl showed significant positive correlations with the crown shoot volume density (r=.629 *) and mean shoot volume (r=.719 **), the correlation with the crown shape ratio was insignificant (r=.373). Also the total shoot length was positively correlated with the mean crown shoot volume density (r=.561 *). A weak negative correlation was evident between the total shoot length and specific needle area (r=−.561 *).

On the other hand, trees characterized by dense needle packing into shoots were those with a broad crown, low needle mass and small shoots occupying a small amount of the total crown volume. This can be concluded since the mean shoot needle mass density was negatively correlated with the crown shape ratio (r=−.612 *), crown shoot volume density (r=−.529 *), and mean shoot volume (r=−.774).

The mean shoot inclination did not show any marked correlation with any characteristic. However, it was weakly negatively correlated with the crown form ratio (r=−.36 p=.24), which implies that in many cases the shoots in broader crowns are more vertically inclined when compared to narrow crowns. There was no correlation between the mean branch inclination and mean shoot inclination or between the mean branch inclination and the mean angle of a shoot to its parent shoot.

Table 6. Correlations between components of above ground biomass portions and components of tree architecture.

Characteristic	Biomass			
	total	stem	branch	needle
Length of living crown	.821***	.837***	.711**	.772**
Number of branches per whorl	.797***	.727**	.682**	.801***
Mean shoot volume	.660**	.554*	.569*	.685**
Total shoot length	.520*	.311	.588*	.512*
Crown shoot volume density	.665**	.457	.626*	.712**
Shoot needle mass density	−.503*	−.332	−.424	−.583
Crown shape ratio	.647*	.632*	.527	.647*
F-vertical	.255	.450*	.096	.199
F-horizontal	−.689**	−.667**	−.574*	−.680**

Characteristics related to high above ground biomass

Length of living crown and number of branches per whorl were the crown characteristics most strongly positively correlated with biomasses of all above-ground yield components (Table 6, Fig. 8). High crown shoot volume density implicated high branch and needle masses, but the correlation with stem mass was weaker and insignificant. The mean shoot needle mass density showed a negative correlation with the total mass. Thus, an even spatial needle distribution inside the crown was related to a high total yield (Fig. 8).

High F-value for horizontal shoot location between and within whorls showed a negative correlation with masses of all measured above-ground biomass components, and thus also with the number of branches per whorl, mean shoot volume, total branch length and crown shoot volume density, indicating a small size and nonlayered structure.

High F-value for vertical shoot location between and within whorls was positively correlated with high stem biomass, and accordingly also with high branch inclination (implicating horizontally inclined branches), high number of branches per whorl and big shoots with low needle mass density.

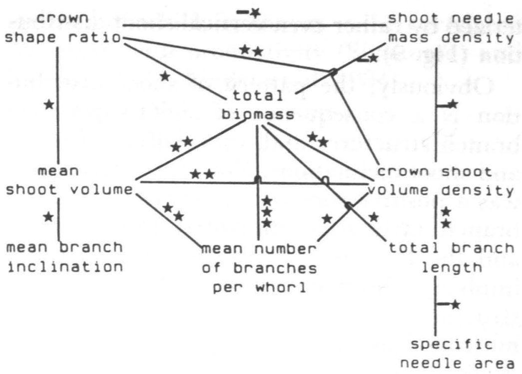

Fig. 8. Relationships between characteristics of tree architecture. The statistical signifigance of the relationships are indicated as follows: *, p<0.05; **, p<0.01 and ***, p<0.001.

5. Discussion

The results of this study demonstrate the existing consistencies as well as the considerable variation in the phenotypic architecture of young Scots pine from different origins. Because of the small size and wide spacing of the trees it was assumed that within-tree shading was determined by the structure of the tree itself. Accordingly it was assumed that the inherent growth model of each tree was to a high degree realized (Halle et al. 1978).

In general, both branches and shoots became more horizontally inclined from the top of a tree downwards, and the youngest shoots were on average more vertically inclined than the older shoots. The shoot needle mass density increased from older to younger shoots within whorl age classes and from the top of trees downwards within shoot age classes. Thus, the distribution of shoot inclinations and shoot structure within the crown was a function of both shoot location and age, which are also interdependent factors. Distribution of branch orientations was uniform as detected earlier by Kellomäki and Oker-Blom (1983).

