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Estimation of volume, total and projected area of Scots pine needles from their regression on length

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Abstract

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Breadth, thickness, perimeter and area of serial transverse sections (TS) of Scots pine (*Pinus sylvestris* L.) needles from non-fertilised (O) and combined NPK-fertilised (F) and irrigated-fertilised (IL) trees of northern Swedish origin were measured by projection microscopy. The accuracy and precision of the method were analysed. Regressions of the above characters and of total (A_t) and projected (A_p) area and volume on the length of single needles were calculated, to make possible their non-destructive estimation from length. Needles were semi-fusiform, rather than semi-cylindrical, as is assumed for some conversion factors from projected to total area. The assumption of a semi-cylindical form caused total needle area to be systematically overestimated. The mean basic dimensions of the longer (F, IL) needles exceeded those of (O) needles: breadth by 11%, thickness by 21%, TS area by 32% and perimeter by 9%. Regressions of A_t and A_p on length were linear over the range 15–70 mm; that of volume was curvilinear. Both (O) and (F, IL) needles lay on the same regression line. Joint regressions gave estimates of mean A_t, mean A_p and mean volume having 95% confidence limits of ± 2.3, ± 2.0 and ± 4.4%, respectively. Comparisons with published sources suggest that the regressions should be applicable outside the range of northern morphological types within Scandinavia, but that overestimates of area and volume may occur if they are applied to material of Central European origin.

Keywords: Pinus sylvestris, needles, fertilised.

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Introduction

In studies of carbon assimilation by conifers, the two needle characters it is most useful to be able to determine readily are area (conventionally, projected area) and volume. From these, other characters, such as area per unit volume, may be obtained. A variety of devices for measuring leaf area has now been available for a number of years. Most of these were not originally devised for use on needle-leaved species, but for species with plane leaves, in which projected area is a straightforward concept. In conifers, "projected area", as measured by such devices, currently implies the mean projection on a plane surface, of randomly oriented needles. For converting projected to total area, the ratio between total and projected area, such as that determined for Scots pine (*Pinus sylvestris* L.) by Rutter (1957), has often been used. Some confusion is implicit in this, since Rutter's original conversion factor was based on the projection of the flattened needle surface. Furthermore, such conversion factors may involve arbitrary assumptions about needle form, and make no allowances for its variation over the range of a species or as a result of experimental treatment, e.g. fertilisation.

As publications concerning methods for indirect estimation of needle area indicate (e.g. Drew & Running, 1975), area meters may not perform satisfactorily when dealing with individual, narrowly linear objects a millimetre or less in breadth (cf. also Smith, Waring & Perry, 1981), i.e. with typical conifer needles. Given the initial uncertainty in determining projected area, it is not remarkable that estimates of total area, derived from it and a general conversion factor, should be unreliable (cf. Zelawski, 1976).

The individual areas thus determined are frequently used in estimating the total needle area of shoots, trees and stands. This involves multiplying the area of a "mean" needle — derived from a sample which may or may not be representative — by a factor which in Scots pine may range from $2 \cdot 10^2$ to $2 \cdot 10^8$ or 10^9 (cf. Burger, 1947; Ovington, 1957; Flower-Ellis & Olsson, 1978). Demands on the precision and accuracy of the initial measurements are therefore great, and a lack of reliability in the means of conversion between projected and total area, is unsatisfactory.

Earlier direct attempts at determining needle area made use of basic needle dimensions and of relationships between them (Amilon, 1925; Huber, 1925; Grahle, 1933). Dimensions were usually obtained by measuring needle length, and breadth and thickness with a micrometer screw gauge or microscopically on serial transverse sections cut at right-angles to the long axis of the needle. It was often assumed that individual needles of two-needled pines, such as Scots pine, were semi-ellipses or semi-cylinders; total surface area was calculated by the appropriate formula, with (Tirén, 1927) or without (Rutter, 1957) correction for the deviation of needle form from the chosen model.

The relationship between basic needle dimensions and length was clearly recognised by e.g. Dengler (1908*b*), Amilon (1925) and Tirén (1927). However, the expressions developed by Amilon and Tirén required measurement of both needle length, and of breadth at midpoint at the least, causing them to be laborious, therefore largely neglected by later workers. Other estimators, such as those of Grahle (1933), expressed in terms of a range without explicit relation to length, are difficult to apply in a specific situation.

In the estimation of the area of all needles on a branch or tree (e.g. Tirén, 1927; Burger, 1947; Rutter, 1957), the relationship between the area of the individual needle and its weight, fresh or dry, has often been employed.

For some time it has been evident that the relationship between area and dry weight in Scots pine needles must vary, not only (a) between trees (Troeng & Linder, 1982) but also (b) with season, in consequence of the seasonal cycle of starch accumulation and breakdown in the needle (Tamm, 1955; Rutter, 1957; Ericsson, 1979); and (c) with needle age. Since seasonal variations in the Scots pine needle's content of starch and soluble sugars may cause its dry weight to fluctuate by 30–35% or more in the course of a year, specific needle area will vary in proportion. Such dry weight variations, associated with the starch cycle, are known from several evergreen plant species (Flower-Ellis, 1980; Reader, 1978), and it is probable that this applies to needles of most conifers. There is also growing evidence that the dry weight of evergreen leaves increases with age (e.g. Flower-Ellis, 1993), as a result of the continued incorporation of vascular tissue (Ewers & Schmid, 1981; Ewers, 1982), the accumulation of mineral elements, metabolic by-products or all of these (van Laar, 1976; Schulze, Fuchs & Fuchs, 1977; Morrow & Timmer, 1981; Madgewick & Tamm, 1986). A means of determining needle area independently of these sources of error must therefore be found (cf. Zelawski, 1976).

Detailed studies on photosynthesis and on the dynamics of assimilate and mineral nutrients in Scots pine (e.g. Linder & Troeng, 1980; Ericsson, 1979; Aronsson & Elowson, 1980) in conjunction with demographic analysis of needle populations within the Swedish Coniferous Forest Project (SWECON), concentrated attention to individual needles. These studies called for a simple, non-destructive means of estimating the area of living needles as well as needles in the litter.

In the SWECON project, the effects of mineral nutrient supply on carbon acquisition were studied. It is well known that the length of conifer needles can be substantially increased by fertilisation (e.g. Brix & Ebell, 1969; Miller & Miller, 1976; Brix, 1981). Photosynthetic production increases with increasing needle length, and fertilisation is believed to increase the photosynthetic rate per unit area (almost invariably expressed as projected area), cf. Linder & Ingestad (1977), Linder & Troeng (1980), Linder & Rook (1984): but part of the increase in the rate of photosynthesis per unit area may be attributable to concomitant increases in needle dimensions which are not satisfactorily accounted for by projected area (in whichever sense it is used).

The study reported here had three aims: (1) To describe a procedure for measuring basic needle dimensions on transverse sections, and to assess sources of error associated with it. (2) To discover to what extent the application of mineral nutrients affects the basic dimensions of Scots pine needles. (3) To establish relationships between a readily measured character, such as needle length, and the volume, total and projected area of individual needles.

This investigation is part of a series of studies on the structure and dynamics of Scots pine, reported elsewhere (Flower-Ellis, Albrektson & Olsson, 1976; Flower-Ellis & Olsson, 1978; Flower-Ellis, 1982).

