Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Prospects for Improvement by Site Amelioration, Breeding, and Protection [and Discussion]

J. D. Matthews and E. J. Gibson

Phil. Trans. R. Soc. Lond. B 1975 **271**, 115-138
doi: 10.1098/rstb.1975.0039

Email alerting service Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: **http://rstb.royalsocietypublishing.org/subscriptions**

This journal is © 1975 The Royal Society

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Phil. Trans. R. Soc. Lond. B. **271**, 115–138 (1975) [115]
Printed in Great Britain

Prospects for improvement by site amelioration, breeding, and protection

By J. D. Matthews
Department of Forestry, University of Aberdeen

Five characteristics of wood that greatly effect its technical properties for joinery, structural and non-structural purposes are density, texture, grain direction, size and number of knots and fibre characteristics. These are influenced by rate of growth, straightness and taper of the stem, distribution of dry matter between foliage, branches, stem and roots and the resistance of trees to the damaging effects of wind, insects, disease and animals. The prospects for improving the yield and technical properties of wood depend mainly on climate, soil, methods of cultivation, supplementary nutrition, spacing and thinning, knowledge of genetical and physiological factors and control of insect pests, diseases and animals. There are numerous pathways to improvement and gains of 30 % over current norms appear practicable.

1. Introduction

There are several ways of improving the yield of forests in Britain. The growth of existing crops can be improved by adding nutrients and applying the well-tried techniques of thinning so as to concentrate increment on good stems. Site amelioration involving cultivation, drainage, supplementary nutrition and weed control can speed the establishment and subsequent growth of plantations. Tree breeding provides a means of producing improved cultivars capable of yielding timber with properties suited to a wide range of end uses.

Much timber is lost through the effects of wind, the attacks of insects and diseases and through damage by animals such as squirrels and deer. Increased knowledge of the reaction of trees to wind and other site factors and of the biology of damaging insects, diseases and animals can be applied in forest practice to reduce losses. Finally, there are the possibilities provided by more efficient and complete harvesting and utilization of trees.

In this paper some promising ways of improving yield are examined and their future potential assessed. It is already evident that on many sites the quantity of wood produced can be increased and its technical properties improved, but there are still wide gaps in our knowledge of the genetics and physiology of trees that must be filled before the full potential of many species and sites can be realized. The end uses of timber and the relationship of technical properties to certain characteristics of wood are described. The variation in such characteristics within trees is described and the requirements that should be met by the grower are listed. Advances in silviculture and forest genetics are dealt with and future possibilities appraised. Greatest attention is given to the larger sizes of trees. Some reference is made to the so-called 'small roundwood' but most silviculture in Britain is directed to the production of sawlogs, for which there is a very large market. It must also be stressed that because foresters in Britain have concentrated during the past half century on the silviculture of conifers most information is available for these species. But much of the knowledge gained can also be applied to broad-leaved trees and indeed has already been so applied.

The Royal Society is collaborating with JSTOR to digitize, preserve, and extend access to
Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences.
www.jstor.org

Downloaded from rstb.royalsocietypublishing.org

2. THE NEEDS OF FOREST INDUSTRIES

Three major consumers of solid timber in Britain are the industries using it for joinery, structural and non-structural purposes. In 1972 members of these sections of industry met growers of timber and from this discussion (Holmes 1973; Brazier 1973) there emerged several conclusions important to the theme of this paper.

Although their specifications differ in detail, these large users can describe the timber they are seeking in terms of its strength, behaviour during drying, stability in service, performance during sawing and machining, its capacity to take nails and hold them and its durability and treatability with preservatives. Each manufacturer and construction enterprise needs a supply of battens, boards, box shooks or pallet wood cut and finished to the correct sizes and with technical properties close to specification. For structural purposes mechanical stress grading, which exploits the relation between the strength of timber and its modulus of elasticity, provides a reliable way of grading wood and the phrase 'tested timber' has a distinct marketing advantage (Endersby 1974).

The technical properties of timber depend on several measurable wood characteristics. There is a close relation between strength properties and the density of the timber – the denser pines (*Pinus* spp.), larches (*Larix* spp.) and Douglas fir (*Pseudotsuga taxifolia*) being stronger and stiffer than the less dense spruces (*Picea* spp.), Silver firs (*Abies* spp.) and Western hemlock (*Tsuga heterophylla*). The grain of timber is not always straight and when it is inclined from the vertical strength is reduced, because of the way in which logs normally are converted. Strength also is affected by the size and number of knots, being greatest when the knots are small, few and dispersed and weakest when they are large, numerous and clustered in whorls. The strength of timber is related to the structure and organization of the constituent cells. In conifers the tracheids are especially influential, comprising as they do the great bulk of the timber. Important factors are tracheid length, wall thickness and structure of the cell wall.

Timber for external use, such as cladding buildings, is dried to a moisture content of 15–20 %; that used within buildings must be dried until the moisture content is 10–12 %. As it is dried the timber shrinks – more in the transverse than in the longitudinal direction – and the amount of shrinkage and final shape and condition of a piece depend on its density, the direction of the grain (whether straight or inclined) and the dimensions, structure and organization of the constituent cells. When placed in its final position the timber must remain stable and the most important factors affecting stability in service are the direction of the grain and the dimensions, structure and organization of the wood cells.

The ease with which timber can be sawn and machined depends on its density, texture (resulting from density variation within and between annual growth rings), inclination of the grain and the size and number of knots. A timber which is light, of even texture, straight-grained and with few small knots is easier to saw and finish than one which is dense, varied in texture, with crooked grain and many large knots. When timber is made into boxes and constructional components such as roof trusses, it is nailed or fastened in various ways and so must readily take nails or fasteners without splitting, and hold them. The characters of timber which influence nailing and nail holding are density and texture.

Some timbers are selected because they are naturally durable, the most durable part being the heartwood and the least durable being the sapwood. The less durable timbers can be impregnated with chemicals to raise their resistance to decay and to damage by insects,

Downloaded from rstb.royalsocietypublishing.org

treatability being dependent on the permeability of timber to gases and liquids. This in turn is governed by characteristics of the cells, and in conifers the number and structure of the bordered pits in the walls of the tracheids are particularly important (Petty 1970).

3. Variation in wood characteristics within trees

It will be seen that the five important features of wood that affect technical properties are density, texture, grain direction, knot size and number, and fibre characteristics. Each of these is now examined with particular emphasis on their variation within trees.

In describing the characteristics of timber produced by plantation-grown conifers it has proved necessary to divide the stem into at least two zones about the pith – an inner 'core' or 'juvenile' zone and an outer 'adult' zone. The zone of corewood, centred on the pith, extends from base to apex of the tree and outwards from between 5 and 15 annual rings, being related to age rather than to linear distance from the pith. 'It has been proposed that the core wood should be defined as the wood formed within the immediate environment of the live crown' (Elliott 1970). The zone of corewood also is coincident with the inner heartwood.

(a) *Texture*

As already noted, important benefits can accrue from reduced variability in density within and between annual rings because an even distribution of density results in even-textured wood, which in turn tends to give less degrada in drying, less splitting on nailing, improved surface-finishing on planing and, in the manufacture of pulp and paper, more uniform sheet properties.

In conifers, the tracheids of the earliest formed wood in one annual ring have a greater radial diameter and a thinner wall than those differentiated later in the season. The terms 'early-wood' and 'late-wood' are used respectively to distinguish between the initially less dense and the subsequently more dense wood formed during a season's growth. Within a given annual ring, cells of late-wood type appear first in the lower stem and gradually extend to higher levels as the annual cycle of growth progresses.

Many conifers, such as Scots pine (*Pinus sylvestris*), the larches and Douglas fir, within an annual ring show a clearly defined zone of late-wood with density more than twice that of the early-wood. In such species density of the early-wood decreases from the pith outwards while the density of the late-wood increases from the pith, over a period comparable with corewood formation. In Norway and Sitka spruce (*Picea abies* and *P. sitchensis*) and the Silver firs, the late-wood is not so clearly defined; moreover there is no substantial development of late-wood in the zone of corewood. Outside the zone of corewood in both groups of species density of late-wood increases at an accelerating rate with increasing age so that in the zone of adult wood, whole ring density is strongly influenced by the width and density of late-wood. Brazier (1970*a*) has suggested that in Sitka spruce attention should be directed in silviculture and breeding to raising the minimum density of the early-wood within the zone of corewood. The possibilities of improving the properties of the timber of Sitka spruce and other species depends in part on knowledge of the physiology of cambial activity, as a brief digression will show.

New cambial activity is associated with the onset of bud activity in spring, and subsequent cambial growth and differentiation are related to the patterns of shoot growth and bud dormancy. The details of the correlation between primary and secondary growth vary between

Downloaded from rstb.royalsocietypublishing.org

ring- and diffuse-porous broadleaved trees and between these and the conifers, but attention is focused here on the conifers.

Brown (1971) has summarized the knowledge of hormonal and nutritional aspects of the formation of growth rings in seedlings and young coniferous trees as follows: 'any condition that enhances bud break, rapid shoot growth and continued leaf development, results in high levels of auxin production and large diameter cells of the early-wood type. Conversely low temperatures, drought, or short photoperiods which adversely affect shoot extension and leaf development, lower the levels of diffusible auxin, and bring about the formation of smaller or radially flattened tracheids of the late-wood type. The increase in cell wall thickening . . . may be explained in terms of seasonal assimilation. Environmental factors such as light intensity and temperature, through their effects on photosynthesis and respiration, directly affect net assimilation and the synthesis of cell wall material.' However, Brown then goes on to question whether this explanation is sufficient 'to account for the complicated patterns of cellular differentiation in older trees and especially in angiosperms that produce multiple rings or no rings at all' . . . 'It becomes increasingly more obvious that the seasonal levels of several types of growth promoters such as auxin, gibberellins and cytokynins, operating in the presence of different levels of natural inhibitors . . . control the complex physiology of differentiation and growth ring formation.'