The spatial distribution of shoots, shoot volume and needle mass showed considerable between-tree variation. The analysis of variance of the spatial shoot distribution pattern revealed that two trees deviated remarkably from the rest of the sample population, one being a descendant of exceptional father tree E1101 (Mikola 1984), with a high F-test value for vertical and a low F-test value for horizontal shoot location within, and the other tree from Northern Finland with an opposite relationship between these two variables. The results would imply that deviations from the mean pattern of shoot distribution in young Scots pine occur either towards a layered structure where shoots are situated in narrow horizontal whorl-layers, or towards a nonlayered or "bushlike" structure, characterized by rather even vertical shoot distribution (Fig. 9).

Obviously, the pattern of shoot distribution is a consequence of shoot-supporting branch structures and, especially, of branch and shoot inclinations. Not suprisingly, there was a positive correlation between the mean branch inclination measured from vertical and the F-value for vertical shoot location, implying a layered structure. The nonlayered structure represented by high F-value for horizontal shoot location appeared to be connected to a small size of all biomass components, while the layered structure with high F-value for vertical shoot distribution was correlated only with high stem mass, implicating differences in photosynthate allocation when compared to the nonlayered structure.

Several methods have been utilized to describe the vertical distribution of foliage biomass in tree canopies. The normal distribution has been used (Ford and Newbould 1971), but also skewed and two-peaked distributions have been documented (Beadle et al. 1982, Ford 1982, Whitehead 1978); Kellomäki et al. (1980) used the beta distribution for young *Pinus sylvestris* L. These model approaches are, however, inappropriate if one wants to describe the vertically uneven and whorl-concentrated distribution of needle mass as characteristic of young Scots pine trees.

The correlation analysis of tree structure revealed that the high variability of tree architecture as detected between individual trees was not random, and that several measured components of structure changed in a predictable manner in relation to each other (Kellomäki 1986). For example, characteristics such as the crown shape ratio, crown shoot volume density, number of branches per whorl and mean shoot volume were positively correlated with each other and with the total above ground biomass. Also the reciprocal relationship between the crown shoot volume density and shoot needle mass density displayed the existing variation in shoot structure and also in the spatial within-crown needle distribution of young Scots pine from different origins. In general, it appeared that in the variation of the phenotypic tree architecture of Scots pine the characteristics of tree structure changed in a predictable way in relation to each other. Therefore, there seem to exist certain easily measurable characteristics of the architecture of Scots pine that could be utilized with wide applicability to predict other structural tree characteristics which are more difficult to measure.

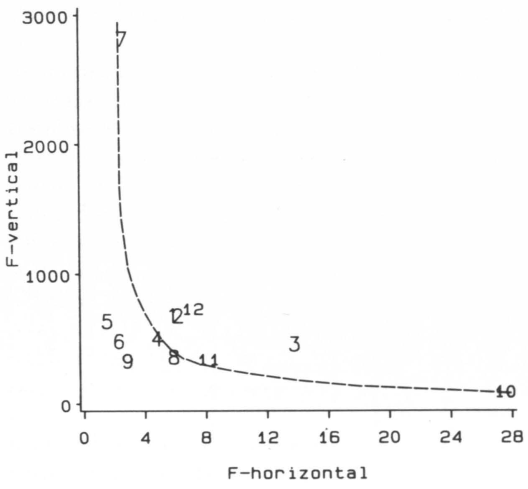

Fig. 9. Vertical and horizontal F-test values of the sample trees.

The detected relationships between structural features and high yield are mostly reported also earlier. For example, Knowles and West (1985) used succesfully the crown length of young *Pinus radiata* to predict basal area increment at stand level. Total shoot length is obviously closely related to needle mass which obviously correlated closely with the total biomass. In Scots pine Velling (1982) reported a positive correlation between branch number per whorl and growth, and Cannell (1974) found that high number and great lengths of branches were related to a high rate of growth in *Pinus contorta* and *Picea sitchensis*. Also a narrow crown has often been related to efficient growth (e.g. Rubner 1943, Schmidt-Vogt 1972, Velling and Tigerstedt 1984).

The connection between a high yield and shoot size and spatial distribution of shoots has not, however, been reported earlier, although these factors may be important. This is because a more homogenous needle distribution within the crown, as reflected by big shoots with low needle density and a high crown shoot volume density, acts by increasing the amount of intercepted radiation, when compared to a more grouped needle distribution (Kellomäki et al. 1984), the amount of which is shown to be correlated positively with productivity (Sivakumar and Virmani 1983, Linder et al. 1984).

References

Beadle, C.L., Talbot, H. & Jarvis, P.G. 1982. Canopy structure and leaf area index in a mature Scots pine forest. Forestry 55: 106–123.

Brünig, E.F. Tree forms in relation to environmental conditions. In: Cannell, M.G.R. & Last, F.T. (eds.). Tree physiology and yield improvement. Academic Press. London, New York.