Abbreviations

The following abbreviations are used:

(O)	Non-fertilised
(F)	Fertilised
(IL)	Irrigated + complete fertiliser supplied in water
TS	Transverse section(al)
r	Needle thickness at 90° to flattened surface, mm
b	Breadth across flattened needle surface, mm
p	Length of perimeter of needle TS, mm
$\bar{r}$	Mean needle thickness, mm $\left(\frac{1}{n}\sum_{i=1}^{n} r_i\right)$
$\bar{b}$	Mean needle breadth, mm $\left(\frac{1}{n}\sum_{i=1}^{n} b_i\right)$
$\bar{p}$	Mean perimeter, mm $\left(\frac{1}{n}\sum_{i=1}^{n} p_i\right)$, where n is the number of TS per needle
L	Needle length, mm
A_t	Total needle area, mm^2
A_p	Projected needle area, mm^2
V	Needle volume, mm^3
f_v	Volume form factor (the quotient between observed volume, and volume calculated assuming the needle to have a semi-elliptical cross-section).

Material and methods

Situation and stands

The needle samples were collected from the SWECON research area at Jädraås (60°49′N, 16°30′E, 185 m above sea-level). The tree stand consisted of self-sown Scots pine (*Pinus sylvestris* L.), approximately 15 years old in 1973. It had been cleaned to give an even spacing and height distribution (1 095 $\pm$ 31 trees·ha^{-1}, mean height in 1974 2.11 $\pm$ 0.09 m for trees $\geq$1 m). Soil and vegetation have been described by Axelsson & Bråkenhielm (1980), the structure of the stand by Flower-Ellis et al. (1976).

Experimental treatment

An experiment laid out on the site consisted of control plots and three treatments, viz. irrigation, fertilisation and combined irrigation and fertilisation with a complete nutrient solution, beginning in 1974. Solid fertiliser was applied annually, combined irrigation and fertilisation throughout the growing season each year (for details, see Aronsson & Elowson (1980)).

The (F) and (IL) treatments resulted in substantial increases in tree height (Flower-Ellis, 1982) and in an approximate doubling of needle length after 1974 (Flower-Ellis, unpubl.).

Sampling

Needle pairs were plucked from the first-order axis (cf. Flower-Ellis et al., 1976) of branches on the southern side of the lower crown. Previous year's (C+1) and older needles were collected, 30 pairs from the control and a total of 30 pairs from (F) and (IL) treatments. Samples were collected in the winter of 1976, and stored at −20 °C until processed.

Processing

Needle fascicles were separated into individual needles. The length of a single needle from every pair was measured to 0.2 mm, including that part normally within the bracts of the short shoot. Needles were marked for sectioning at 1 mm from the tip, and at 10, 30, 50, 70 and 90% of their length (tip = 0). They were sectioned on a freezing microtome to give 30 μm TS, cut at right-angles to the long axis. The TS from each position were stored in water with added thymol, then mounted in glycerol on slides.

According to Tirén (1927), TS in water increased their linear dimensions by 2–3% compared with initial values determined by micrometer screw gauge. Micrometer measurements are, however, an uncertain base for such a comparison. In the present study, TS mounted in glycerol after storage in water showed no measurable change in dimensions 1 h after mounting.

For practical reasons, TS could not be cut at 10 and 70% of length on some of the shorter needles. However, in almost all cases a needle was represented by 6 TS.

The TS were back-projected on to tracing paper mounted on a vertical, transparent screen, using a Leitz "Micropromar" projection microscope with planar lenses to give an image free from radial distortion. Magnification at the screen was adjusted to (a) 140X (O), (b) 200X (F, IL), using a stage micrometer. The perimeter of all TS was traced.

Two batches of tracing paper were used. These had a nominal weight of (a) 82 $g{\cdot}m^{-2}$ and (b) 95 $g{\cdot}m^{-2}$, respectively.

The perimeter of each TS was measured with a map-measuring instrument, after which the breadth and thickness (Fig. 1) were measured on the tracing to 0.5 mm (0.004 and 0.003 mm, respectively, at true scale). Each traced TS was excised, and stored in a desiccator over silica gel until it was weighed to 0.1 mg. During weighing, tracings were handled with forceps only.

From each batch of tracing paper, replicate samples 100 × 100 mm were cut out and treated as above, to provide area-weight conversion factors.

The map-measuring instrument was calibrated by repeatedly measuring the length of straight lines and the perimeter of circles of equivalent circumference. Since some "slip" occurred when measuring the perimeter of circles, the length of all traced needle perimeters was multiplied by 1.0447 (mean of 30 determinations) to correct for the resulting underestimate.

Sources of error

The measurement of linear dimensions and area of TS involves various types of error, which may affect the accuracy and comparability of results. These are as follows:

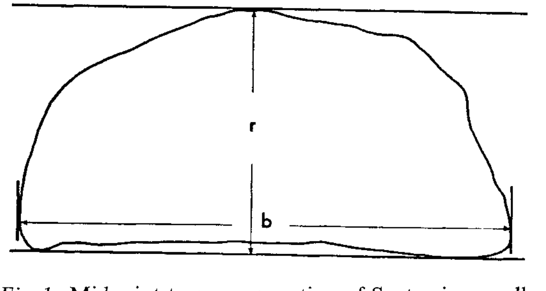

Fig. 1. Midpoint transverse section of Scots pine needle from non-fertilised (O) tree, to define measurement limits for breadth (b) and thickness (r).

1. Swelling or shrinkage of TS in mountant (cf. Tirén, 1927),
2. Failure to cut TS at 90° to the axis (cf. Amilon, 1925),
3. Inaccurate tracing of the perimeter,
4. Inaccurate measurement of dimensions on tracings,
5. Inaccurate excision of TS and area: weight standards,
6. Variations in the area: weight ratio of the paper,
7. Differential uptake of moisture by paper tracings,
8. Weighing errors,
9. Number of TS per needle.

The precautions taken should have minimised errors under (1)–(2), (5) and (7). To avoid error due to different observers, the same person traced all perimeters (3). Observer bias may have occurred, but this error component was not analysed.

The precision of measurents on tracings (4) lay within acceptable limits. Repeated linear measurements by ruler, e.g. of b and r, were within 0.5 mm. Repeated instrumental measurements of perimeters, over the range of perimeter length in the material, had a SE of 0.27 scale units ($n=30$), e.g. 0.48% of the mean length of the traced perimeter at needle mid-point.

Variations in the area per unit weight of the paper (6) depend on manufacturing tolerances. For batch (a), the error in estimating TS area from weight was equivalent to 0.20% of the area of the TS of mean area at true scale; for batch (b) it was 0.39%. As to (8), a weighing accuracy of ± 0.1 mg corresponds, e.g. for paper (b), to $< 1\ \mathrm{mm}^2$.

While (9), the number of TS per needle, is not a source of error of the same nature as Nos. (1)-(8), it affects overall precision. For example, the average standard error (SE) of the mean of six determinations of TS area was 0.093 mm^2 (ca. 9% of mean TS area). To reduce this to 5% of the mean at the same risk level would have required the cutting of a considerably larger number of TS per needle. The construction of the microtome made it impossible to determine accurately the exact position on the needle of each section, when the number of TS was increased. A decrease in the number of TS to 3 increased the SE to about 13% of mean TS area. On balance, the number of TS actually cut appears to have been a reasonable compromise between what is desirable and what was practicable (but see Discussion).

