TREE BIOLOGY RESEARCH AND PLANT PROPAGATION

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Several research groups at this station are investigating aspects of tree and forest science from a broad spectrum of interests and approaches, especially in physiology, ecology, genetics and microbiology. The same themes recur: how trees grow and develop, how their responses differ, and how one tree affects another. It is expected that this knowledge will be used to improve and innovate in forestry, and aid the cultivation of ornamental and amenity trees. To a large extent this research is complementary to that of the Forestry Commission Research Division, whose work is particularly related to practical problems associated with commercial forestry species. Fruit tree research in Britain is mainly concentrated at the Long Ashton and East Malling Research Stations.

Compared with herbaceous crop and ornamental plants, much less is known about forest and amenity trees, and new hybrids and cultivars appear infrequently or not at all. Whereas spectacular changes and improvements have occurred for example in the wheat crop during the last 50 years, and countless new forms and colour variants have been developed in the cultivated rose, progress in forest tree improvement has been much slower. However, the importance of the geographical origin or provenance has become widely recognised, and progenies of improved quality have been produced from seed orchards (for example in *Pinus sylvestris, P. radiata* and *P. elliottii*). The considerable number of new forms of species of *Populus* and *Chamaecyparis* are exceptions, but it may be useful to ask why tree research in general has lagged behind. Can anything be done to hasten it?

PROBLEMS IN TREE RESEARCH.

In the first place, the *life-cycle* of herbaceous plants allows a man to see many successive generations of crops, whereas trees, except for certain short tropical rotations, generally grow for 20 to 200 years or more. This makes it difficult to retain the continuity of research aims, and also to adjust to changing requirements. Superficially it might seem that research on young seedlings (some of which are able to grow 10 cm/week and even 5m/year) might enable the best types for particular sites to be distinguished. This may be so when establishment and survival are of overriding importance, but in most instances foresters are concerned with the quality and quantity of the crop at harvest. There is disturbing evidence accumulating which suggests that rapid early growth in trial plots may not necessarily be indicative of later excellence. Thus trees may change their size relative to each other as the crop closes canopy and grows to maturity (3, 5, 24).

Early characteristics may be more reliable indicators of later performance where differences of a qualitative nature are concerned, as for example in stem form, branching habit or foliage colour. However, caution is still needed here for it is well known that a batch of seedlings of *Fagus sylvatica* may sometimes contain a number with bronze coloured leaves, but only a very few of these grow into copper beeches. Similarly, the final height that a tree may attain is unlikely to be predicted from its early patterns of growth unless it has a short life-cycle (for example *Sambucus* spp.). Generally there are too many unknown factors at work, including occasional extremes of climate, for reliable prediction from present knowledge.

Perhaps one of the greatest problems posed by the long life-cycle of forest trees is the scarcity of flowering during the juvenile period, which may extend for the first 10 to 30 years of life (19). Clearly this means that breeding cycles would be very lengthy, and also that it is usually necessary to graft scions of older trees on to seedling rootstocks in order to bring selections together for crossing. Such grafted plants are often described as "mature," because they retain a number of the flowering and vegetative characteristics of older trees, which contrast with the "juvenile" shoots from younger trees. A further complication is that many mature plants do not flower annually.

A second area of difficulty arises from the *large size* which trees attain, with complex shoot and root systems. One cannot hope to study a big tree, still less the entire structure of a forest, from one point on the ground. Thus for example the HORMONAL CONTROL project, one of six at the Bush Station, uses tall ladders and tripods for its flower induction experiments, and has developed a mobile, Landrover-mounted tower of unit scaffolding. A more permanent system of scaffolding and towers is used in a 15 year old plantation of *Picea sitchensis* by the project investigating the EFFECT OF THE PHYSICAL ENVIRONMENT ON TREE GROWTH.

Conditions for growth at the top of a tree are often very different from those at its base, particularly if the forest is tall and dense enough for substantial gradients to exist. Continuous measurement of the micro-environments at various positions in the stand can help to explain how growth is controlled, particularly if aspects of growth are monitored as well as climatic data. In this project many of these measurements are automatically recorded and, using a computer, it is feasible to unravel the many interactions between the trees and their environment. Root systems pose greater problems still, and are notoriously little understood. Extensive sampling, digging or winching operations are needed even for moderate-sized trees, followed by time-consuming washing and separation of root fragments. On certain soils wind-thrown specimens may illustrate an exposed and relatively intact pattern of roots, but these by their nature may provide a biased sample.