Denne (1973*a*) studied the relations between primary and secondary growth in trees from a single provenance of Norway spruce (*Picea abies*) growing in Wales. The canopy had not yet closed, the trees were 14 years old and varied in their rate and duration of shoot elongation. Denne found, as expected, that final shoot length was closely correlated with the width of the annual ring. Both rate of shoot elongation and rate of xylem increment were correlated with mean tracheid diameter and with the tracheid diameter in comparable parts of the growth ring.

Now Brazier (1970*a*) has shown that in Sitka spruce in Britain increase in rate of growth is associated with increase in the proportion of early-wood in the annual ring, together with reduction in the minimum density and average density of the early-wood. Denne's work on Norway spruce confirms that the proportion of early-wood increases as rate of shoot elongation increases and also that the amount of cell wall material per unit area of wood (wall area divided by tracheid area) decreases with increased shoot vigour. Part of the practical interest of these observations lies in the possibility of predicting wood density from measurements of the rate of shoot elongation and this point is taken up again in § 4*b* of this paper.

Considerable interest also attaches to the data collected by Denne (1973*b*) from the four Norway spruce trees with earliest bud break when compared with similar data from trees with latest bud break. The late-flushing trees began their shoot elongation about 6 weeks after the earliest, bud break in the later trees occurring when the shoots of the earliest trees had extended to about 85 % of their final length. The time difference in shoot elongation was mirrored by a difference in the time of appearance of late-wood – which became evident in the early-flushing trees some 4 weeks before that in the late-flushing trees. Denne (1974) suggests 'that the increase in wall thickness across the growth ring is due to change in substrate availability or growth regulator balance associated with the periodic growth of shoots or roots, and not due to the direct effect of light or temperature on wall thickening'.

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(*b*) *Density*

The density of a dry piece of timber (calculated from oven dry mass divided by green volume) indicates the amount of wood substance contained in it. In anatomical terms density is a function of the ratio of cell wall volume to cell void volume and consequently is affected by the structure of the cell wall, the dimensions of the cell and lumen, the amount of resin and extractives present and the volume of non-fibrous elements such as medullary rays.

The pattern of variation in density of annual rings in coniferous trees has been thoroughly described by Elliott (1970), who based his review of published information on a three-part system of sampling, devised by Duff & Nolan (1953, 1957). The latter comprised an oblique series sampled within a given annual ring down the stem from the apex, a horizontal series outward from the pith within a given internode and a vertical series at a given number of rings from the pith at different internodes.

When variation in density with height in the stem is considered (in the vertical series), two basic patterns can be recognized. In the area close to the pith (that is, in the 'core' or 'juvenile' zone) the vertical variation in density is slight. Outside this zone the density of whole rings increases with decreasing height in the tree.

When an annual ring is sampled within the oblique series, the density of the whole ring decreases initially with increasing number of internodes from the apex of the tree until a minimum value is reached at or near the limit of the live crown. Thereafter density of the whole ring increases down the stem.

In the horizontal series of the three-part sampling system, the density varies considerably within a given horizontal section of the tree as distance from the pith increases. Coincident changes also occur in the width of the annual ring, the proportion of late-wood in each ring and in the dimensions of the tracheids. Elliott (1970) makes a neat summary of a complex situation when he writes: 'density at first decreases to a minimum within the first 15 rings from the pith and thereafter increases, whereas ring width at first increases to a maximum between 3 and 12 rings from the pith and decreases thereafter'. But Panshin & de Zeeuw (1970) show that this pattern of change in density, although common in the conifers, is not universal and give examples of three other patterns.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

(*c*) *Fibre characteristics*

Dinwoodie (1961) summarized much of the evidence then existing on the pattern of variation within conifers and broadleaved trees in the length of tracheids and fibres. Taking first the variation in tracheid length across an annual ring, the average cell length of the late-wood is always greater than that of the early-wood, the percentage difference being lower in the conifers than in broadleaved trees. But the variation across the growth ring is seldom linear in mature timber and it is possible to find both very long and very short cells in the middle of the ring. In Sitka spruce, Dinwoodie (1963) found that, except for the first three rings from the pith in which tracheid length increases linearly across the ring, the last formed tracheids are 5–11 % longer than those at the beginning of the ring and 17–30 % longer than those of minimum length in the centre of the ring. He concluded that the location of minimum tracheid length in this species coincided with the boundary between early and late-wood.

According to Dinwoodie (1961) every investigator of the variation in tracheid length outwards from the pith at any one level in the tree (the horizontal series) has found that length near the

Downloaded from rstb.royalsocietypublishing.org

pith is very short (0.5–1.5 mm in conifers) but increases rapidly outwards in the first few rings; after this the rate of increase declines until a maximum tracheid length is attained which it generally from three to five times greater than the initial length. In young plantation-grown conifers there is an *apparent* maximum tracheid length; according to Brazier (1967) it occurs at about the 26th ring in Sitka spruce in Britain. Thereafter there are minor fluctuations in tracheid length which are caused by variations in rate of growth.

Within a given annual ring (the oblique series) tracheid length increases upwards in the stem for a certain distance and then progressively decreases, the average length at the top of each ring being generally less than that at ground level. In Sitka spruce the position of maximum tracheid length occurs at about one third the height of the tree.

Finally, there is variation in tracheid length upwards in rings at a fixed distance from the pith (the vertical series). With the exception of the first ring from the pith, tracheid length increases with increasing height up to some point in the stem, after which length remains constant.

Dinwoodie (1961) recorded considerable divergence of opinion about the relation between cell length and rate of growth but Brazier (1967) from his examination of 12 mm core samples from 116 trees of Sitka spruce growing on 19 sites located on the western side of Britain considered that rate of growth, expressed either as size of stem or width of annual ring, had little effect on tracheid length. He also showed that tracheid length and width varied independently of each other, as also did tracheid length and density. Thus it is possible to select trees with either long or narrow or long and wide tracheids and to raise density without reducing cell length. However, density and cell width were negatively correlated and selection for high density would tend to produce wood with narrow cells.

(*d*) *Reaction wood*

One important cause of variation of timber properties within trees is the occurrence of reaction wood – an abnormal type of tissue with distinctive anatomical characteristics. Compression wood, the reaction wood of conifers, is found typically on the lower side of leaning or crooked stems and of branches. Tension wood, the reaction wood of broadleaved trees, occurs typically on the upperside of the same organs.

In conifers, compression wood appears as concentric, crescent-shaped zones conformable with the annual rings and giving the appearance of unusually wide bands of late-wood. Compression wood tracheids are shorter than normal. In comparison with the three-layered structure (outer S 1, middle S 2 and inner S 3) present in normal tracheids, the secondary wall of compression wood tracheids consists only of two layers, corresponding to the S 1 and S 2 layers. The inner layer, corresponding to the normal S 3 layer, is absent or only feebly developed.

The most important defect of compression wood is its very high longitudinal shrinkage on drying, and this was considered by Dadswell (1960) to be caused by two special features of the structure of the S 2 layer of the cell wall, the first being the abnormally large angle at which the microfibrils are inclined to the long axis of the cell and the second being 'a radial discontinuity of structure' which is visible as spiral markings in the cell walls.

When compression wood and normal wood are present in the same piece of timber the exceptionally high longitudinal shrinkage of the former may lead to serious distortion or splitting during seasoning.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

Compression wood has a higher lignin and lower cellulose content than normal wood and for a wide range of species most of the strength properties are generally lower than would have been expected for normal wood of similar density. Because of its greater density, compression wood is more difficult to work and nail than normal wood, and in both sulphate (alkaline) and sulphite (acid) pulping the higher lignin and lower cellulose content adversely affect the yield, chemical purity, bleach requirements and strength of pulp.

The experimental studies on the factors affecting compression wood formation have included its induction in vertical stems by application of the hormone indoleacetic acid and have led to the suggestion that compression wood has a regulatory function, being stimulated by the disturbance of an inherent equilibrium between the various parts of the tree crown, the orientation of the equilibrium pattern being established by gravity and controlled by the distribution of growth substances (see Low 1964).

In trees exposed to a strong prevailing wind, compression wood may be developed on the leeside as a result of their stems becoming inclined. The information on the amount and distribution of compression wood within trees is limited and conflicting (Low 1964) but it appears to occur more commonly near the base than in the higher parts of the stem. Information on the relation between the deviation of the stem from the vertical and the proportion of compression wood is also limited, but it does seem that straight and cylindrical stems often are associated with localized and mild development of compression wood.

(*e*) *Stem characteristics*

Four important attributes of tree stems (in addition to knot size and number) are size, circularity in cross section, straightness and taper. These greatly affect the efficiency of conversion and the quantity and quality of the output of sawn timber and other products (Juvonen 1961).

If the taper is assumed to remain constant, size of log is defined by the diameters at top and bottom and length. For logs of the same grade, the proportion of the original log 'recovered' as sawn material rises with increasing diameter due to sawing wider and thicker boards with less waste in the form of sawdust. Each sawmiller must determine the minimum size of log he can profitably convert and the maximum size he can profitably handle and between these limits he will seek logs that are straight and with a low rate of taper.

Straightness is important because the recovery of boards and battens from a given size of log falls as crookedness of stem increases. Dobie (1964*a*) studied the output and quality of sawn timber from Douglas fir logs in British Columbia and reported that crooked logs yielded on average 15% less sawn timber than straight logs of the same top diameter and length. The effects of slight crookedness can be reduced by sawing techniques but Dobie (1964*a*) found that his crooked logs required 40% more time at the head saw than straight logs to produce equivalent volumes of sawn timber. Reaction wood is associated with crookedness and Hallock & Jaeger (1964) have shown that the accuracy of sawing suffers when compression wood occurs. Moreover the sawn timber can have a hard surface and this makes the pieces less acceptable.

Concerning length of log Grayson (1961) found that for a given diameter a longer log can be sawn at a lower cost per unit of production, and a long length of clear bole also carries many advantages in harvesting as well as in primary conversion.