Statistical treatment

Needle breadth, thickness and TS area

Within the range of Scots pine in Sweden, there is considered to be both an absolute decrease in mean needle length with increasing latitude (Sylvén, 1910, 1916; but cf. Zelawski & Niwinski, 1966) and a relative increase in needle breadth (Andersson, 1844; Sylvén, 1916). According to Sylvén (1916), the ratio of needle length: breadth (i.e. breadth at midpoint, b_{50}) had a modal value of 17.5:1 for northern, and 37.5:1 for southern populations. However, the relationship between length and breadth at midpoint was not explicitly quantified in earlier investigations.

On the principle of co-relation between the dimensions of organs (Galton, 1888), it might also be expected that needle thickness (r) would vary in proportion to breadth, hence also TS area (cf. Dengler, 1908*a*). These basic relationships must be taken into account when constructing regressions for estimating needle area and volume from length.

Means and standard deviations (SD) were therefore calculated for b, r and TS area at all relative positions, as also the mean of the quotients r/b.

Mean needle breadth ($\bar{b}$), mean r ($\bar{r}$) and mean TS area ($\overline{TS}$) were calculated for every needle. The relationship between b and breadth at midpoint (b_{50}) was also calculated.

The regression of $\bar{b}$, $\bar{r}$ and $\overline{TS}$ on needle length (L) was investigated, where

$$\bar{b} = \beta o + \beta 1 \cdot L + \varepsilon \qquad (1)$$

βo being a constant, $\beta 1$ the coefficient of length and ε the error term; and similarly for $\bar{r}$ and $\overline{TS}$.

Perimeter in relation to breadth

Amilon (1925) found that the relation of perimeter to breadth at the same relative position was approximately equal for all needles studied by him. Hence the length of the perimeter could be estimated by measuring breadth alone.

This relationship is important for determining the ratio of total: projected area, for which reason the regression of mean perimeter ($\bar{p}$) on mean breadth ($\bar{b}$) was calculated.

Total area in relation to length

It has earlier been assumed that the Scots pine needle may be regarded as a semi-cylinder for the purpose of calculating total area, the expression

$$\text{Area} = L \cdot b(1 + \pi/2) \tag{2}$$

being used (Rutter, 1957). This reduces to the familiar expression

$$A = L \cdot b(2.571) \tag{3}$$

However, it is evident that $2r > b$ (e.g. Dengler, 1908*b*; Tirén, 1927; Zelawski & Gowin, 1966). The needle is in fact semi-fusiform, i.e. resembles rather a spindle split longitudinally, than a semi-cylinder. The area calculated according to the approximation above must therefore be corrected for the disparity between the assumed and the true form of the needle (compare the "surface form factor" of Tirén (1927)).

The geometrical approach to the estimation of total needle area, cf. Tirén (1927), Rutter (1957), was tested. However, in the present paper the total area of needles was obtained by dividing intervals between section points into 1-mm slices and summing the perimeters for each interval (cf. Amilon, 1925), the tip being treated as a pyramid with triangular base. The longitudinal section of the needle was thus regarded as a polygon, and perimeters were estimated by linear interpolation between section points. Since the graph of perimeter on relative length (RL) in fact describes a cubic parabola, this approximation may lead to error.

The "observed" area thus obtained for every needle in the material was treated as the dependent variable in a regression of total area on length. Graphical examination of the relationship between total area and length suggested that a linear model was appropriate. Separate regressions were calculated for the (O) and (F, IL) materials, and tested for differences in slope before they were combined. In view of the lack of overlap in length of the (O) and (F, IL) materials, the decision to combine the materials must also be supported by additional information. This was provided by the relationship between single-needle dry weight and length (Flower-Ellis unpubl.), in which separate regressions for (O), (I), (F) and (IL) treatments on the same occasion and for the same age-class, did not differ significantly.

Projected area in relation to length

The projected area of the needle was calculated by summing successive unit breadths (b) by sections, as described above for perimeter. This presupposes that the projected area consists of the vertical projection onto a plane surface, of the flattened surface of the needle. Estimates of the ratio of projected to total area were based on the same assumption (cf. Grahle, 1933; Rutter, 1957). However, the needles of many Scots pine provenances exhibit marked torsion (although northern provenances are considered to have a high proportion of straight needles; cf. Örtenblad, 1888), which will tend to reduce the projected area as determined by scanning devices.

After graphical examination of the material, a regression of projected area on needle length was calculated.

Volume in relation to length

Needle volume was determined by summing unit TS areas for successive sections of the needle, as for perimeter. After graphical inspection, regressions having observed volume as dependent, and length as independent variable, were calculated.

For comparison with the volume estimates of Tirén (1927), geometrical expressions for needle volume were also calculated. The first of these was identical with Tirén's function (8), viz.

$$\text{Volume} = f_v \cdot ((\pi \cdot L)/4) \cdot b \cdot r, \tag{4}$$

where f_v is a correction term, the "volume form factor", analogous to the "area form factor" according to Tirén (1927), being the quotient between observed volume and volume calculated assuming the needle to possess a semi-elliptical cross-section.

In the second relationship, volume was generated from length and from the regression of breadth on length, as follows:

$$\text{Volume} = L \cdot [\pi(\beta o + \beta 1 \cdot L)2/2]/k, \tag{5}$$

where k is a correction term derived from the mean of the ratios r : b (since $2r > b$).

Finally, volume was generated from length and from the regression of TS area on length, viz.

$$\text{Volume} = L \cdot (\beta o + \beta 1 \cdot L) \tag{6}$$

Surface area per unit volume

The relation between the surface area and the volume of the needle has been used as an index of xeromorphism, although the basis for its calculation has varied (Grahle, 1933). Mean values are usually given, without indication of variation with length.

Using the total surface areas and volumes of individual needles as calculated above, area per unit volume ($mm^2 \cdot mm^{-3}$) was calculated. After graphical examination of the relationship between this character and length, a regression was calculated, with area per unit volume as dependent variable.

For all regression relationships, goodness of fit was assessed, both by graphical study of the residuals (cf. Draper & Smith, 1980) and from the standard error of estimate ($s_{\hat{Y}\cdot x}$). The applicability of the relationships found to needles from other parts of the range of Scots pine was tested by comparison with previously published material (Dengler, 1908*b*; Sylvén, 1916; Amilon, 1925; Tirén, 1927; Grahle, 1933; Zelawski & Gowin, 1966).

Statistical terminology follows Snedecor & Cochran (1980). Significance is shown as follows:

NS not significant at the 5% level,
* significant at the 5% level, not significant at the 1% level,
** significant at the 1% level, not significant at the 0.1% level,
*** significant at the 0.1% level.