A third problem with trees is their very great *variability*. This is often so large that it obscures the effects of treatments, requires many replicates to be used, and restricts valid prediction from information gained in particular circumstances. Whereas someone buying a packet of tomato seed knows with a degree of certainty the type of crop to be obtained, the same person sowing birch has no assurance of success. Three-quarters of the seeds may never germinate, and those that grow into saplings will probably not closely resemble the carefully selected parent tree. In a sense there is no such thing as The Birch Tree; instead there are trees showing a wide variety of birch-like attributes. In the PHYSIOLOGY OF GENOTYPES project, some factors underlying variability are being investigated in *Pinus contorta* and *Picea sitchensis,* particularly those controlling shoot growth and branching patterns.

Looked at in another way, the existence of all this variation puts growers of trees in a much stronger position as regards the future than tomato growers, having this large potential for selection and as a basis for breeding. But in order to select one must first understand the reasons for variation (Fig. 1). All too often, however, it has been impossible to find out whether a selected tree has grown well because it is inherently vigorous under those conditions, whether it has been specially favored by its local environment, or whether its response is confined to one part of the tree or its life-cycle (i.e. due to internal factors).

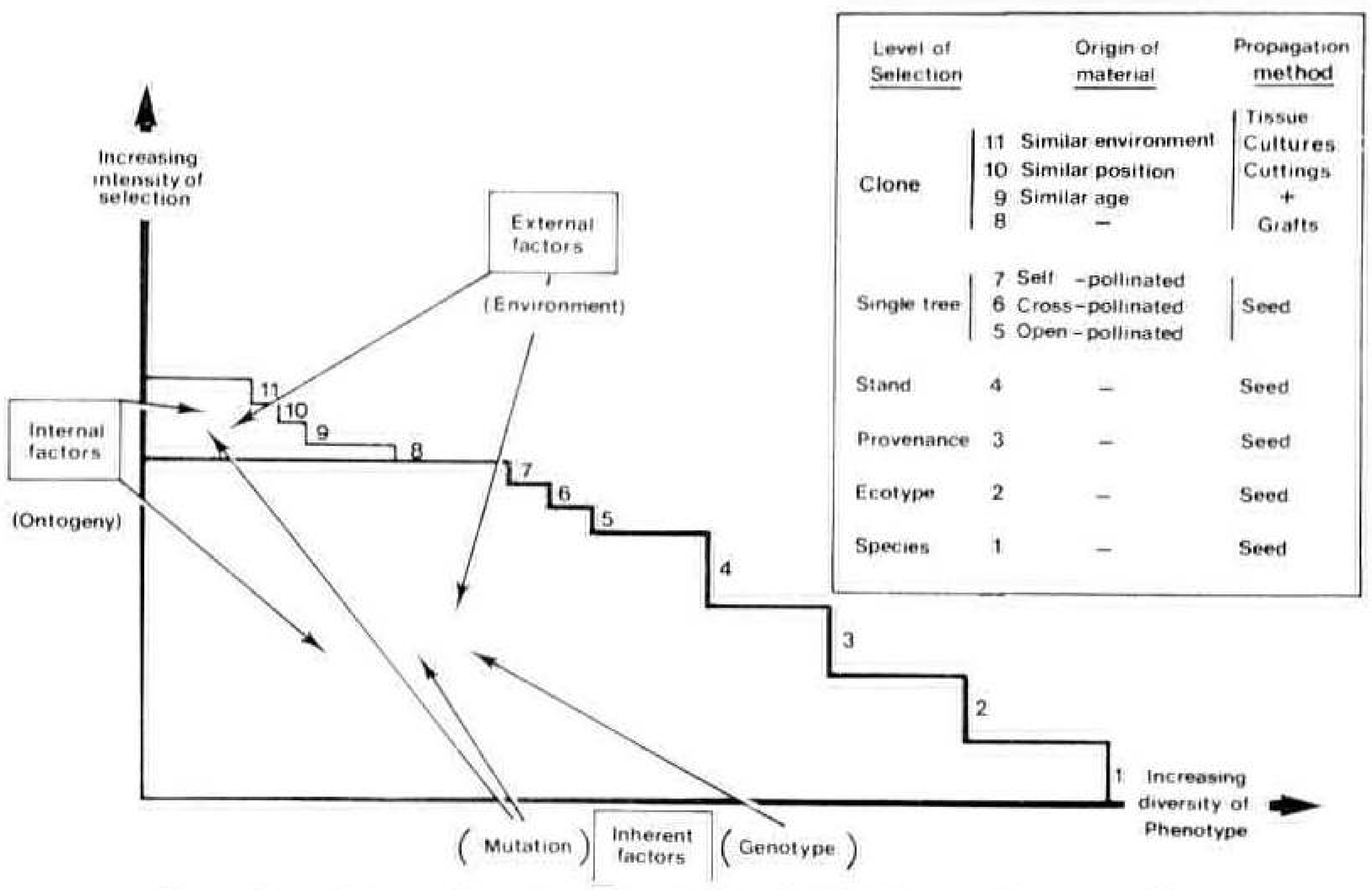

Figure 1. Variation and selection in trees. Variability depends upon an interaction between external, internal and inherent factors. Greater diversity is obtained by selecting near the bottom of the chart; more uniform trees by selection near the top.

Experience with other perennial crops, including apples, citrus, rubber, etc., suggests that a considerable proportion of tree variability is often genetical and distinct forms can, therefore, be established by vegetative means. With forest trees, it is not surprising that the recognition of new types has progressed much faster with *Populus* and *Chamaecyparis,* for they are propagated by cuttings. Grafting selected "plus" trees and ornamental cultivars of many other genera has amply demonstrated the large inherent component of forest tree variation, and indeed it is typically much greater than in other crops. Species of forest trees usually have a wide geographical range; they are generally out-breeding and therefore populations are heterogenous; and there has been a smaller element of selection in their cultivation.

As soon as several replicates of a single genotype are produced, the inherent differences from other clones of the same tree species can be seen, as happened with a collection of four clones of *Pinus sylvestris,* produced by grafting scions from mature "plus" trees. Unintentionally these potted grafts were exposed to gale-force winds, after which it was found that needles on one clone were extensively browned, whereas those of the other three were not affected. The effect was unequivocal, and yet with a single representative of each genotype it would probably not even have been noticed.