Larson (1963) defined stem taper as the rate of change in stem diameter with increasing tree height. The rate of change in stem diameter is extremely variable and it is necessary to consider

Downloaded from rstb.royalsocietypublishing.org

the tree as having three parts – the crown, the clear bole and the butt or root swell. The taper of the clear bole depends on its length as well as diameter at top and bottom. Logs with rapid taper take longer to convert and yield more small sized material than logs with low taper and Dobie (1964*b*) reported that in Douglas fir in British Columbia it took 12 % longer to convert the logs with rapid taper because of the increased amount of re-sawing. According to Sunley (1963) two other difficulties associated with rapid taper are, first, that grain inclination is increased in the sawn pieces thus reducing their capacity to bear loads, and secondly, that it is more difficult to avoid the occurrence of 'wane' (irregular edges to cut pieces).

Variation in stem taper within trees is 'reasonably well correlated with crown size and the length of the branch free bole' and Larson (1963) described these relations:

'The stem within the crown is strongly tapered because of the progressive increase in branch numbers downward from the apex and the cumulative contribution of these branches to stem growth.

'In open-grown trees with long, vigorous crowns the rapid stem taper either continues or diminishes rather slowly down the branch-free bole. As the crown base recedes upwards and the clear bole elongates with increasing tree age or stand closure the stem becomes more cylindrical. This tendency towards cylindricity results from a concentration of growth in the general vicinity of the crown base although many factors influence the overall distribution. As a rule, favourable growth conditions tend to shift increment downward on the stem whereas unfavourable conditions shift stem increment upward. The greater cylindricity of lesser crown classes as opposed to dominants or the downward progression of annual increments during extremely favourable growth seasons, for example, may be explained on this basis. These rules, however, are by no means immutable, and unfavourable factors, such as poor site, may frequently promote stem taper, particularly when the unfavourable conditions strongly suppress height growth.'

(*f*) *Knot size and number*

Size and number of knots and the incidence of reaction wood and distorted grain associated with knots are mainly the result of the diameter of the branches, the angle at which they are held, the number of branches per whorl, the number of whorls per year and per unit length of stem. The diameter of a branch usually is closely and positively correlated with its length, hence crown width is related to branch diameter (Ehrenberg 1970). Branches with flat angles are more easily shed and more rapidly occluded and trees with such branches have a smaller volume of knot wood than those with steeper branch angles.

The habit of branching determines the number of apical meristems actively engaged in leaf production. In the early stages of the growth of trees the number of branches is small. As the tree increases in size and complexity of branching the number of shoot apices producing leaves also increases and this in turn is closely related to the growth rate of the tree.

Thompson (1974) compared the elongation of shoots in two provenances of Lodgepole pine (*Pinus contorta*) in an 11 year old plantation on a heathland site in northeast Scotland. The superior rate of height growth of the coastal 'Long Beach' trees with a uni-cyclic branching habit when compared with that of inland 'Fort Fraser' trees with the same habit was associated with a greater production of needle primordia, which in turn raised the total amount of foliage. 'Long Beach' trees produced more secondary branches than was found in 'Fort Fraser' trees. Both provenances displayed similar mass ratios of branch + stem to foliage but 'Long Beach' trees produced proportionately more branch wood for a given mass of needles.

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Particularly in 'Long Beach' provenance, trees showing superior growth in stem height, volume and dry mass had greater-than-average numbers of primary branches but relatively fewer secondary branches.

(g) *Spiral grain*

Reduction in the number of trees with marked spiral grain should contribute to improved timber quality because trees with spiral grain give on conversion timber which twists on drying, requires more care in machining and has reduced strength properties in comparison with more nearly straight-grained wood of comparable density. Brazier (1967) examined cross sectional disks taken at breast height from 180 trees of Sitka spruce growing on 18 sites throughout Britain. The age varied from 30 to 37 years and the pattern of variation in grain angle (that is, the angle made by the tracheids in relation to the main axis of the tree) was measured along a randomly selected diameter.

In young growth, the spiral was characteristically left-handed or clockwise and increased for 5–10 years, with thereafter a gradual decrease in grain angle with increase in size of tree. According to Brazier (1967) this is a familiar pattern observed in many conifers. Individual trees differed 'in the age at which a maximum grain inclination is reached and although the pattern of grain change described is the most common others occur. Thus, in some trees, grain inclination remains fairly constant or exceptionally shows a gradual increase from the juvenile wood outward to the bark . . . .' Brazier also compared the average grain angle at similar ages of two populations, one chosen for its outstanding rate of growth and the other for its generally slow rate of growth. The pattern of grain change was similar for both, reaching a peak in the zone of corewood and thereafter decreasing slowly in the vigorous trees and more rapidly in the slow grown trees, but at comparable ages the vigorous trees had a consistently greater grain inclination. This tendency for greater spirality to be associated with fast growth has been recorded for other species.

4. The grower's response

Consideration of the information presented thus far makes it possible to describe trees and crops that will produce timber meeting the needs of many end users and enabling the harvesting and primary processing sections of the forestry industry to operate more efficiently.

The first requirement is for rapid rate of growth in height and diameter to large dimensions. The upper limit of current annual increment might be set at 4 annual growth rings per 25 mm to meet the needs of British Standard 4978 for timber used in building. Sitka spruce is one of the faster-growing species in Britain, and the sample of logs from 18 sites throughout the country examined by Broughton (1962) had 3.7–7.9 annual rings per 25 mm with a mean of 6 per 25 mm at 30–37 years of age. The crops from which these samples were taken ranged in metric yield class from 12–24 and it seems that a metric yield class of 20 could still give a high output of trees with more than 4 rings per 25 mm.

Secondly, the stems should be straight and circular in cross section and show a low rate of taper – this making necessary a long length of clear bole for a given breast height diameter. The incidence of spiral grain and its angle should be low.

Thirdly, the distribution of dry matter between foliage, branches, stem and roots should favour stem and roots rather than branches. The branches should be small in diameter, flat in angle and few in number when judged against the growth rate of the tree.

Fourthly, the density and tracheid characteristics of the tree should, within the limits set

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

by the innate propensities of the species, be as uniform as possible, within and between annual growth rings. In Sitka spruce the main need is to raise the basic density of the early-wood.

Fifthly, the tree should possess resistance to the effects of wind, be resistant to the attacks of the most damaging insects and disease organisms and show good recovery from the damage done by animals.

The prospects for meeting these requirements are governed by climate and soil, the silvicultural techniques devised by foresters, the genetical and physiological characteristics of the trees being grown and the damage done by diseases, insects and animals which attack the trees. Each of these is now examined with emphasis on those factors having greatest effect on the amount and technical properties of the timber produced.

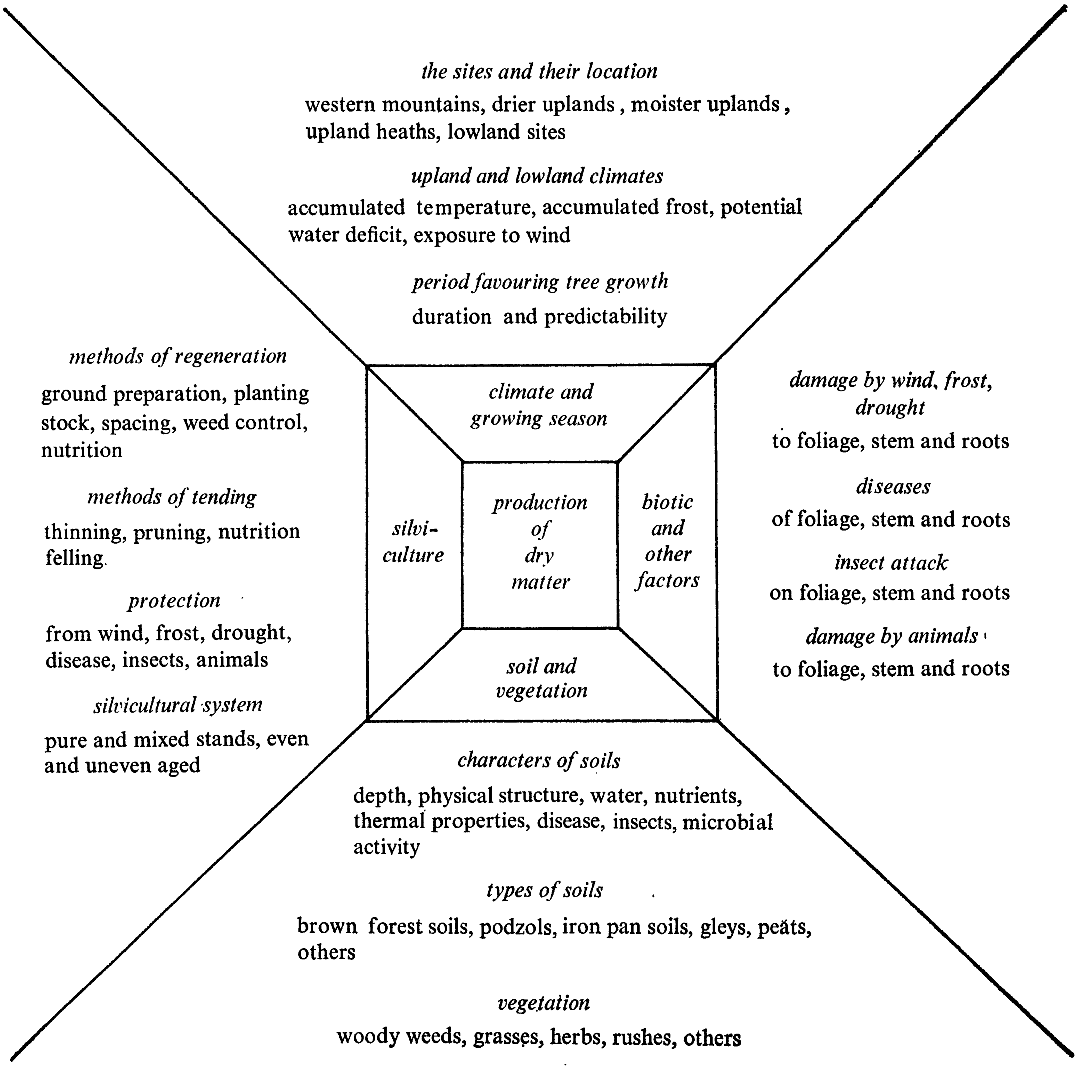

Figure 1. Environmental factors affecting the productivity of trees.