Results

Basic dimensions and relative position

The basic dimensions of the needles (b, r, p, TS) varied regularly with distance from the tip (Table 1). Needle breadth was greatest between

Table 1. *Mean, coefficient of variation (CV%) and number of observations for needle breadth, thickness, perimeter and TS area by relative positions and overall, for (O) and (F, IL) needles. Differences between (O) and (F, IL) are shown below (t-value, significance)*

Item		Position on needle 0	10	30	50	70	90%	$\bar{X}$
Non-fertilised								
Breadth,	$\bar{X}$	0.92	1.40	1.64	1.59	1.43	1.07	1.33
mm	$CV\%$	12.7	6.7	10.1	6.3	7.9	11.1	22.2
Height,	$\bar{X}$	0.58	0.72	0.76	0.74	0.71	0.62	0.68
mm	$CV\%$	11.0	8.1	7.6	6.4	7.9	9.7	4.9
Perimeter,	$\bar{X}$	2.60	3.74	4.22	4.19	3.86	3.03	3.58
mm	$CV\%$	11.7	6.9	6.2	5.9	7.9	10.4	5.3
TS area,	$\bar{X}$	0.437	0.807	0.969	0.951	0.838	0.558	0.753
mm^2	$CV\%$	22.2	12.6	11.4	11.4	13.4	17.4	30.4
n		30	21	28	30	26	30	165
F, IL								
Breadth,	$\bar{X}$	1.17	1.61	1.72	1.64	1.50	1.27	1.48
mm	$CV\%$	8.4	7.6	10.6	8.9	9.3	12.9	16.6
Height,	$\bar{X}$	0.72	0.86	0.87	0.86	0.84	0.78	0.82
mm	$CV\%$	9.9	10.0	10.2	10.2	9.5	11.7	8.4
Perimeter,	$\bar{X}$	3.09	4.13	4.47	4.31	4.01	3.46	3.91
mm	$CV\%$	10.6	10.0	11.1	10.3	11.1	13.7	9.2
TS area,	$\bar{X}$	0.673	1.081	1.207	1.150	1.038	0.828	0.996
mm^2	$CV\%$	16.3	14.2	17.1	14.7	15.8	23.7	25.2
n		30	30	30	30	30	30	180
tdiff								
Breadth		8.93 ***	6.90 ***	1.71 NS	1.54 NS	2.05 *	5.43 ***	5.16 ***
Height		7.96 ***	6.89 ***	5.40 ***	6.36 ***	6.84 ***	8.09 ***	9.78 ***
Perimeter		6.03 ***	4.17 ***	2.43 *	1.29 NS	1.47 NS	4.19 ***	4.49 ***
TS area		8.81 ***	7.44 ***	5.53 ***	5.43 ***	5.38 ***	6.76 ***	9.28 ***

30 and 50% of length. Thickness increased from the tip, but varied little between 10 and 70% of length. The semi-fusiform shape of the needle thus emerges clearly. The observed maximum values of both perimeter length and TS area in the interval 30–50% of length follow from this.

The dimensions of needles from the (F, IL) treatments were consistently greater than those of the (O) needles in all relative positions. While differences between (O) and (F, IL) needles at 1 mm, 10 and 90% of length were all significant (Table 1), the difference between (O) and (F, IL) with respect to needle breadth at 30 and 50% of length was not significant, and was barely significant at 70% of length. Perimeter at 50 and 70% of length did not differ significantly between the materials. The thickness of (F, IL) needles was significantly greater (***) in all positions, largely accounting for their greater TS area.

Two main facts emerge from the above: (1) the lack of a significant difference in breadth at midpoint (b_{50}) in needles the mean length of which differed markedly and significantly (***; (O) 32.7 ± 1.5 mm, (F, IL) 57.4 ± 1.3 mm — mean ± 1 SE); and (2) the greater overall thickness (r) of the (F, IL) needles.

Interrelations between basic dimensions

Thickness and breadth

The quotient r/b described a closely similar course in both materials, with a narrow range of variation (Table 2). It follows from the foregoing (Table 1) that it was generally greater in (F, IL) than in (O).

The contribution of breadth and thickness, respectively, to TS area was analysed with the help of multiple linear regression. In both materials, thickness and breadth contributed significantly to TS area, in the (O) material, about equally (coefficients 0.6517 and 0.6987, respectively). In the (F, IL) needles the contribution of thickness to TS area was ca 2.9 times that of breadth (coefficients 1.2361 and 0.4308, respectively).

Breadth and perimeter

The quotient b/p was greatest between 10 and 30% of length (Table 2), but in absolute terms varied little with position on the needle. Differences between (O) and (F, IL) were significant at 1 mm, 10 and 90% of length, otherwise non-significant. (The reciprocal of b/p corresponds to the quotient of perimeter/projected area by positions.)

The mean of the quotients $\bar{p}/\bar{b}$ by needles was 2.694 (SD 0.054) and 2.630 (SD 0.098) in (O) and (F, IL), respectively. The difference between the means was significant (**).

Relationships with needle length

Breadth

There was no trend of b_{50} on length, and the slope coefficient did not differ from zero. Mean breadth at midpoint in the present material was therefore effectively constant over the range

Table 2. *Mean and coefficient of variation for quotients r/b and b/p by relative positions and overall, for (O) and (F, IL) needles. The reciprocal of b/p corresponds to perimeter/projected area. The difference between (O) and (F, IL) for the overall means of both r/b and b/p was significant (***)*

Item		Position on needle						
		1 mm	10	30	50	70	90%	All
Non-fertilised								
r/b	$\bar{X}$	0.633	0.519	0.467	0.467	0.495	0.578	0.528
	CV%	9.4	7.0	9.9	7.2	7.0	8.4	14.6
F, IL								
r/b	$\bar{X}$	0.616	0.534	0.501	0.523	0.558	0.617	0.558
	CV%	7.7	5.9	5.6	7.2	6.3	7.3	10.5
Non-fertilised								
b/p	$\bar{X}$	0.354	0.373	0.388	0.380	0.369	0.351	0.369
	CV%	4.2	3.4	7.7	3.1	3.9	5.3	6.1
F, IL								
b/p	$\bar{X}$	0.380	0.391	0.388	0.382	0.376	0.368	0.381
	CV%	5.1	6.2	5.0	4.9	6.8	4.1	5.7

15–70 mm, with a joint mean value of 1.61 mm (SD ±0.13).

In the (O) material, mean breadth increased with length, but in the (F, IL) material, it decreased. This was probably a consequence of the relatively large variation in mean breadth in the shorter needles of the (F, IL) sample. In the (O) material, the slope of the regression of mean breadth on length differed significantly from zero (**). It did not do so in the (F, IL) material.

While b_{50} may be considered constant in the present material, it may be useful to be able to estimate mean breadth for a given length. The quotient $\bar{b}/b_{50}$ increased linearly with needle length in the range 25–70 mm and varied within narrow limits about the regression line (Table 3). However, values for the quotient were high in needles shorter than 20 mm in length, which suggests that morphological constraints on minimum needle dimensions may affect the lower range of length. Since the joint quotient varied continuously over the length range 25–70 mm, a joint regression was calculated.

The quotients of perimeter/breadth for individual needles showed no relationship with length in this material. Separate values of the quotient must therefore be used for (O) and (F, IL) needles (see also below).

Thickness

Thickness at midpoint (r_{50}) was significantly greater in the (F, IL) than in the (O) material (Table 1). This result was confirmed when r_{50} was plotted against length. As with b_{50}, there was no trend, and the slope coefficient did not differ from zero. In contrast to b_{50}, variation in r_{50} was discontinuous. The two materials were therefore not united.

As follows from the above, mean thickness ($\bar{r}$) differed significantly between the materials. It tended to increase with needle length in both materials. However, the slope coefficients did not differ significantly from zero. Since variation was discontinuous, the two materials were not united (Table 3).