Calahan, M. Ch. 1981. Provenance and clonal variation in growth, branching and phenology in Picea sitchensis and Pinus contorta. Silvae Genetica 30 (2–3):40–46.

Cannell, M.G.R. 1974. Production of branches and foliage by young trees of Pinus contorta and Picea sitchensis: provenance differences and their simulation J. Appl. Ecol. 11: 1091–1115.

— , Sheppard, L. J., Ford, E.D. & Wilson, R.H.F. 1983. Clonal differences in dry matter production and distribution, wood specific gravity and the efficiency of stemwood production in Picea sitchensis and Pinus contorta. Silvae Genetica 32 (5–6): 195–202.

Flower-Ellis, J., Albrektson, A. & Olsson, L. 1976. Structure and growth of some young Scots pine stands: (1) dimensional and numerical relationships. Swedish coniferous forest project. Technical report 3.

Ford, D. 1982. High productivity in a polestage Sitka spruce stand and its relation to canopy staructure. Forestry 55: 1–17.

— & Newbould, P.J. 1971. The leaf canopy of a coppice woodland. I. Development and structure. J. Ecol. 59: 843–862.

Halle, F., Oldeman, R.A.A. & Tomlinson, P.B. 1978. Tropical trees and forests: An architectural analysis. Springler Verlag. London, New York, San Fransisco.

Jahnke, L.S. & Lawrence, D.B. 1965. Influence of photosynthetic crown structure on potential productivity of vegetation based primarily on mathematical models. Ecology 46(3):319–326.

Kellomäki, S. 1986. A model for the relationship between branch number and biomass in Pinus sylvestris crowns and the effect of crown shape and stand density on branch and stem biomass. Scand. J. For. Res. 1:455–472.

— , Hari, P., Kanninen, M. & Ilonen, P. 1980. Ecophysiological studies on young Scots pine stands: II. Distribution of needle biomass and its application in approximating light conditions inside the canopy. Silva Fenn. 14(3): 243–257.

— & Oker-Blom, P. 1983. Canopy structure and light climate in a young Scots pine stand. Silva Fenn. 17 (1): 1–21.

— , Oker-Blom, P. & Kuuluvainen, T. 1984. The effect of crown and canopy structure on light absorption and distribution in a tree stand. In: Tigerstedt, P.M.A., Puttonen, P. & Koski, V. (eds.). Crop physiology of forest trees. Proceedings of an international conference on managing forest trees as cultivated plants held in Finland, July 23–28, 1984.

Knowles, R.L. & West, G.G. 1985. The use of crown length to predict the effects of pruning and thinning in Pinus–radiata. In: Fujimori, T. & Whitehead, D. (eds.). Crown and canopy structure in relation to productivity. Proceedings of an international workshop held in Japan 14–20 October 1985.

Linder, S., McMurtrie, R.E. & Landsberg, J.J. 1984. Growth of eucalyptus: A mathematical model applied to Eucalyptus Grandis. In: Tigerstedt, P.M.A., Puttonen, P. & Koski, V. (eds.). Crop physiology of forest trees. Proceedings of an international conference on managing forest trees as cultivated plants held in Finland, July 23-28, 1984.

Mikola, J. 1984. Relationships between height growth differences of Scots pine full-sib families and variation in seed size, annual growth ryth and some foliage characteristics. In: Tigerstedt, P.M.A., Puttonen, P. & Koski, V. (eds.). Crop physiology of forest trees. Proceedings of an international conference on managing forest trees as cultivated plants held in Finland, July 23–28, 1984.

Norman, J.M. & Jarvis, P.G. 1974. Photosynthesis in Sitka Spruce (Picea sitchensis (Bong.) Carr.). III. Measurements of canopy structure and interception of radiation. J. Appl. Ecol. 11:375–398.

Rubner, K. 1943. Die praktische Bedeutung unserer Fichtenformen. Forstwiss. Zentbl. 65:233–247.

Schmidt-Vogt, H. 1972. Studien zur morphologishen variabilität der Fichte (Picea abies Karst.). 3. Gesetzmässigkeiten und Theorien. Algem. Forst-Jagdztg. 143:133–144 and 221–240.

Sivakumar, M.V.K. & Virmani, S.M. 1984. Crop production in relation to interception of photosynthetically active radiation. Agrig. and For. Meteorol. 31: 131–141.

Velling, P. 1982. Genetic variation in quality characteristics of Scots pine. Silva Fenn. 16 (2): 129–134.

— & Tigerstedt, P.M.A. 1984. Harvest index in a progeny test of Scots pine with preference to the model of selection. Silva Fenn. 18 (1): 21–32.