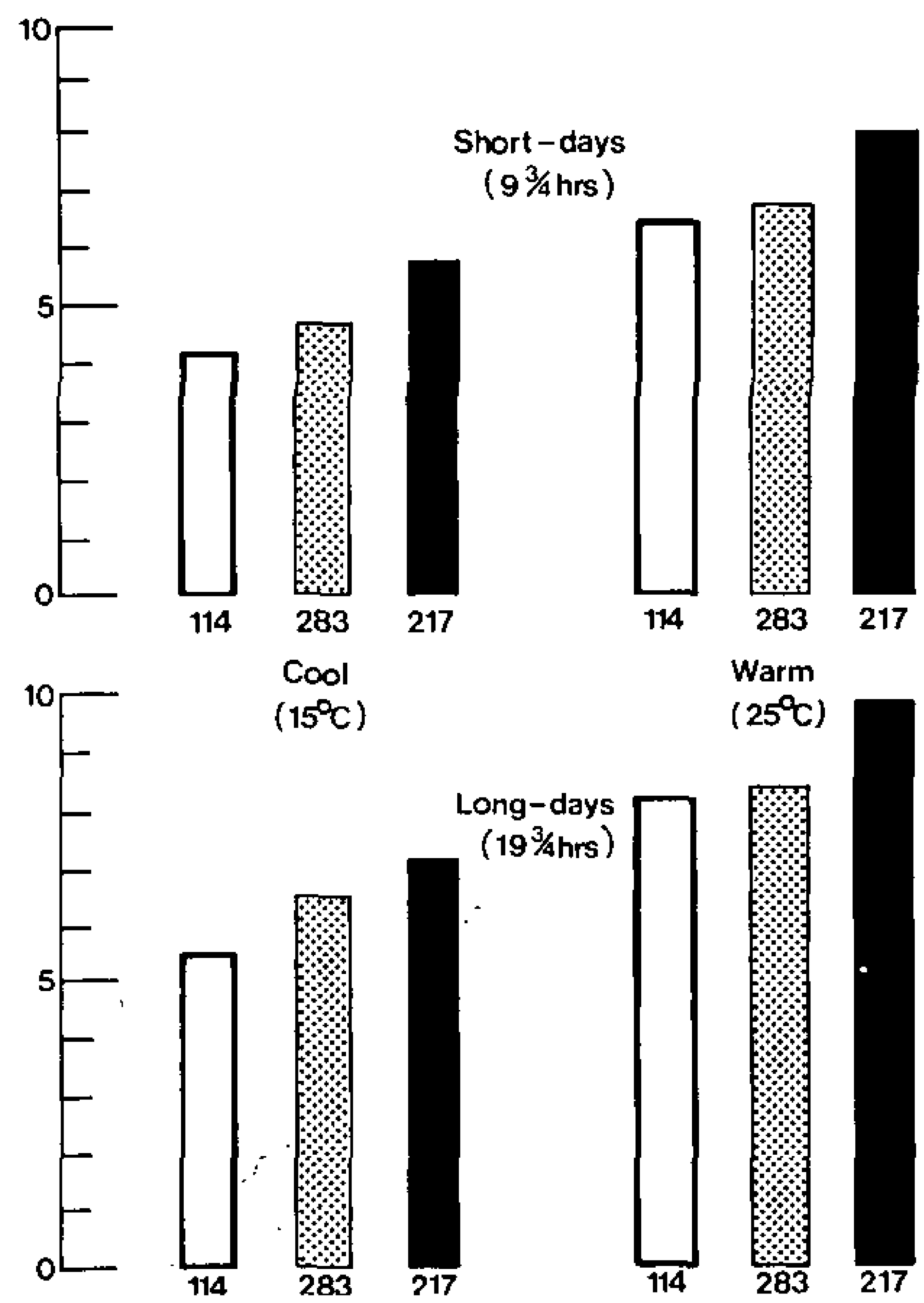

Figure 2. Effects of genotype and environment. Response of 3 clones of Scots pine grafts (scions from mature "plus" trees nos. 114, 283 & 217) to 4 different growth cabinet regimes. ("Needle-display" = average width of shadow cast by current year's needles on a screen, a function of needle length and angle to the main stem.)

When the four clones were grown under four different regimes in growth-rooms (see Fig. 2), the same clone again showed needle-browning, but this was much more pronounced in one of the rooms (long-day; cool). Thus the expression of the genetic character was considerably modified by environment. This is also illustrated in the needle measurements of the other three clones, which were influenced both by temperature and by day-length, besides showing consistent inherent differences (Fig. 2). Indeed, some external and internal effects can be so strong that the genetic component is hard to detect. For example, by selecting the growing conditions and the node position, leaves of a single clone of *Triplochiton scleroxylon* can be produced which differ by as much as 35 times in length, and possess photosynthetic surfaces varying a thousand-fold (Fig. 3). In such circumstances, it will be almost impossible to discover any inherent differences, unless they are qualitative rather than quantitative.