Perimeter

The regression of mean perimeter on length in the (O) material was both positive and significant, while that in the (F, IL) material was

Table 3. *Basic data for regressions of mean breadth, thickness, perimeter and TS area on needle length; and mean breadth/breadth at midpoint ($\bar{b}/b_{50}$) on length. Regressions are shown separately for (O) and (F, IL) needles and, where appropriate, for the joint material. Significance and t_b refer to slope. The limits of length within which each regression is valid are also shown*

Material	Estimated variable, units	Estimator variable: Length mm							
		β_0 $\pm s_b$	β_1 $\pm s_b$	$s_{y \cdot x}$ $s_{\bar{y} \cdot x}$	r^2	t_b	signif.	n	Limits, mm
Control	$\bar{b}$ mm	1.1784 ±0.0507	0.00459 ±0.0015	0.0678 0.0124	0.2505	3.059	**	30	15–44
F, IL		1.6847 ±0.1793	−0.00345 ±0.0031	0.1174 0.0210	0.0424	1.114	NS	30	47–70
Joint		1.8131 ±0.0440	0.00498 ±0.00093	0.1045 0.0135	0.3308	5.355	***	60	15–70
Control	$\bar{r}$ mm	0.6374 ±0.0242	0.00139 ±0.0072	0.0324 0.0059	0.1180	1.936	NS	30	15–44
F, IL		0.7016 ±0.1044	0.00205 ±0.0018	0.0684 0.0125	0.0442	1.138	NS	30	47–70
Control	$\bar{p}$ mm	3.1977 ±0.1236	0.01161 ±0.0037	0.1654 0.0302	0.2643	3.172	**	30	15–44
F, IL		4.3817 ±0.5518	−0.00819 ±0.0095	0.3614 0.0659	0.0256	0.858	NS	30	47–70
Joint		3.2600 ±0.1239	0.01075 ±0.0026	0.2939 0.0380	0.2254	4.108	***	60	15–70
Control	$\overline{TS}$ mm^2	0.6016 ±0.0468	0.00450 ±0.0014	0.0627 0.0115	0.2727	3.240	**	30	15–44
F, IL		0.8899 ±0.2129	0.00191 ±0.0037	0.1394 0.0255	0.0095	0.518	NS	30	47–70
Joint		0.5050 ±0.0482	0.00808 ±0.0010	0.1142 0.0147	0.5205	7.934	***	60	15–70
Joint	$\bar{b}/b_{50}$	0.7204 ±0.0148	0.00321 ±0.00030	0.0288 0.0039	0.6757	10.608	***	56	25–70

negative, but not significantly different from zero. This too probably depended on the dispersion of values in the lower range of length (Table 3, Fig. 2); since both breadth and thickness tended to increase with length, perimeter should also increase.

The SD of $\bar{p}$ showed no trend with length, but was significantly smaller in (F, IL) than in (O) (*). Although the coefficients of variation (CV) were similar, perimeter varied relatively more in (O) than in (F, IL).

The precision of estimates of needle perimeter and TS area, and by extension those of total area and volume, depends on the number of TS per needle. For the TS positions in the present study, the CV of perimeter ($\bar{p}$), e.g. in the (O) material, was 19.6%. Without the use of needle length as estimator, 16 TS per needle must be measured to give a SE equivalent to 10% of mean perimeter, at the 5% risk level. Notwithstanding the relatively weak relationship between length and perimeter, the use of needle length as estimator reduces to one the number of TS per needle required, for the same precision. Similarly, the use of needle length as estimator reduces from 38 to 7 the number of sections per needle required to estimate TS area with equivalent precision.

Derived relationships

Total area

The total area of individual needles (A_t) increased linearly with needle length. Comparison of slope coefficients and constants (Table 4) showed that (O) and (F, IL) did not differ significantly. A joint regression was therefore calculated, and is shown in Fig. 3.

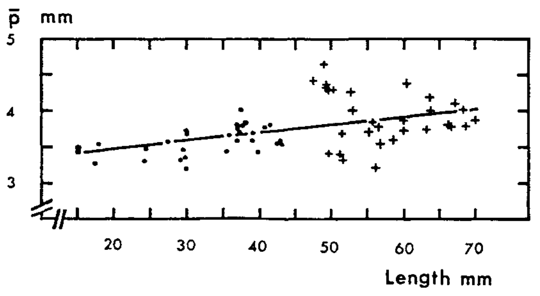

Fig. 2. Regression of mean needle perimeter ($\bar{p}$) on length for Scots pine needles from the non-fertilised (●) and the (F, IL) treatment (+), showing the dispersion of values in the lower range of length for (F, IL) needles. The joint regression line is shown.

For comparison, A_t was also calculated according to Amilon (1925), Tirén (1927) and Rutter (1957), using observed needle dimensions. The "surface form factor" (f_y) according to Tirén (1927), showed no trend on length over the range 20–70 mm (although low values of f_y occurred in needles <20 mm in length). For (O) needles, f_y was 0.918 (SD 0.076), for (F, IL) needles, 0.954 (SD 0.051). Since the two did not differ significantly, the materials were combined. The joint mean of f_y was 0.936 (SD 0.067).

Using this joint mean, A_t for individual needles was estimated from the expression

$$A_t = 0.936(\pi/2) \cdot L(1.137 \cdot b_{50} + r_{50}) \qquad (7)$$

Agreement between observed and estimated A_t was good (r^2 0.981).

When A_t was calculated according to Rutter (1957), i.e. with no correction for needle form, it was systematically overestimated by an average of 7.3%.

When A_t was calculated according to Amilon (1925; function viii), there was good agreement between observed and calculated values for (O) needles (r^2 0.977), less good for (F, IL) needles (r^2 0.867), especially in the upper range of length. Fig. 4 shows observed individual A_t in relation to Amilon's regression line.

Projected area

Projected area (A_p), as defined here, also increased linearly with needle length in both materials (Fig. 5). Since the regressions did not differ significantly, the materials were combined (Table 4).

It is evident from Table 4 that the Scots pine needles used in this study could not be regarded as semi-cylinders. The observed mean quotient of A_t/A_p was 2.758 (SD 0.068) and 2.680 (SD 0.116) in (O) and (F, IL) needles, respectively. The difference between them was significant (**).

Volume

The relationship between needle volume (V) and length was, as expected, non-linear (Fig. 6). Since the relative increase of $\bar{r}$ with length was about twice as great as that of $\bar{b}$, relationships based on needle breadth considerably underestimated the volume of long needles.

Volume calculated according to Tirén (1927;

Table 4. *Basic data for regressions of A_t, A_p and volume on needle length, for (O) and (F, IL) separately, and jointly where appropriate (bold type indicates estimative relationships underlying Figs. 3, 5 and 6). The regression of volume on length is of the type $V = L \cdot (\beta 0 + \beta 1 \cdot L)$, compare Table 3. The standard deviation for this regression was obtained from the sum of squares of the differences between observed and calculated values*

Material	Estimated variable units	Estimator variable: Length mm β_0 $\pm s_b$	β_1 $\pm s_b$	$s_{y \cdot x}$ $s_{\bar{y} \cdot x}$	r^2	t_b	signif.	n	Limits, mm
Control	A_t mm^2	−10.6973 ±4.8350	4.0196 ±0.1434	6.4738 1.1819	0.965	28.036	***	30	15–44
F, IL		19.2671 ±32.4052	3.6440 ±0.5605	21.2246 3.8751	0.601	6.501	***	30	47–70
Joint		**−15.6835** **±6.6655**	**4.2235** **±0.1408**	**15.8242** **2.0429**	**0.939**	**29.989**	***	**60**	**15–70**
Control	A_p mm^2	−3.8988 ±1.7956	1.4574 ±0.0532	2.4042 0.4389	0.964	27.398	***	30	15–44
F, IL		9.9041 ±9.4999	1.3110 ±0.1643	6.2222 1.1360	0.694	7.978	***	30	47–70
Joint		**−7.5874** **±2.1155**	**1.5992** **±0.0447**	**5.0173** **0.6477**	**0.956**	**35.785**	***	**60**	**15–70**
Joint	Vol. mm^3	**0.5050** **±0.04818**	**0.00808** **±0.00102**	**6.6372** **0.8569**	**0.898**	–	***	**60**	**15–70**

function (8)), but without correction for needle form, was systematically overestimated. For the needle of mean length in the joint material, the overestimate was 14.5%. When the joint "volume form factor" (fv; 0.873, SD 0.091) was introduced as a correction, agreement between observed and calculated values improved substantially (r^2 0.955).