Whitehead, P. 1978. The estimation of foliage area from basal area in Scots pine. Forestry 51:137–149.

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Appendix

Table A1. Mean branch inclinations measured from vertical in sample trees in the uppermost whorl (1), in lower whorls (2+) and in all whorls included (All). Var = variance, N = number of measurements.

Whorl		Tree number											
		1	2	3	4	5	6	7	8	9	10	11	12
	$\bar{x}$	55.9	46.4	63.0	50.5	83.1	51.7	55.6	60.0	45.0	60.7	55.0	48.5
1	var	329	170	479	342	1565	452	297	770	279	362	421	895
	N	11	11	10	11	13	12	9	11	8	7	8	10
	$\bar{x}$	76.7	84.5	80.8	85.8	88.3	81.1	96.1	84.3	91.0	79.7	79.4	81.9
2+	var	226	286	479	376	583	326	209	161	252	249	218	331
	N	38	29	25	36	32	35	32	28	30	19	24	29
	$\bar{x}$	71.8	74.0	77.9	78.3	84.6	73.6	87.2	77.4	81.3	74.6	73.3	73.3
All	var	344	546	368	579	574	518	510	439	612	340	372	674
	N	49	40	35	37	45	47	41	39	38	26	32	39

Table A2. Mean shoot inclinations as measured from the vertical in sample trees by whorls; var = variance; N = number of measurements.

Whorl		Tree number											
		1	2	3	4	5	6	7	8	9	10	11	12
	$\bar{x}$	50	35	70	35	60	100	45	40	30	75	50	25
1	var	–	–	–	–	–	–	–	–	–	–	–	–
	N	1	1	1	1	1	1	1	1	1	1	1	1
	$\bar{x}$	61.9	56.2	77.5	56.4	66.4	66.4	104.4	70	67.1	85.0	63.3	61.4
2	var	564	241	675	423	731	781	967	743	690	900	897	914
	N	8	8	4	7	7	7	8	8	7	7	6	7
	$\bar{x}$	72.9	64.2	81.7	73.6	77.6	77.8	93.9	83.4	88.2	72.7	66.7	81.6
3	var	323	395	207	579	479	432	218	694	509	603	659	381
	N	34	25	30	33	21	28	27	40	37	20	35	34
	$\bar{x}$	83.7	85.5	90.1	87.7	84.9	90.8	94.7	86.4	81.0	77.2	83.9	98.3
4	var	294	317	332	789	456	598	130	375	431	602	409	539
	N	91	38	110	64	42	64	29	69	40	32	57	70
	$\bar{x}$	84.1			77.9	76.6	89.9				83.9		
5	var	120			206	416	251				434		
	N	34			12	16	52				124		

Table A3. Mean shoot inclinations in (1) first years shoots and in (2+) older shoots. Var = variance, N = number of measurements.

Shoot age		Tree number											
		1	2	3	4	5	6	7	8	9	10	11	12
	$\bar{x}$	76.1	67.2	87.4	74.9	72.9	83.2	94.5	84.3	80.3	77.5	71.6	86.0
1	var	292	443	214	642	573	482	420	464	621	585	552	759
	N	88	39	85	67	36	69	38	75	56	75	68	73
	$\bar{x}$	85.0	82.4	88.4	87.8	84.7	90.2	95.2	83.3	86.5	84.3	86.3	98.3
2+	var	295	419	485	755	377	476	145	651	359	430	547	365
	N	80	33	60	50	51	83	27	43	29	109	31	39

Table A4. Mean shoot needle mass densities of trees (0.01g/cm^3) in 1st year shoots (1), older shoots (2+) and all shoots (All). Var = variance, N = number of measurements.

		Tree number											
Age	class	1	2	3	4	5	6	7	8	9	10	11	12
1	$\bar{x}$	.43	.50	.42	.32	.33	.30	.26	.34	.43	.35	.40	.31
	var	.001	.004	.000	.005	.001	.001	.001	.002	.001	.001	.003	.005
	N	88	39	85	67	36	69	38	74	47	73	68	73
2+	$\bar{x}$	.36	.25	.34	.25	.24	.33	.29	.36	.34	.34	.35	.24
	var	.002	.020	.001	.001	.011	.001	.007	.003	.002	.002	.000	.000
	N	61	32	59	45	44	63	20	32	21	69	24	34
All	$\bar{x}$	.40	.39	.39	.29	.28	.31	.27	.35	.41	.34	.39	.29
	var	.003	.026	.002	.005	.008	.002	.003	.002	.003	.001	.003	.004
	N	149	71	144	112	80	132	58	106	68	142	92	107