(*a*) *Climate*

In Britain much of the land readily available for forestry lies at relatively high altitudes and the climate and soils of the uplands strongly influence the amount and technical properties of the timber that can be grown.

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

In the British Isles generally – and particularly in Scotland – climate is influenced by increasing altitude. Temperature and sunshine decrease; rainfall, liability to frost and snow and, broadly speaking, windiness, all increase; the onset of the 'growing season' is progressively delayed and its total length reduced. Because of the general lower level of temperature in Scotland, the critical temperature thresholds of 5.6 °C at which plant growth commences and 0 °C at which frost damage can occur will be reached at lower altitudes than farther south, hence land subjected to low temperature hazards will be encountered at lower altitudes in Scotland than in England (Meteorological Office 1972).

The deterioration in climate associated with increasing altitude is matched by a reduction in rate of tree growth and range of species that can be grown and, in the absence of the appropriate silviculture treatments, by deterioration in some of those characters of trees which affect timber properties. Malcolm & Studholme (1972) assessed the performance of trial plantations of Sitka spruce and European larch (*Larix decidua*) planted before 1945 on 17 sites above 460 m in Scotland. They found that the most marked effect of increasing altitude on Sitka spruce was reduction in height growth and they used additional data to show that 'for areas of marked relief the reduction is linear (with altitude) from sea level upwards'. But the reduction in yield of timber was not so great because trees at the higher altitudes had larger stem diameters than would normally be expected from their heights. This change in the relation of stem diameter to height was also seen in the European larch plantations, but whereas the taper of the stems of Sitka spruce became more rapid with increasing altitude that of the stems of European larch did not alter. Mayhead (1973) also studied the effect of altitude on yield class of Sitka spruce and his data were drawn from plantations growing throughout Great Britain. Mayhead reported that the decrease in yield class with rise in altitude, as expressed by linear repression equations, was not constant for the whole of Britain but was most pronounced in the northern parts and least in south west England. It follows that upper limits for tree growth will also differ, and if a metric yield class of 7 is taken as a minimum for profitable plantations (Hummel & Grayson 1962) the limits for Sitka spruce appear to be 550 m in Scotland and 600 m in England and Wales.

It has proved difficult to explain the effects of altitude on tree growth because not only do all the climatic elements change but soil type also is closely related to altitude. Anderson & Edwards (1955) stressed the importance of exposure to wind and of air and soil temperatures and the first of these has received much attention. Birse & Robertson (1970) defined 'exposure' as 'the influence of air movement over an extended period of time on the development and survival of living organisms. It is the velocity of the air movement together with such parameters of the air mass as salt content near the coast, temperature at high altitude and relative humidity, which accentuate or diminish its effect.'

Millard (1974) made a detailed study of the production of dry matter and its distribution between foliage, branches, stem and roots in Sitka spruce planted in 1964 at Durris forest, Aberdeenshire. The trees were growing at four altitudes ranging from 240 to 330 m on two vegetation types. Millard assessed exposure to wind, tree growth and nutrient status and considered that much of the variation in dry matter production could be attributed to the variation in exposure to wind. Total dry matter production on the lowest, most sheltered grass heath site exceeded that on the highest and most exposed grass heath site by 3.3 times, despite the closely similar quantities at the two altitudes of nitrogen, phosphorus and magnesium in the foliage of the trees and in the soil. The exposure to wind was assessed by the reduction in area of

Downloaded from rstb.royalsocietypublishing.org

standard pieces of fabric (tatter flags), the rates being 1.5 cm²/day at 240 m and 3.9 cm²/day at 330 m.

Exposure affects tree growth in mechanical and physiological ways. Whitehead (1968) considered that the main physiological effects result from disturbance of the internal water balance of trees and the development of water deficits even under conditions of good supply of soil moisture. Fourt (1968) grew 'one-plus-one' transplants of Sitka spruce for 6 months and subjected them to three moisture regimes and three levels of side shelter. The trees receiving shelter combined with plentiful soil water grew best and height growth decreased progressively with restrictions on both shelter and soil water. Both these treatments affected the internal water balance of the plants and Fourt suggested that they responded by closure of stomata with consequent reduction in photosynthesis.

As already noted in §3*d*, wind induces the formation of reaction wood, thus increasing the variability of the timber. Low (1964) obtained samples from 114 trees representing four size classes in seven Scots pine plantations 24–40 years old in northeast Scotland. He estimated that the amount of compression wood in these trees comprised from 5.4 to 57.1 % of the total under bark volume to a top diameter of 7 cm. In the seven stands sampled from 21 to 41 % of total timber volume consisted of compression wood and Low concluded that its formation was largely due to the prevailing winds having at an early age caused the stems to lean.

Strong winds also blow down tree crops and much work has been done to establish the relation between soil type, rooting habit and stability of crops (Pyatt 1968). Windthrow occurs principally in shallow-rooted crops growing on soils with impeded drainage. Damage becomes important after a critical top height has been attained and some estimates of the windthrow hazard on different soil types in Wales (Pyatt, Harrison & Ford 1969) have been expressed in terms of the likelihood of some damage occurring before or after the tree crops have attained heights of 18 m. Armstrong & Read (1973) compared soil aeration and water potential with yield and stability of Sitka spruce on a peaty-gley soil in the Kielder region of Northumberland and found a strong positive correlation between the oxygen status of the soil in the winter and early part of the growing season and such factors as crop stability, stem and root mass and the diameter of the stem at breast height (1.3 m) and mid height. The survey and analysis by Neustein (1971) of the damage done by the very severe westerly gale which blew across central Scotland on 15 January 1968 emphasized the influence of topography on windthrow in the more mountainous western forests. In the smoother topography of the central and eastern spruce forests shallow rooted crops were the most vulnerable.

The deleterious effects on timber production of exposure to wind can be reduced by several silvicultural techniques. First in importance when forming plantations is selection of species, provenances and cultivars resistant to the mechanical and physiological effects of wind. Sitka spruce has long been thought of as a species resistant to defoliation and deformation of the stem (Zehetmeyr, 1954) although in windy conditions Sitka spruce does suffer mechanical damage, particularly in early summer when fresh laterals and leaders are readily broken (Malcolm & Studholme 1972). Bending of the lower part of the stem, called basal sweep, is a widespread defect of trees growing in the climate of northern Britain and in areas subject to frequent gale-force winds Lodgepole pine of south coastal U.S.A. provenances frequently show a high incidence of basal sweep when planted on peat soils or compacted mineral soils that have not been completely cultivated. But Lines & Booth (1972) report an instance in which 6-year-old hybrid trees of Lodgepole pine derived from controlled crosses of coastal and inland provenances and

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

of similar height to south coastal trees were virtually free from basal sweep while the latter were badly swept.

A second group of silvicultural techniques involves choice of spacing at planting and subsequent control of spacing by thinnings. On sheltered ground initial spacing is determined primarily by costs, because most of the costs of establishment are reduced by widening the spacing. On exposed upland areas the early development of mutual shelter between trees is beneficial in reducing the physiological and mechanical effects of wind and, according to Low (1973), 1.8 × 1.8 m is now a common spacing on such sites. Initial spacing does not appear to affect stability of crops, this being more dependent on subsequent thinning practice.

A third and very important technique is cultivation, which in combination with drainage, supplementary nutrition and control of competing vegetation has greatly improved the establishment and subsequent growth of plantations in the uplands of Britain. The objects of cultivation and drainage are to encourage the development of roots and improve the growth of trees by regulating the movement of water, improving soil aeration, reducing compaction and mobilizing nutrients, especially nitrogen (Taylor 1970). Cultivation can also improve the establishment of tree crops by providing planting spots with a loosened soil, reducing competition from the natural vegetation and providing a favourable sheltered micro-climate for the young trees. Better survival of the young trees, quicker and more uniform early growth, earlier yield of timber and better stability to wind are important benefits which can accrue from cultivation and drainage.

(*b*) *Soils and cultivation*

The extent to which the objects of cultivation and drainage can be achieved and the kind of ploughing depend on the limiting features of the soil, and Taylor (1970) and Pyatt (1970) have related soils and ploughing practice in detail.

The development of *brown earths* is associated with base-rich rocks, permeable loamy-textured drifts, steep slopes, low rainfall, low altitudes and southerly aspects. Brown earths provide many of the best soils available for forestry in upland Britain but there are shallow variants overlying bedrock or indurated parent material. In the latter case additional depth of rooting to increase crop stability may be gained by deep ploughing. Superficial ploughing to suppress vigorous and dense swards of grass often is justified. Although fertilization at planting is not usual, responses to applications of phosphorus and other elements may be obtained as the trees grow older.

The true *podzols* are freely drained and give good conditions for rooting, but variants with compact or cemented subsoils at relatively shallow depth are common. On these latter soils ploughing is done to destroy the surface matt of ericaceous vegetation and mix the markedly stratified upper soil horizons, so providing better rooting conditions.

The essential features of *iron pan soils* are the presence of a horizon which is waterlogged for substantial periods and which rests sharply on a thin ironpan. There may also be a peaty upper horizon with thicknesses up to 45 cm. The object of ploughing is to shatter the ironpan, aerate the surface peat and destroy the surface matt of vegetation, in which heather (*Calluna vulgaris*) often is the dominant species. It is on the ironpan soils that the benefits of cultivation have been most clear cut.

On *surface water gleys with clay subsoils* a peaty overburden often is present and vertical drainage is impeded. Without adequate drainage the root systems of most tree species are severely restricted and early windthrow may be expected. These are difficult soils to improve for tree

Downloaded from rstb.royalsocietypublishing.org

growth and a combination of turf ploughing and drainage is needed. Phosphorus must be applied at planting. The *surface water gleys with indurated subsoils* also have a perched water table. The indurated horizon restricts the downward movement of water and presents an impenetrable barrier to roots. If the depth of relatively loose material over the induration is sufficient, drainage alone may provide conditions adequate for the stability of trees, but in many cases the depth of rootable soil is insufficient and must be increased by cultivation. Lodgepole pine and Sitka spruce are the main species and both phosphorus and potassium are needed to sustain their growth. *Ground water gleys* are of limited occurrence in upland forest areas but *deep peats* or bogs are very plentiful. The depth of peat exceeds 45 cm and the underlying mineral material usually is beyond the reach of tree roots. Peats vary considerably in their nutrient status, in composition and in the degree of humification but all are difficult to drain because of the slow rate of water movement within them. It is necessary to recognize five main types:

(1) Fen peat, which accumulates on sites flushed by water from calcareous rocks.