On closer examination, the difference between the mean values of f_v for (O) and (F, IL) was found to be significant (***; 0.811, SD 0.054 and 0.936, SD 0.077, respectively). From this it was concluded that a joint value of f_v should not be used.

Volume was most simply estimated by means of length and the regression of mean TS area on length. No significant reduction of the residual mean error was achieved by the use of separate regressions for (O) and (F, IL), as compared with the joint regression (Table 4).

Area per unit volume

The area per unit volume of needle decreased with needle length, from ca. 5.1 to 3.6 $mm^2 \cdot mm^{-3}$ between 20 and 70 mm. The range of variation in the (F, IL) material was considerable. Although the rate of decrease declined with needle length, a linear approximation was calculated. This had a slope coefficient of -0.029 ± 0.0026 $mm^2 \cdot mm^{-3}$ (± 1 SE) per millimetre of needle length within the above limits.

Discussion

Comparability with earlier studies

Although existing studies on the basic dimensions of Scots pine needles have employed essentially the same method, viz. microscopic measurement of serial TS, the description of details is often insufficient for them to be reproduced. Whereas e.g. Amilon (1925) and Tirén (1927) discussed the effects of the mounting medium and of time on the stability of TS dimensions, few later studies report such details. Thus, while individual studies are internally consistent, uncertainty as to the sources of experimental error hinders both the comparison of results and their application elsewhere (cf. Zelawski, 1976).

It is therefore still relevant to describe a method for determining the area and volume of individual needles, in sufficient detail for it to be reproduced, and to analyse sources of error associated with it. Notwithstanding the ease of use of leaf area meters, and the increasing availability of integrating sensors for measuring leaf area index (LAI) in the field, the results pro-

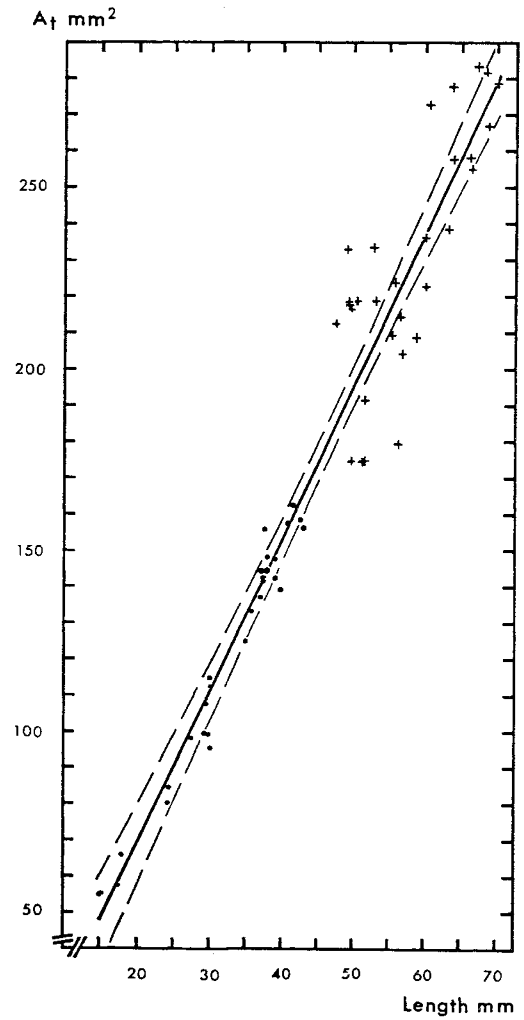

Fig. 3. Regression of A_t on length for Scots pine needles from the non-fertilised (●) and (F, IL) treatment (+). The joint regression line (—) and 99% confidence limits for the mean (---) are shown.

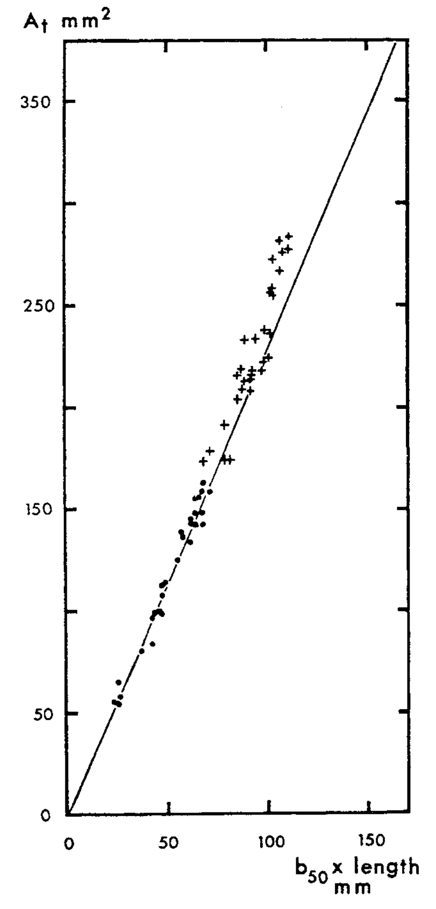

Fig. 4. Observed total needle areas (A_t) for the non-fertilised (●) and (F, IL) treatment (+) for Scots pine needles from Jädraås, superimposed on the regression line from Amilon (1925), viz. $A_t = 2.293 \cdot L \cdot b_{50} - 3.19$. Note the good agreement between the observed values and the regression line for (●) and the shorter (F, IL) needles, and the deviation of (F, IL) needles >50 mm in length from the regression line. Basic diagram after Amilon (1925).

duced by such devices must still be checked independently.

The present study was modelled on that of Tirén (1927), but differed in that glycerol replaced ethanol as mountant. Glycerol appears to be neutral with respect to the dimensional stability of TS. It is, however, still not clear what relation measured dimensions bear to true dimensions: since the breadth and thickness of living needles probably also vary, e.g. diurnally and as a result of water stress, this question is not readily resolved.

The number of TS per needle is of central importance to both accuracy and precision in determining needle perimeter and TS area, hence also to total and projected area and volume. If the requirements as to precision are set at a SE equivalent (at the 5% risk level) to 10% of mean perimeter ($\bar{p}$) and TS area, respectively, then the number of TS per needle actually measured in the present study matched the number required, when length was used as estimator. Greater precision would have necessitated the cutting of many more TS than was practicable.

In Amilon's study, the number of TS per needle was proportional to needle length (Amilon, 1925), but the average number of TS per needle was similar to that in the present study. The SDs should therefore be comparable

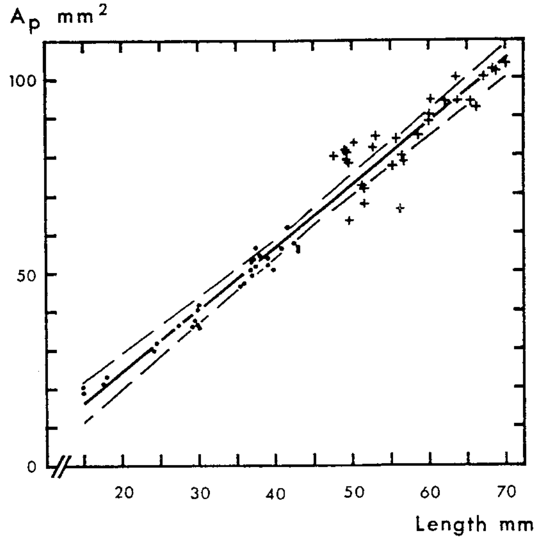

Fig. 5. Regression of projected needle area (A_p) on length for Scots pine needles from non-fertilised (●) and (F, IL) treatment (+). The joint regression line (—) and the 99.9% confidence limits for the mean (---) are shown.