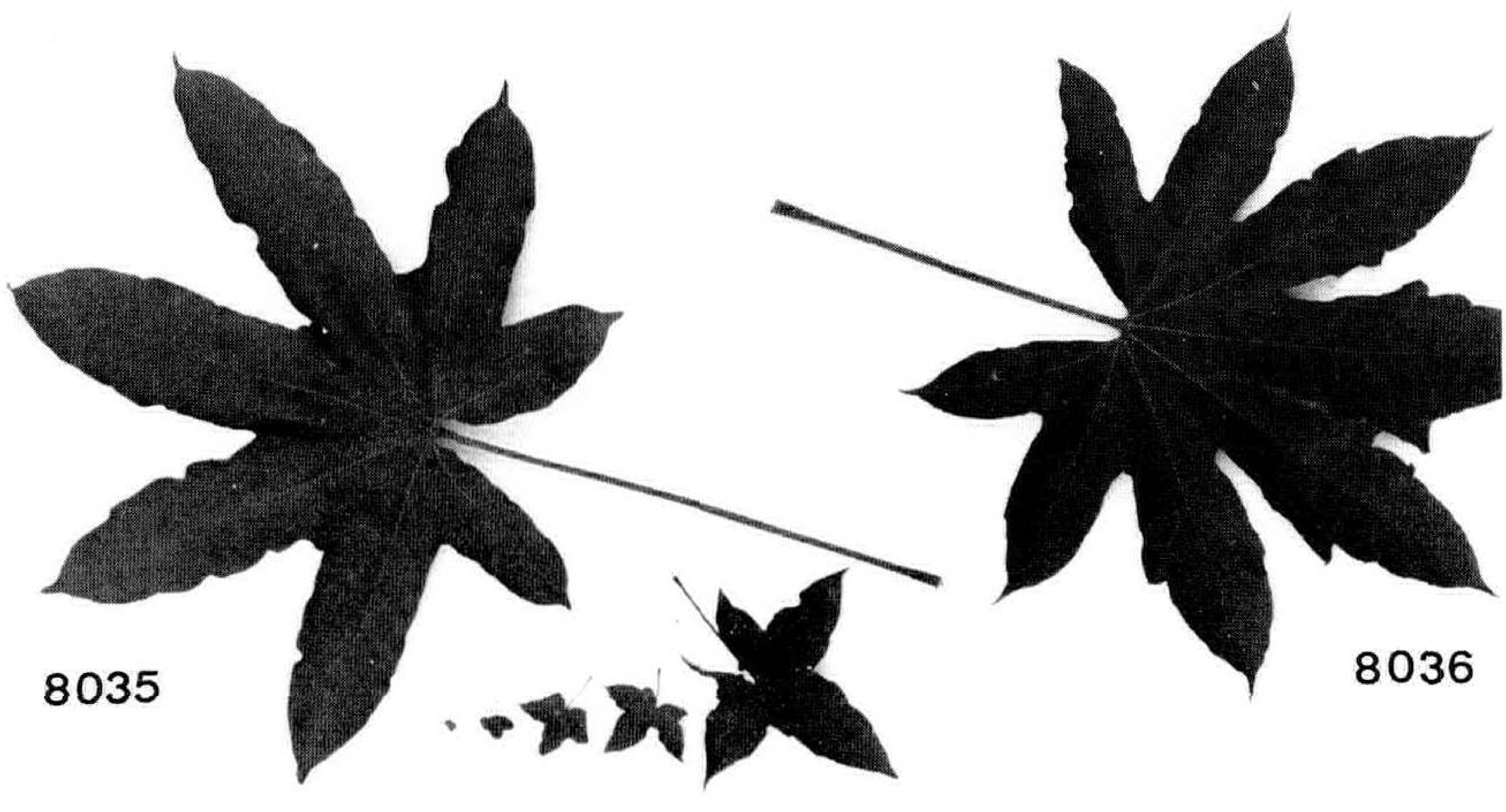

Figure 3. Effects of environment and ontogeny. Fully expanded leaves of Obeche, selected to show variation within a single clone (8035). The smaller leaves were taken from weak shoots on plants in small pots, pruned back and left in a shady place at 15-23°C. The large leaf originated from a vigorous shoot on a plant growing in a large container under supplementary lighting at 25-30°C. Note the differing numbers of lobes, and also the genetical difference shown by the large leaf of clone 8036, with its characteristic secondary lobing. (Scale: 15 cm or 6 in. long.)

During the last few years it has become clear that it is possible to distinguish between genetical and environmental components of variation, now that cuttings can be rooted using material from young forest trees. For instance, over 25 temperate and tropical tree species have been rooted at the Bush during the last two years, using standard hormones and mist propagation with bottom heat (see Table 1). Juvenile cuttings can often provide more elegant research material than seedlings, and they have far-reaching implications in clonal forestry, a subject which is being actively debated at present (15, 25). The major forest species in use in Britain can now be rooted from young trees, and methods have been developed by the Forestry Commission's Physiology Branch for producing in a few months cuttings which have better structured root systems than standard nursery transplants raised from seed (2). There is a real prospect