(2) Flushed basin peat, occurring in basins or concave sloping sites where there is strong flushing from non-calcareous rocks. Phosphate fertilizer is applied at tree planting and potash usually is needed later.

(3) Molinia bog, usually seen in concave sloping sites, the characteristic species being *Molinia coerulea*. Phosphate fertilizer is applied at planting and potash usually is needed later. Additional phosphorus may also be needed to sustain the growth of spruce.

(4) Un-flushed sphagnum bog develops from the previous types when the accumulation of peat raises the bog surface above the influence of flushing. This type of peat is very low in nitrogen, phosphorus and potassium and repeated applications of all three nutrients are needed for sustained growth of spruce.

(5) Hill peat or un-flushed slope bog is found on flattish or convex hilltops or slopes which may exceed 5°. In Scotland and northern England the vegetation often is dominated by heather; in Wales *Vaccinium myrtillus* may replace *Calluna*. Phosphorus is essential when trees are planted; potassium is required at an early stage and subsequent applications of NPK may be needed to sustain the growth of spruce.

Drainage is essential for the deep peats and is accomplished by a combination of turf ploughing, to provide well-aerated planting sites, and more widely spaced deep drains for subsoil drainage.

Soils on calcareous rocks are slightly or moderately acid, and often are shallow and subject to drought. Shallow ploughing to suppress natural vegetation is done, but not deep ploughing.

Taylor (1970) presented data for the response of Sitka spruce during 20 years to cultivation of ironpan soils in northeast Scotland, where the ground vegetation had been dominated by *Calluna vulgaris*. Increasing the volume of soil disturbed by 3.1 times from 1100 to 3500 m^3/ha raised the metric yield class from 7 to 11. All the trees were given phosphorus at planting and in all cases the Sitka spruce was grown in mixture with either Scots pine or larch to reduce the competition from the heather. But tree crops are not completely harvested for at least 40 years and an important question for the forest manager is the duration of improved growth of trees following cultivation. All the major cultivation experiments of the Forestry Commission's Research Division are being closely followed and Savaser (1972) assessed height and diameter increment and the fresh masses of foliage, branches, stem and roots of Sitka spruce and Scots pine growing in an experiment established in 1946 on upland heath at Fetteresso forest, Kincardineshire. The soil was a peaty gleyed podzol with an indurated subsoil at 40 cm and

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

had been cultivated to three intensities by deep spaced furrows 1.5 m apart to a depth of 30–37 cm, shallow complete ploughing to 13–18 cm and deep complete ploughing to 30–37 cm. Savaser found no evidence of a fall in volume increment in Sitka spruce at 25 years.

One cultivation experiment which has greatly influenced silviculture on the upland heaths of eastern Britain was established at Teindland forest in Morayshire, to compare the effects of six types and intensities of cultivation on the growth of Scots pine, a mixture of Lodgepole pine and Japanese larch (*Larix leptolepis*) and four possible alternative species, Douglas fir, Sitka spruce, Norway spruce and Western hemlock all grown in mixture with Japanese larch. When analysing progress after 20 years Thomson & Neustein (1973) considered that the Lodgepole pine – Japanese larch mixed crop had gained 20–25 % in timber volume over the less intensive treatments, but from 15 to 20 years the current increment in stem height and diameter had fallen below that of trees on the spaced furrow and shallow complete cultivation treatments. However, an application of PK fertilizer made before the start of the 19th year might be correcting this trend.

A further stage of development of cultivation and drainage is in progress in which ploughs capable of penetrating to a depth of 90 cm are being tested and the method and intensity of cultivation are being further studied. The prospects for improving yield and stability of crops from the use of cultivation and drainage remain good. On some soils supplementary nutrition and weed control are also essential techniques (Mackenzie 1974).

(*c*) *Supplementary nutrition*

Fertilizers are applied to planting stock in nurseries, when establishing plantations in the forest and to established crops at various stages in their development. The nutrition elements and the rates and proportions applied vary with climate, soil, ground vegetation, tree species and stage of development of the crops and much experimental evidence and practical experience is needed to guide the silviculturist in using supplementary nutrition to control the rates of growth of plantations and the quality of timber produced. Nevertheless steady progress is being made and Toleman & Pyatt (1974) describe how site classification is being used to guide choice of species, cultivation, supplementary nutrition and weed control.

Binns & Grayson (1967) reviewed the information then available on the fertilization of established crops and considered that the nutrient elements that can limit their growth in Britain are nitrogen (N), phosphorus (P) and potassium (K). Magnesium (Mg) deficiencies are common in forest tree nurseries and may also exist in the forest. Calcium (Ca) may be required on some deep peats but the phosphate fertilizers currently applied all contain calcium.

N, P and K may be applied singly or in combination, by hand or tractor-mounted spinners, or may be blown into the forest by compressed air or dropped from aircraft. The latter method has been extensively used to apply fertilizers to established crops (Davies 1967, 1969; Atterson & Davies 1967; Dannatt, Davies & McCavish 1971). The controlled nutrition of nursery plants has been thoroughly described by Benzian (1965) and Aldhous (1972) and the current prescriptions for supplementary nutrition in establishing plantations are recorded by Pyatt (1970) and Taylor (1970) and were summarized in § 4*d* of this paper. The intention now is to examine information on the effects of supplementary nutrition on rate of growth, stem and wood characters.

In September 1966, 400 ha of Sitka spruce plantations in Kilmory forest, Argyllshire, were top dressed with coarse Gafsa phosphate (12–13 % P) by helicopter at the rate of 375 kg/ha.

Downloaded from rstb.royalsocietypublishing.org

The trees had been planted in 1954 and 1955 at elevations of 90–240 m on a site open to westerly winds off the Atlantic ocean and with an annual rainfall between 1500 and 2000 mm per year. The soils were very variable, ranging from deep unflushed peat, through shallow peat to mineral soils derived from phyllites and mica schists and very little phosphate had been applied at planting. The tree crops were growing at an average rate equivalent to metric yield class 5–7 (Dannatt *et al.* 1971).

Four years after treatment the increments in length of the leading shoots and stem diameter were assessed and the average rate of growth was estimated as equivalent to metric yield class 14–16. Two surprises in this extensive trial were the strong response of trees on ill-drained sites as well as on the most fertile mineral soils bearing bracken, *Pteridium equilinum.*

In 1956 Lodgepole pine and Sitka spruce were planted as part of a system of shelterbelts on the newly established Peatland Experiment Station at Glenamoy in North Mayo, Eire. The trees were planted on mounds and fertilized with 57 g per plant of ground mineral phosphate (14.5 % P). Establishment and early growth were satisfactory but by 1961 the young trees had gone into the condition known as 'check'. A combined dressing of NPK, Ca and Cu was applied in the spring of 1961 and the colour of the foliage improved within 6 weeks. Mean annual growth of the leading shoot of Sitka spruce three years later was 38.6 cm for the treated trees and 12.4 cm for the untreated control (O'Hara 1967). According to Fielding (1967) the characteristic effect of an application of fertilizer which stimulates tree growth is an increase in the amount of foliage and an improvement in the colour – 'an effect in conifers, which, from the viewpoint of the relation of the crown and of auxin gradients to wood properties should be associated with increased production of earlywood cells and lower density'. In this connexion, Harding (1973) summarized the objects and results of an investigation into the density of wood produced by Sitka spruce growing at Glasfynydd forest in South Wales. The trees had been treated with combinations of NPK, Ca and Mg fertilizer in 1959 and the subsequent assessments showed that only phosphorus had caused a significant increase in volume increment, with nitrogen having the effect of reducing growth. Core samples of stemwood were taken 11 years after treatment from standing trees and disks from felled trees in plots receiving P but no N, N+P, N but no P and untreated controls. Unfortunately the effects of fertilizer application on tree growth and wood density had been confounded by an increasing tendency to eccentric growth in the trees on the whole site, but it was tentatively concluded that in plots containing P but no N the normal relation between growth rate and wood density had not been altered.

One of the most comprehensive studies on the nitrogen nutrition of polestage crops in Britain is that of Miller (1966), who applied nitrogen at 84, 168, 336 and 504 kg/ha from 1964 to 1966 to a 36 year old stand of Corsican pine (*Pinus nigra* var. *maritima* Ait) growing on the aeolian sand dunes of Culbin forest in Morayshire. Miller also applied phosphorus and potassium to all the plots to reduce the risk of secondary deficiency.

Recently Miller & Cooper (1973) described the distribution of the increases in stem growth induced by the fertilizer. When the experiment was laid out, the trees were very deficient in nitrogen and growth was declining as a mor humus layer developed, but during the 7 years to 1971 this condition had been alleviated. Height growth reached a maximum of 1.4 times that of the untreated controls when the level of nitrogen in the foliage was 1.6 %, following the application of N at 168 kg/ha for 3 years. Stem diameter growth was highest at 2.4 times the control when foliar nitrogen reached 2.2 %, the amount of N applied being 504 kg/ha for 3 years. Volume growth was highest at 2.6 times the control, the foliar nitrogen level being 2.0 %

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Downloaded from rstb.royalsocietypublishing.org

and the amount of N applied 336 kg/ha for 3 years. Stem taper altered only slightly, but usually decreased.

At present it appears that although improvements in rate of growth can follow from applications of phosphorus at planting and during the rotation (with the addition of potassium on deep peats), the influence of supplementary nutrition on other characters affecting the technical properties of timber are not yet clear. However, two points can be made: first, that fertilizers will normally be applied to slow-growing crops, mainly those below metric yield class 14 and as noted earlier a metric yield class of 20 could still give a high output of stems conforming to British Standard 4978, and secondly, that the statements made in §3*a* about the relation between shoot and cambial growth in spruce suggest that silviculturists may have a visual aid to guide them in devising fertilizer regimes which combine steady rates of tree growth with acceptable whole-ring density.