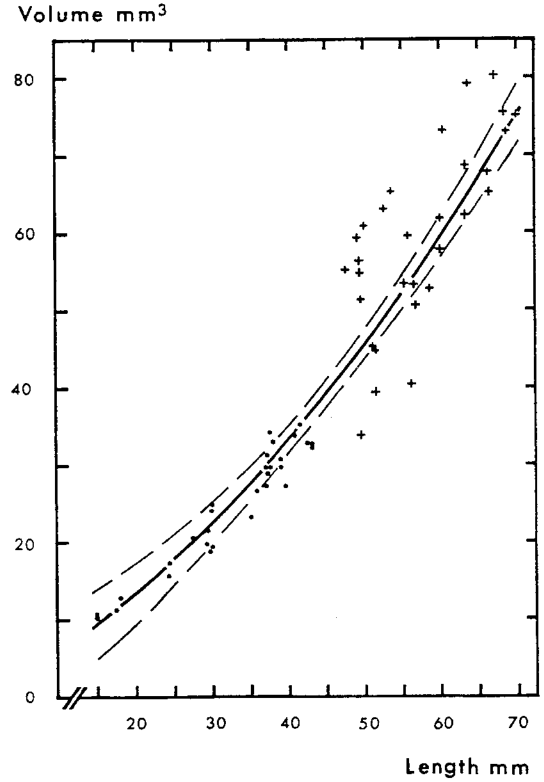

Fig. 6. Regression of needle volume on length for Scots pine needles from non-fertilised (●) and (F, IL) treatment (+). The joint regression line (—) and 95% confidence limits for the mean (---) are shown. Note the dispersion of values in the shorter (F, IL) needles.

(compare also Grahle, 1933, for which, however, experimental details are not given). These materials, and that of Tirén (1927), should have about the same precision as the present study, and should therefore be directly comparable with it, although their accuracy may differ as a result of differences in procedure.

Effects of fertiliser treatments on needle dimensions

A further aim of the study was to describe the effects of mineral nutrient supply on the basic dimensions of Scots pine needles. Since the regressions of b_{50} and r_{50} on length were not significant, midpoint means for the two materials may be compared directly. Breadth at midpoint was slightly (ca. 3%) but not significantly greater in the (F, IL) than in the (O) material. Thickness at midpoint was significantly greater in (F, IL) than in the (O) needles. While the absolute increase was small, it was considerable in relative terms (16%).

The increase in thickness at midpoint contributed largely to the greater (by ca. 21%) transverse-sectional area of the (F, IL) needles. Needle perimeter at midpoint differed little in the two materials, the perimeter of the (F, IL) needles being only ca. 3% longer than that of the (O) needles. Taken together with the increased TS area at midpoint of the (F, IL) needles, this resulted in the (O) needles' having a surface area : volume ratio highly significantly greater than that of the (F, IL) needles (by 17%).

Comparison of differences at midpoint alone is, however, misleading. Differences in mean breadth, TS area and perimeter between (F, IL) and (O) needles were substantially greater than is indicated by the midpoint comparison: Breadth was 11%, TS area 32% and perimeter 9% greater in (F, IL) than in (O) needles (Table 1), while thickness was not affected by the change in the basis of comparison. While in published sources, midpoint dimensions may be the only dimensions given, the present results indicate that they may not adequately express differences resulting from experimental treatment.

According to Grahle (1933), the area per unit volume of Scots pine needles was 40.7 $cm^2 \cdot cm^{-3}$ for a needle length of 47 mm (compare 43.2 $cm^2 \cdot cm^{-3}$ in the present material), and

$54.3\ cm^2 \cdot cm^{-3}$ for a needle 67 mm long (compare $37.3\ cm^2 \cdot cm^{-3}$ in the present material).

While the first of Grahle's values is in good agreement with that for the present material, the second is not. Judging by the values of b_{50} for needles of "southern" origin, the value $54.3\ cm^2 \cdot cm^{-3}$ probably represents a needle markedly narrower in relation to its length (b_{50} ca. 1.205 mm) than those from Jädraås. Where perimeter increases with length, area per unit volume will also increase, in contrast to a semi-cylinder in which breadth is constant while length increases.

The ratio of total : projected area was significantly greater in the (O) than in the (F, IL) needles. Although the difference was 2–3% only (depending on the base for calculation), it should be taken into account when converting measured projected area to total area, e.g. when comparing photosynthesis or dry matter production per unit needle area in fertiliser experiments.

The volume form factor (f_v) was very significantly greater (by 15%) in the (F, IL) as compared with the (O) material, i.e. the (F, IL) needles approximated more closely to semi-cylinders.

Since perimeter increases with needle length, the increase in the area of the (F, IL) needles was greater than it would have been had length alone increased. Fertilisation, and combined irrigation and fertilisation, caused a mean increase of ca. 25 mm in needle length in the stand at Jädraås (Flower-Ellis, unpubl.). This was accompanied by an increase of $106.7\ mm^2$ in mean A_t. Without the increase in needle perimeter, the increase in A_t associated with the observed increase in length would have been $91.7\ mm^2$. The difference ($15.0\ mm^2$, 14%) is associated with the increase in perimeter. The increase in mean breadth, corresponding to projected area, was ca. 9%. An increase in one dimension of an organ is usually accompanied by proportionate increases in others (cf. Galton, 1888), which serve to maintain structural integrity.

From the above it is concluded that needle form in the (F, IL) treatments differed from that of the (O) material, and that the differences were a result of the treatment. The present material does not, however, permit the effects of fertilisation and of irrigation combined with fertilisation, to be separated. The results suggest that the examination of a larger material might lead to the recommending of separate estimative regressions for fertilised and non-fertilised needles.

Applicability of relationships

The relationships reported here are intended for estimating A_t, A_p and volume for single Scots pine needles, whether detached or in situ. They must be capable of being applied to a range of provenances, as well as to material from fertilised stands. At this point the position of the Jädraås material relative to the range of variation in Scots pine needles must be examined.

The length of Scots pine needles is known to decrease with increasing latitude and altitude (e.g. Dengler, 1908*b*; Sylvén, 1916). It also varies with position in the tree, with tree age, with shoot type and order, with aspect and between years (e.g. Renvall, 1914; Troeng & Linder, 1982; Junttila & Heide, 1981). For needle breadth at midpoint, the underlying trend with latitude is unclear. It has been emphasised that the greater breadth of needles of northern origin is relative rather than absolute (cf. Dengler, 1908*b*; Andersson, 1844; Sylvén, 1916). Between-year variations in breadth are known to occur (Zelawski & Gowin, 1966; Zelawski & Niwinski, 1966), also variations with position and shoot type within the tree.

Jädraås is geographically situated in the transitional zone between the "northern" and "southern" morphological types recognised by Sylvén (1916; cf. also Langlet, 1959), but its altitude places it in a relatively more northerly climatic zone. Regressions based on material from Jädraås may therefore be expected to represent a northern, rather than a southern or intermediate, morphological type.