that before long practical growers may be able to reproduce repeatedly a set of desirable characteristics which they have selected in a forest tree. Each of the following research projects uses cuttings for precisely these reasons.

Table 1. Tree species rooted as cuttings for research at I.T.E., Bush, 1973-75.

Species	Age of Vegetative Stock-Plants	Comments
Temperate conifers:		
Cupressus macrocarpa	old	fairly difficult?
Metasequoia glyptostroboides	old	easy
Picea sitchensis	young	easy
Pinus contorta	young & old	most clones easy
P. sylvestris	young	fairly difficult
Thuja plicata	young & old	easy
Temperate dicotyledons:		
Acer pseudoplatanus	young	difficult
Betula alleghaniensis	young	easy
B. pubescens	young	easy
B. verrucosa (B. pendula)	young	easy
Crataegus monogyna	young	some clones fairly easy
Fagus sylvatica	young	difficult
Fraxinus excelsior	young	difficult
Malus silvestris	young	fairly easy
Prunus avium	young	difficult
Quercus robur	young	some clones fairly easy
Salix capraea	young	easy
Sambucus nigra	young & old	easy
Sorbus aucuparia	young	fairly difficult
Ulmus glabra	young	some clones fairly easy
Tropical dicotyledons:		
Cedrela odorata	young	fairly easy
Chlorophora excelsa	young	easy
Gmelina arborea	very young	easy
Shorea albida	young	easy?
Terminalia ivorensis	very young	easy
T. superba	young	easy
Triplochiton scleroxylon	young	easy

The absence of a tree species from this list does not imply that it cannot be rooted. For further information, see Kommissarov (10); Hinds and Krugman (7); Longman (15).