(*c*) *Spacing and thinning*

Fielding (1967) and Evert (1971) point out that the growing space available to a tree influences directly the environment of that tree and especially solar radiation, moisture, nutrients, frost and wind – factors which have a direct influence on rate of growth and the development of crown and stem. In 1935 and 1936 the Research Division of the British Forestry Commission planted more than 60 sets of plots at spacings of 0.9 m × 0.9 m, 1.4 m × 1.4 m, 1.8 × 1.8 m and 2.4 × 2.4 m and in subsequent years the factors investigated included survival, growth in height and stem diameter, stem taper and the yield of timber both in total and in assortments.

Some results obtained by Brazier (1970*b*) from one of these sets of spacing plots are important. He studied the relation between spacing and both yield and characters of the wood produced by Sitka spruce in the Forest of Ae, near Dumfries in Scotland. One series, called P, had been thinned so as to minimize the effect on the final crop of trees of differences in the initial spacings (such a treatment involves removal of many stems from the close spacings and relatively few from the wider spacings). The second series, called Q, were thinned so as to maintain or accentuate the effects of the initial spacing, thinning being minimal at the lowest initial spacing and heaviest in the widest initial spacing. The figures for total volume and drywood production appear in table 1.

Brazier concluded that when the primary concern is to produce wood substance for, say, a

Table 1. Total yields from Sitka spruce spacing plots, aged 30 years

	planting distance			
thinning treatment	2.4 m	1.8 m	1.4 m	0.9 m
P (effect minimized)				
standing crop				
volume/m^3 ha^{-1}	365	302	299	217
mass drywood/10^3 kg ha^{-1}	123	102.8	100.8	78.6
total yield to date				
volume/m^3 ha^{-1}	382	359	370	313
mass drywood/10^3 kg ha^{-1}	128.1	123	128.5	102.6
Q (effect accentuated)				
standing crop				
volume/m^3 ha^{-1}	121	145	170	311
mass drywood/10^3 ha^{-1}	41.2	54.3	59.2	118
total yield to date				
volume/m^3 ha^{-1}	224	264	282	343.5
mass drywood/10^3 kg ha^{-1}	76.3	97.7	99.8	130.6

Downloaded from rstb.royalsocietypublishing.org

pulp mill, wide initial spacing is justified. But he went on to compare the density of the wood produced by trees of three size categories grown in each spacing and thinning treatment and found that the largest trees at the wider spacings had produced a high proportion of low density timber of uncertain value for use as sawn timber. He advocated identification and removal of these trees in early thinnings so that growth increment can be concentrated on stems with higher density and one of several carefully defined systems of thinning which produces this result is that described by Macdonald (1954, 1961, 1963).

The relation between growing space and branch development is a major factor in the effect of initial spacing on wood properties. When pines are planted in Britain at spacings wider than 1.8 m × 1.8 m the branches become rather large (Low 1973). In a fast growing crop of Sitka spruce in Northern Ireland, Jack (1971) found that the number of branches per whorl at a height of 2 m on the stem rose from just over 5 at 3000 stems per hectare (1.8 m × 1.8 m) to somewhat more than 7 at 750 stems per hectare (3.6 m × 3.6 m). Klem (1952) harvested and converted Norway spruce in Norway which had been planted at spacings ranging from 1.25 m × 1.4 m to 3.5 m × 3. 5m and found that the grade yield of sawn boards decreased with increasing spacing and all the reductions in grade were due to knots.

The taper of the lower and middle parts of the stem may increase with wider initial spacing regardless of size of tree (Evert 1971; Hamilton & Christie 1974). Concerning damage and spacing Low & Taylor (1967) reported a case where widely spaced Sitka spruce had suffered more severely than closely spaced trees on a frosty site. After forming a complete canopy the crops at 2.4 m × 2.4 m showed marked stem malformation which diminished progressively to the 0.9 m × 0.9 m spacing.

To sum up, the lower limit of spacing usually is determined by economic factors and the upper limit by considerations of timber quality. It appears that in Britain the effect in wood properties becomes marked only at initial spacings wider than 2.0 m. On exposed upland areas, as already noted, 1.8 m × 1.8 m is now a common spacing.

(*d*) *Genetic and physiological factors*

In addition to the limitations imposed by climate and soil foresters may be restricting production by their choice of species and only a potentially high yielding species, provenance or cultivar is likely to respond to efforts to improve site. According to Binns *et al.* (1973), in the drier half of southern Britain at moderate elevations Corsican pine is giving way to Western hemlock and to Douglas fir on more fertile and sheltered sites. Further west Sitka spruce is the preferred species. Two other pines growing faster than Corsican pine in the south and west of England are *Pinus radiata* and *Pinus muricata* in its blue, northern form.

Wareing & Matthews (1973) identified and discussed some physiological and genetical factors determining productivity in forest trees. Dealing with the conifers they emphasized the importance of rapid production of leaves during the early stages of growth in plantations and the work of Pollard & Wareing (1968), Thompson (1974) and Cannell (1974) has defined the components of rate of increase in total leaf area in provenances of Lodgepole pine and other species. After closure of the canopy the conditions for optimal dry matter production are a high rate of photosynthesis in association with a deep crown, but a relatively narrow crown is needed to reduce stem taper and size of knots. Wareing & Matthews suggested that special attention should be given to the possibility of increasing the rate of photosynthesis at cool temperatures (see Ludlow & Jarvis 1971; Nielson *et al.* 1972).

Downloaded from rstb.royalsocietypublishing.org

Two more important factors influencing the rate of dry matter production are the pattern of the annual growth cycle in relation to the length of growing season and the ontogenetic changes occurring within the tree during its life cycle. There is ample evidence from the comparative trials of provenances of Sitka spruce and several other conifers in Britain (Lines & Mitchell 1966; Lines *et al.* 1973) of the importance of the first of these factors and of the relative ease with which it can be exploited to increase timber production. Concerning ontogenetic changes, those occurring in the zone of core wood provide one example and another is provided by the marked contrast in the patterns of current annual increment (c.a.i.) in height and stem diameter seen in Sitka spruce and Douglas fir when grown on the same site for 50 years. It is probable that increased definition and knowledge of these and other ontogenetic changes will lead to results of practical value.

Finally, Wareing & Matthews (1973) discussed the influence of the way dry matter is distributed within trees on the yield of timber and evidence is appearing which emphasizes the potential importance of this factor. In §4*b* reference was made to the work of Savaser (1972) on the growth of 25 year old Sitka spruce on a peaty gley podzol cultivated to three intensities. His figures for the ratio of root mass to shoot mass (foliage + branches + stem) on shallow and deep complete cultivation were 0.29 and 0.27, similar to those of Fraser & Gardiner (1967) for Sitka spruce on sites in Wales. By contrast the ratio of root to shoot mass on the deep spaced furrows was 0.41, emphasizing the high proportion of total mass found in the roots of trees growing on soil cultivated by this method. However, Millard (1974) in her study of the production of dry matter and its distribution within trees planted on sites at four altitudes prepared by deep spaced cultivation observed that the mean distribution of dry matter remained remarkably stable on all plots except one, where there was abnormal root development.

In tree breeding the pace and amount of progress made in producing improved cultivars depends on the effectiveness with which parent trees are selected and progenies are screened and the success in producing seed of the desired cultivars (Faulkner 1965). Tree physiologists and geneticists are required for all three parts of the process and an example is provided by the work of Samuel, Johnstone & Fletcher (1972), who made a complete dialled cross among six Sitka spruce trees and assessed several characters of the seedlings during the first growing season of an early progeny test in a glasshouse, using procedures devised by Herbert (1971). Straightness of stem, number of buds and branch angle were found to be inherited in a predominantly additive fashion while plant height, number and length of branches and total dry mass were under additive, dominance and maternal control. Use of early progeny tests such as these in the improvement of a crop grown on a rotation of 45 or more years naturally raises doubts about the permanence of superiority in youth and in this connexion an observation of Brazier (1967) is important. He compared the rate of growth of Sitka spruce trees selected as 'candidates' for use in the tree breeding programme with that of neighbouring 'satellites' and wrote: 'at all stages in their development the candidate trees exceeded the satellites in average size. This suggests that if dominance is achieved soon after establishment it is maintained at least during the 30 years or so, of early vigorous growth.'

It is essential to obtain improvements in timber properties within a framework of rapid rate of growth, good stem form and resistance to climatic and biotic damage. Henderson & Petty (1972) compared width of annual ring, density of early and late wood, and tracheid length and width of two provenances of Lodgepole pine planted in 1938 at Millbuie Forest in Easter Ross. The trees of coastal 'Long Beach' provenance had closely similar dimensions to those of inland

Downloaded from rstb.royalsocietypublishing.org

'Prince George' provenance at 34 years of age. The density of the Long Beach timber was 20 % higher but tracheid length was about 20 % lower in trees of Prince George provenance. Henderson & Petty estimated that the timber of Long Beach trees would have up to 20 % greater strength in compression and would yield about 20 % more sulphate pulp, but the tendency to basal bowing and stem crookedness, due to wind, was associated with the formation of compression wood to an extent and degree which would reduce the usefulness of the produce as structural timber.

(*e*) *Pests and diseases*

Recently Crooke (1972) reviewed the status of insect pests of conifers in Britain and made the point 'that very many of the conifers grown in Britain are exotics and it follows from this that, since many of the insects associated with these conifers are restricted to one host genus, our conifer-feeding fauna has its origin mainly, but not exclusively, in continental Europe and is already fairly large and varied'.

Crooke went on to assess the impact of these insects on the coniferous forests in Britain and concluded that no catastrophic incidents have been caused by them. He presented evidence in support of the opinion that 'any serious entomological troubles will come either from leaf-eating insects such as lepidopterous or hymenopterous defoliators or, less probably, from secondary pests such as the pinhole borers associated with crop harvesting'.

Both Crooke (1972) and Phillips (1974) were agreed that although the control of insect pests by chemical means is justified in emergency situations, in general, solutions to pest problems must be sought along other lines. For this to be so more must be learned about the population dynamics of the pest insects in the ecological conditions created by the site amelioration treatments (particularly cultivation and supplementary nutrition), harvesting practices and other techniques of forest management.