Since the regressions are based on length, they should be capable of accomodating length variations within their domain (15–70 mm). Not more than about 20% of needles in the Eurasian range of Scots pine lie outside these limits (cf. Pravdin, 1969; Table 4). It remains to be seen how well the regressions accomodate variation in other needle dimensions.

Values of b_{50} and r_{50} extracted from Dengler (1908*b*), Amilon (1925), Zelawski & Gowin (1966), Zelawski & Niwinski (1966) and Pravdin (1969) were compared with observed values from Jädraås. With the possible exceptions of the Finnish provenance (61°N) and the Norwegian coastal provenance ("precise latitude not given", Dengler 1908*a*), all material in the comparison originated south of the limit of the "northern" type of Scots pine (Sylvén, 1916).

Absolute mean breadth at midpoint was lower in the material of southern origin, than in the joint material from Jädraås. Since, however, b_{50} increased with needle length in material of southern origin for which the relationship between the characters could be examined (contrast the Jädraås material), direct comparison of the means may be inappropriate. For r_{50}, the results of the comparison were closely similar (Fig. 7).

Material for comparison of TS area is scanty, provenances of Polish origin alone being available (Zelawski & Gowin, 1966; Zelawski & Niwinski, 1966). The TS area at midpoint was consistently lower in material of Polish origin, than in that from Jädraås.

Thus the mean basic dimensions of needles in the Jädraås material, i.e. even in the non-fertilised needles, were clearly greater than those in material of more southerly origin. The range of length covered by both sets of material was similar. The regressions of A_t, A_p and volume on length, based on the Jädraås material, must therefore be considered likely to overestimate these characters for needles of southern origin.

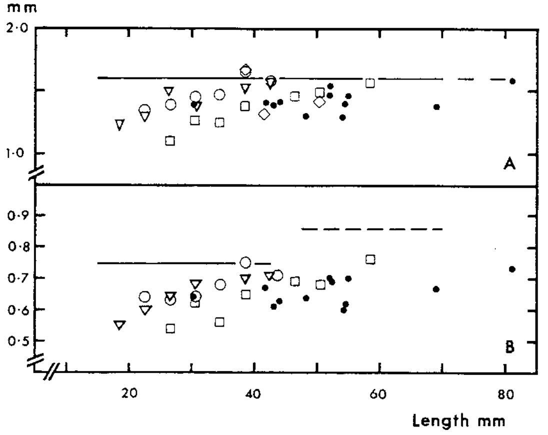

Fig. 7. Comparison between the joint mean for needle breadth at midpoint (b_{50}), in relation to length, for the Scots pine needles from Jädraås (—) and (A) b_{50} values extracted from Dengler, (1908*b*; Eberswalde □; Finland ○, Norway ▽), Amilon (1925; Stockholm and 2 south-eastern Swedish materials, not distinguished ◇), Zelawski & Gowin (1966; 3 Polish provenances for 2 years ●) and Zelawski & Niwinski (1966; same provenances as Zelawski & Gowin, 1966 ●). (B) As above, but excluding Amilon (1925), for thickness at midpoint (r_{50}). Non-fertilised Jädraås material (—), (F, IL) material (---). Cf. also Perterer & Körner (1990; Table 3).

While there is little published material for comparisons concerning A_t, that available originates south of the distribution area of the "northern" morphological type of Scots pine. Agreement was good between observed A_t values extracted from Amilon (1925), and values calculated using the regression of A_t on length, despite the fact that values of b_{50} in Amilon's material were lower than those from Jädraås. Agreement between observed A_t for the longer (F, IL) needles and Amilon's regression (based on non-fertilised material), was poor (Fig. 4).

Tirén's material was closely similar in origin to that of Amilon. The present regression of A_t on length gave results almost identical with those obtained by Tirén's method (Tirén, 1927; function (6)), for both (O) and (F, IL) materials. However, when the (O) material from Jädraås was compared with the regression based on data extracted from Tirén's graph of total area on length (Tirén op. cit., Fig. 10), there was a systematic difference of ca. 35 mm^2 over the range of needle length 20–50 mm. The regression lines were parallel, but that based on Tirén's observations lay, relative to the Jädraås material, on the lower 95% confidence limit for a new observation.

Such a discrepancy could have its origin in a sample of needles having substantially lower breadth and thickness than those from Jädraås; but information about these characters cannot be extracted from Tirén's paper. Against this interpretation must be set (a) the similarity of origin of Tirén's and Amilon's materials, and (b) the good agreement between the Jädraås material and that of Amilon. Tirén's relationship may therefore contain a systematic error.

Comparison between Tirén's material and the (F, IL) needles of the present material is not possible, since the ranges of length do not coincide.

From the above it is concluded that estimates of A_t in the length range 15–50 mm for needles from the Jädraås material agree well with those of Amilon (1925). The origin of the lack of agreement with respect to A_t between the Jädraås material and that of Tirén (1927) cannot, however, be identified.

Since values for A_p and volume were not reported by Amilon (1925) or Tirén (1927), comparison of these characters with the Jädraås material is not possible.

Conclusions

The method described here allows the basic dimensions of single Scots pine needles to be determined with good accuracy and precision. Values of A_t, A_p and volume for single needles estimated from length should be accurate to $1\ mm^2$ and $1\ mm^3$, respectively, when needle length is measured to 0.5 mm. For the needle of mean length in the joint material, A_t was estimated with 95% confidence limits for the mean equivalent to $\pm 2.3\%$, A_p to $\pm 2.0\%$ and volume to $\pm 4.4\%$. These estimates may be made in situ by means of any scale that permits needle length to be measured with an accuracy of ± 0.5 mm.

Fertilisation, and irrigation combined with fertilisation, increased needle length, breadth and thickness. The (F, IL) needles differed from (O) needles in TS area, "volume form factor" (f_v), surface area : volume ratio and in the ratio of total : projected area. Any separate effects of fertilisation or of irrigation combined with fertilisation, were not isolated. Further study of the effects of individual constituents of the (IL) treatment on needle form is desirable.

The use of a general conversion factor from projected to total needle area led to systematic overestimates of A_t. Since the error was greater in the (O) than in the (F, IL) material, the use of a general conversion factor for non-fertilised needles should be avoided. The use of the regression of A_t on length, in combination with mean needle length, is to be preferred.

For the same range of length, mean basic dimensions were greater in the Jädraås needles than in those originating outside the area of the "northern" morphological type of Scots pine. Nevertheless, agreement was good between calculated values of A_t, and values extracted from Amilon (1925), i.e. for material of "southern" origin. The regressions of A_t and A_p on needle length should therefore be valid within Sweden beyond the range of the "northern" morphological type. For material of Central European or more southerly origin, A_t and A_p may be overestimated by the regressions presented here. The validity of the regression of volume on length may be similarly restricted.

It is recommended that A_t, A_p and volume be estimated from needle length, expressed in millimetres, by the following regressions (Table 4):

$$A_t = 4.2235(\text{Length}) - 15.6835$$

$$A_p = 1.5992(\text{Length}) - 7.5874$$

$$\text{Volume} = \text{Length} \cdot [0.00808(\text{Length}) + 0.505]$$

If A_p is used, the restricted definition on which it is based must be borne in mind. A priori, it may be expected to predict larger values for projected area at a given mean length, than will be produced by integrating optical devices operating on randomly oriented needles. It is recommended that A_t be determined, in preference to A_p, as being a better defined and more appropriate expression for needle area.

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