The review by Murray (1972) of the diseases of conifers in Britain omitted consideration of viruses, mycorrhizae and staining fungi and concentrated on rather more than 20 fungal diseases which are important in plantations and in the nursery. He pointed out that only in few cases has a disease precluded wholly or partially the use of a tree species, and quoted *Cronartium ribicola* on five-needled pines, *Scleroderris lagerbergii* which has limited the use of *Pinus nigra* in the uplands and in the north of Britain, larch dieback which caused so much failure in early plantings of European larch and *Fomes annosus* which limits the use of western hemlock on certain sites.

Several other diseases either limit production of nursery stock or reduce yield in plantations, but Murray (1972) emphasized that knowledge of important aspects of the biology of most common conifer diseases is still limited, thus making difficult such procedures as assessments of economic loss, forecasts of incidence of disease and genetic control. Two important exceptions to this situation were recorded by Phillips (1974). In the case of the root and butt rot fungus, *Fomes annosus*, which enters the crop mainly through stumps produced by felling operations, colonization of the stump surfaces may be largely prevented by painting them with a solution of urea. In the case of pines however, stump protection by chemical means is no longer necessary, as suspensions of oidia of the competing fungus *Peniophora gigantea* can be painted on instead. *P. gigantea* then colonizes the stump tissues and prevents the entry of *F. annosus*.

In the case of larch canker, a disease caused by the fungus *Trichoscyphella willkommii*, genetic control in practicable. European larch generally is susceptible to the disease while Japanese

Downloaded from rstb.royalsocietypublishing.org

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

larch and the first generation hybrid *Larix* × *eurolepis* are resistant. Sudeten and Polish provenances of European larch also show resistance and a breeding programme begun in Britain in 1949 has resulted in the production of cultivars showing rapid rate of growth, good stem and crown characters and resistance to the disease. Introduction of the best cultivars into general cultivation has unfortunately been delayed by difficulties in mass controlled cross-pollination.

5. The prospects for improvement

In Britain the techniques of site amelioration, that is, cultivation, drainage, supplementary nutrition, control of natural vegetation and choice of initial spacing are all intended to encourage the rapid build up of foliage which will bring young crops rapidly into the thicket stage so as to gain the benefits of high interception of light and reduced competition from the vegetation, mutual shelter between trees to reduce the effects of wind and an early appearance of marketable produce. It is inevitable that the trees in fast-grown plantations will put on a considerable volume of core wood in youth, but such plantations will ordinarily produce a greater volume of adult wood in later years than comparable slow-grown ones.

The dimensions of the zone of core wood and its volume relative to that of the whole stem are affected by the length of rotation. As the rotation lengthens the average width of ring decreases and the proportion of core wood and of wood with spiral grain both fall, while density, tracheid length and the proportion of heartwood all increase. If a short rotation is chosen the properties of the timber may be appropriate only for pulp and boards; choice of a longer rotation can result in timber suited to a wider range of products, including joinery, structural and non-structural purposes.

For conifers, rotations of 40–45 years or more are general in Britain, and if the intention is to grow structural timber this situation will continue.

In assessing the scale of improvement it is necessary:

(1) to state a reference point;

(2) consider whether the methods when used in combination are additive in their effects or not; and

(3) estimate the speed at which improvements can be gained in practice.

For improvement of the amount and properties of timber a suitable datum is provided by Johnston (1975), who gives metric yield class 5 as the national average for broadleaved species and 10 for conifers. As the emphasis in this paper is on the conifers it is necessary to confine the estimates of prospects to them.

In the short term, the gains in amount and properties of timber will be derived from improvement of existing crops. The methods to be used are drainage, supplementary nutrition, thinning, and protection from disease, insects and animals. All of these *appear* additive in their effects when used in combination but more information is needed about the interactions between them.

In the longer term, the gains will come through choice of species, provenance and cultivar coupled with spacing, cultivation and drainage, supplementary nutrition, weed control and thinning. All of these also appear additive in their effects.

Gains can also be made by increasing the proportion of total yield that is harvested, utilized and marketed. King & Smith (1974) used a tree of 30 cm diameter at breast height to demonstrate that 23 % of the total dry matter is contained in the root and stump, 22 % in the branches and top of the stem and 55 % in the harvested stem measured to a top diameter of 8 cm. When

Downloaded from rstb.royalsocietypublishing.org

the harvested stem is converted to sawn timber and pulpwood further losses occur in debarking and sawing and only 18 % of the original tree becomes sawn timber. King & Smith listed the potential markets for wood waste, which are very large.

Another important potential source of gains lies in the skills and attitudes of the managers, technicians and craftsmen engaged in forestry. Substantial advances in their productivity have already been made; continued education and training should bring more.

Consideration of the evidence presented in this paper suggest that a mean improvement in yield of 30 % is feasible, giving a national average metric yield class of 13 and a higher output of timber suited to a wide range of structural and non-structural purposes.

REFERENCES (Matthews)

Aldhous J. R. 1972 Nursery practice. *Bull. For. Comm. Lond.* **43**, 184.

Anderson, M. L. & Edwards, M. V. 1955 What are the limits of possible afforestation in Scotland? *Scott. geogr. Mag.* **71**, 94–103.

Armstrong, W. & Read, D. J. 1973 A comparison of soil aeration and water potential with yield and stability of Sitka spruce on a peaty-gley site in the Kielder region of Northumberland. *For. Commn Rep. Forest Res.* 1973, pp. 148–150.

Atterson, J. & Davies, E. J. M. 1967 Fertilisers – their use and methods of application in British forestry. *Scott. For.* **21**, 222–228.

Benzian, B. 1965 Experiments on nutritional problems in forest nurseries. *Bull. For. Commn, Lond.* **37**, 251.

Binns, W. O. & Grayson, A. J. 1967 Fertilization of established crops: prospects in Britain. *Scott. For.* **21**, 81–98.

Binns, W. O., Mackenzie, J. M., Everard, J. E. 1970 Maximum site amelioration project (Project 381). *For. Commn Rep. Forest Res.* 1970, pp. 77–78.

Binns, W. O. *et al.* 1973 Nutrition of forest crops. *For. Commn Rep. Forest Res.* 1973, 50–60.

Birse, E. L. & Robertson, L. 1970 *Assessment of climatic conditions in Scotland* 2. Based on exposure and accumulated frost. Pp. 41. Aberdeen: The Macaulay Institute for Soil Research.

Brazier, J. D. 1967 Timber improvement. I. A study of the variation in wood characteristics in young Sitka spruce. *Forestry* **40**, 117–128.

Brazier, J. D. 1970*a* Timber improvement. II. The effect of vigour on young-growth Sitka spruce. *Forestry* **43**, 135–150.

Brazier, J. D. 1970*b* The effect of spacing on the wood density and wood yields of Sitka spruce. In *The wood we grow*. Supplement to *Forestry*, pp. 22–28.

Brazier, J. D. 1973 Better softwoods from existing forests. *Commonw. Forestry Rev.* **52**, 125–132.

Broughton, J. A. H. 1962 Properties of 30–37 year old Sitka spruce timber. *Forest Prod. Res. Bull.* **48**, 24.

Brown, C. L. 1971 Secondary growth. In *Trees, structure and function*. pp. 67–123. Berlin: Springer Verlag.

Cannell, M. G. R. 1974 Production of branches and foliage by young trees of *Pinus contorta* and *Picea sitchensis*. *J. appl. Ecol.* **11**, 1091–1115.

Crooke, M. 1972 Insect pests of conifers in Britain. In *Conifers in the British Isles*, pp. 86–89. London: The Royal Horticultural Society.

Curry, W. T. & Endersby, H. J. 1965 The effect of pruning on the value of home grown softwoods. *Forest Prod. Res. Spec. Rep.* **22**, 16.

Dadswell, H. E. 1960 Tree growth–wood property inter-relationships. *Proceedings Special Field Institute: Forest Biology*. Chapel Hill, North Carolina: University of North Carolina Press.

Dannatt, N., Davies, E. J. M. & McCavish, W. J. 1971 An investigation into fertiliser response. *Scott. For.* **25**, 101–108.

Davies, E. J. M. 1967 Aerial fertilisation at Kilmory forest. *Scott. For.* **21**, 99–104.

Davies, E. J. M. 1969 Further experiences with aerial fertilisation in the West Scotland Conservancy. *Scott. For.* **23**, 87–101.

Denne, M. P. 1973*a* Tracheid dimensions in relation to shoot vigour in *Picea*. *Forestry* **46**, 117–124.

Denne, M. P. 1973*b* Cambial activity in relation to shoot growth and light intensity in *Picea abies*. *International Symposium on Dormancy in Trees*, pp. 1–8. Polish Academy of Sciences, Institute of Dendrology and Kornik Arboretum.

Denne, M. P. 1974 Effects of light intensity on tracheid dimensions in *Picea sitchensis*. *Annals Bot.* **38**, 337–345.

Dinwoodie, J. M. 1961 Tracheid and fibre length in timber. A review of literature. *Forestry* **34**, 125–144.

Dinwoodie, J. M. 1963 Variation in tracheid length in *Picea sitchensis* Carr. *Spec. Rep. Forest Prod. Res. D.S.I.R.* **16**, 55.

Dobie, J. 1964*a* Log taper related to lumber production. *Br. Columbia Lumberm.* May 1964.

Downloaded from rstb.royalsocietypublishing.org

Dobie, J. 1964*b* Log sweep and lumber production in the British Columbian interior. *Br. Columbia Lumberm.* October 1964.

Duff, G. H. & Nolan, N. J. 1953 Growth and morphogenesis in the Canadian forest species. I. The controls of cambial and apical activity in *Pinus resinosa* Ait. *Can. J. Bot.* **31**, 471–513.

Duff, G. H. & Nolan, N. J. 1957 Growth and morphogenesis in the Canadian forest species: II. *Can. J. Bot.* **35**, 527–572.

Ehrenberg, C. 1970 Breeding for timber quality. *Unasylva* **24**, 2–3.

Elliott, G. K. 1970 Wood density in conifers. *Tech. Commun. Commonw. For. Bur.* **8**, 44.

Endersby, H. J. 1974 Stress grading home-grown softwoods. Building Research Advisory Service. *BRE Information* IS 5/74, 3.

Evert, F. 1971 Spacing studies – a review. Canadian Forestry Service. Forest Management Institute. *Information Rep.* FMR-X-37, 95.

Fielding, J. M. 1967 The influence of silvicultural practices on wood properties. *Int. Rev. For. Res.* pp. 95–126.

Fourt, D. F. 1968 Sitka spruce, shelter and moisture. *For. Commn Res. Devel. Pap.* **72**, 8.

Fraser, A. I. & Gardiner, J. B. H. 1967 Rooting and stability in Sitka spruce. *For. Commn Bull.* **40**, 28.

Faulkner, R. 1965 Seed orchards in Britain. *For. Commn Rep. Forest Res.* 1964, pp. 211–243.

Grayson, A. J. 1961 Influence of log size on value. *Timber Trades J.* 75–78.

Hallock, H. & Jaeger, E. 1964 Some aspects of sawing accuracy in circular mills. *USDA Forest Service Res. Not.* FPL 029, 9.

Hamilton, G. J. & Christie, J. M. 1974 Influences of spacing on crop characteristics and yield. *For. Commn Bull.* **52**, 91.

Harding, T. 1973 The joint research programme on home grown timber, Princes Risborough Laboratory and Forestry Commission. *For. Commn Rep. Forest Res.* 1973, 139–142.

Henderson, J. & Petty, A. J. 1972 A comparison of wood properties of coastal and interior provenances of lodgepole pine. *Pinus contorta* Dougl. ex. Lond. *Forestry* **45**, 49–57.

Herbert, R. B. 1971 Development of glasshouse techniques for early progeny test procedures in forest tree breeding. *For. Commn Forest Rec.* **74**, 34.

Holmes, G. D. 1973 Wood quality – consumers' needs, growers' response. *Commonw. For. Rev.* **52**, 123–132.

Hummel, F. C. & Grayson, A. 1962 Production goals in forestry with special reference to Great Britain. *Eighth British Commonwealth Forestry Conference, East Africa*, Pp. 16.

Jack, W. H. 1971 The influence of tree spacing on Sitka spruce growth. *Irish For.* **28**, 13–27.

Johnston, D. R. 1975 Tree growth and wood production in Britain. *Phil. Trans. R. Soc. Lond.* B **271**, 101–114.

Juvonen, K. S. 1961 Recovery in sawmilling. *J. South African For. Ass.* **37**, 16–21.

Klem, G. G. 1952 The influence of spacing on wood quality. *Medd. Norske Skogsforsøkvosen* **11**, 473–506.

King, N. J. & Smith, C. A. 1974 Problems of wood-waste. *For. Home Grown Timber* **3**, 46–48.

Larson, P. R. 1963 Stem form and development in forest trees. *Forest Sci. Monogr.* **5**, 42.

Lines, R. & Mitchell, A. F. 1966 Differences in phenology of Sitka spruce provenances. *For. Commn Rep. Forest Res.* 1965, pp. 173–184.

Lines, R. & Booth, T. C. 1972 Investigation of basal-sweep of lodgepole and shore pines in Great Britain. *Forestry* **45**, 59–66.

Lines, R., Pearce, M. L. & Mitchell, A. F. 1973 Sitka spruce, IUFRO Collection. *For. Commn Rep. Forest Res.* 1973, pp. 42–44.

Low, A. J. 1964 Compression wood in conifers. A review of literature. *For. Abstr.* no. 25, 3 and 4, pp. xxxv–li.

Low, A. J. & Taylor, G. G. C. 1967 Spacing in plantations. *For. Commn. Forest Res.*, 78–79.

Low, A. J. 1973 Spacing of conifers at planting. *For. Commn. Rep. Forest Res.* 38.

Ludlow, N. M. & Jarvis, P. G. 1971 Photosynthesis in Sitka spruce *Picea sitchensis* (Bong.) Carr. I. General characteristics. *J. appl. Ecol.* **8**, 925–953.

Macdonald, J. A. B. 1954 Crown thinning in practice. *Scott. For.* **8**, 85–89.

Macdonald, J. A. B. 1961 The simple rules of the Scottish eclectic thinning method. *Scott. For.* **15**, 220–226.

Macdonald, J. A. B. 1963 Thinning to meet today's problems. *Forestry* **36**, 165–171.

Mackenzie, J. M. 1974 Fertilizer–Herbicide trials on Sitka spruce in East Scotland. *Scott. For.* **28**, 211–221.

Malcolm, D. C. & Studholme, W. P. 1972 Yield and form in high elevation stands of Sitka spruce and European larch in Scotland. *Scott. For.* **26**, 296–308.

Mayhead, G. J. 1973 The effect of altitude above sea level on the yield class of Sitka spruce. *Scott. For.* **27**, 231–237.

Meteorological Office 1972 *The climate of Scotland – a brief review.* Select Committee on Scottish Affairs, 5. Appendices to the minutes of evidence and index appendix A 36, pp. 175–187. London: H.M.S.O.

Millard, H. J. M. 1974 Factors affecting the growth of *Picea sitchensis* (Bong.) Carr. in Durris Forest Aberdeenshire. Unpublished Ph.D. thesis, University of Aberdeen.

Miller, H. G. 1966 Current research into the nitrogen nutrition of Corsican pine. In *Physiology in Forestry*, Supplement to *Forestry*, pp. 70–77.

Miller, H. G. & Cooper, J. M. 1973 Changes in amount and distribution of stem growth in pole-stage Corsican pine following application of nitrogen fertiliser. *Forestry* **46**, 157–190.

Downloaded from rstb.royalsocietypublishing.org

Murray, J. S. 1972 Diseases of conifers in Britain. In *Conifers in the British Isles*, pp. 90–98. London: The Royal Horticultural Society.

Neustein, S. A. 1971 Damage to forests in relation to topography, soil and crops. In 'Windblow of Scottish forests in January 1968'. *For. Commn Bull.* **45**, 42–48.

Nielson, R. E. Ludlow, M. M. & Jarvis, P. G. 1972 Photosynthesis in Sitka spruce *Picea sitchensis* (Bong.) Carr. II. Response to temperature. *J. appl. Ecol.* **9**, 721–745.

O'Hara, P. J. 1967 Leader growth and foliar composition in Sitka spruce in relation to fertilizer application on blanket peat. *Proc. 5th* Colloquium of International Potash Institute, pp. 111–121.

Panshin, A. J. & De Zeeuw, C. 1970 *Textbook of wood technology*, 3rd ed. London: McGraw-Hill.

Petty, J. A. 1970 The relation of wood structure to preservative treatment. In *The wood we grow*. Supplement to *Forestry* 1970, pp. 29–35.

Phillips, D. H. 1974 Control of diseases and invertebrate pests in forestry in Great Britain: chemicals and their alternatives. Tenth Commonwealth Forestry Conference, United Kingdom, 1974, p. 10.

Pollard, D. F. W. & Wareing, P. F. 1968 Rates of dry matter production in forest tree seedlings. *Annls Bot.* **32**, 573–591.

Pyatt, D. G. 1968 Forest management surveys in forests affected by winds. In *Wind effects on the forest*. Supplement to *Forestry*, pp. 67–77.

Pyatt, D. G., Harrison, D. & Ford, A. S. 1969 Guide to site types in forests of north and mid Wales. *For. Commn Forest Rec.* **69**, 35.

Pyatt, D. G. 1970 Soil groups of upland forests. *For. Commn Forest Rec.* **71**, 51.

Samuel, C. J. A., Johnstone, R. C. B. & Fletcher, A. M. 1972 A diallel cross in Sitka spruce. Assessment of first year characters in an early glasshouse test. *Theor. appl. Genet.* **42**, 53–61.

Savaser, B. G. 1972 A study of cultivation and tree growth on an upland heath in east Scotland. Unpublished M.Sc. thesis, University of Aberdeen.

Sunley, J. G. 1963 Factors affecting timber quality. *Commonw. For. Rev.* **42**, 129–136.

Taylor, G. G. M. 1970 Ploughing practice in the Forestry Commission. *For. Commn Forest Rec.* **73**, 44.

Thomson, J. H. & Neustein, S. A. 1973 An experiment in intensive cultivation of an upland heath. *Scott. For.* **27**, 211–221.

Thompson, S. 1974 Shoot growth and dry matter production in two contrasted provenances of *Pinus contorta* Douglas. Unpublished Ph.D. thesis, University of Aberdeen.

Toleman, R. D. L. & Pyatt, D. G. 1974 Site classification as an aid to silviculture in the Forestry Commission of Great Britain. Tenth Commonwealth Forestry Conference, United Kingdon, 1974, p. 21.

Wareing, P. F. & Matthews, J. D. 1973 Physiological and genetic factors determining productivity in species of forest trees. *Proc. 15th* Congress of I.U.F.R.O., Gainesville, Florida, pp. 136–143.

Whitehead, F. H. 1968 Physiological effects of wind exposure in plants. In *Wind effects on the forest*. Supplement to *Forestry*, pp. 28–38.

Zehetmayr, J. W. L. 1954 Experiments in tree planting on peat. *For. Commn Bull.* **22**, 110.

Discussion

E. J. GIBSON (*Princes Risborough Laboratory, Building Research Establishment, Princes Risborough, Aylesbury, Bucks HP17 9PX*)

You have emphasized the importance of uniformity and have shown how to grow straight stems with fewer knots. However, you have not discussed tree taper, which is very important when it comes to obtaining good yields of sawn timber, particularly from the smaller diameter logs. Are there yet indications of how we can reduce the taper on sawlogs?

J. D. MATTHEWS.

I agree that stem taper is very important, because rapid taper reduces efficiency of conversion in sawmills and the proportion of the log 'recovered' as sawn material. Silviculturists can reduce stem taper by adjusting initial spacing, intensity of thinnings and favouring trees with deep, narrow crowns.