GENETICS OF TREE NUTRITION

A feature of this project is the growing of "mini-cuttings" of birch on an aseptic medium in small tubes. Seedlings are raised on agar jelly, and are then cut up into a number of single-node fragments, which can be stimulated to form visible roots in as little as three days. After about 2 months propagation is repeated, and when the clonal cuttings are sufficiently numerous they are used to study variability in response to mineral nutrients. It is interesting that it has been found that seedling plants are too variable for these experiments, even when they originate from single trees (see Fig. 1). There is still considerable variation in size within the batches of clonal cuttings, principally due to the node position from which they were derived. However, as the cuttings continue to grow these initial effects appear to become less important (13).

In Table 2 a typical example is given from a series of mineral nutrition experiments. With large amounts of phosphate, both clones tended to make similar amounts of shoot growth, no matter whether stem length, leaf length, leaf area or shoot dry weight were measured. However, with very small amounts of phosphate definite genetical differences could be observed. For example, clone A made less than half the leaf growth, whereas clone B grew nearly as well as with high phosphate. A possible reason for the capacity of clone B to thrive under limited nutrients was that these plants produced almost three times the number of roots.

Table 2. Differences in the responses of two clones of *Betula pendula* to low phosphate. From data of Pelham and Mason (20).

Measurement	Clone	High P (26.0 ppm)	Low P (0.4 ppm)	Change caused by lowering P
Leaf area (cm^2)	A	7.9	3.5	− 55%***
	B	8.8	8.0	− 10%
Root number	A	14.4	18.6	+ 30%
	B	19.5	56.4	+190%***

Means of 16 plants after 10 weeks in sand culture.
*** indicates a highly significant change.

If the low nutrient tolerant clones flourish in long-term field trials on phosphate-deficient soils, this ability could be of great practical importance, considering the poor nutrient status of many planting sites for both forest and amenity trees. In the case of birch it would also be possible to multiply any selected clone very rapidly. Taking the normal 8 cuttings every 8 weeks with over 90% success, it is theoretically possible to obtain a million cuttings in a little over a year, assuming facilities and staff are available. Alternatively, ordinary mist propagation could be used, as young birch clones root very readily with hormone treatment, as pointed out at an earlier meeting of the Society (6).

In natural conditions tree roots encounter many different micro-organisms, some of which may affect the availability and uptake of mineral nutrients. In particular, many trees form close mycorrhizal associations with specific fungi, and these modified roots are quite different from an uninfected root system. Birch seedlings which had not previously been contaminated with any micro-organisms formed mycorrhizas when inoculated with strains of *Amanita muscaria* (the poisonous fly agaric toadstool). There is considerable variation in both the tree and the fungal strain in their ability to form associations, and some combinations give more vigorous tree growth than others. This is an important discovery, which may prove to be of general relevance to the successful establishment of trees, and perhaps also in their later growth on poor sites.

Ultimately, it is intended that the inheritance of the capacity to utilize mineral nutrients will be studied in the tree, mycorrhizal association and fungus. This should be possible by developing the methods just described, and because birch seedlings can be induced to form flowers in 1 to 3 years from sowing. (See Table 5.)

AMENITY TREES FOR INDUSTRIAL WASTELAND

Choosing the most suitable individuals from the total range available within a species is also the theme of this project, which is concerned with selecting trees for improving the appearance of derelict spoil heaps. It has been clearly established that herbaceous plants colonizing bare ground around abandoned metal mines are often tolerant of the particular metal ions and of the generally very exacting conditions (1). This tolerance has probably arisen as a result of rapid, intense natural selection, and the same may apply to isolated trees which have managed to survive on coal tips, etc., though evolution may not have proceeded to the same extent, in view of the longer interval between generations. Successful establishment of trees would obviously have much to offer in terms of landscape improvement, stabilising the terrain and providing new habitats for wildlife.

For these purposes, clonal stocks are being built up by rooting cuttings of selected trees of many species (see Table 1). These will later be tested on spoil heaps and compared with material originating from unselected seedlings. If the selected plants survive and grow better, they could improve success rates in future reclamation projects, and at the same time reduce costs. Further improvement could then be sought through continued selection and breeding.

Tropical Tree Improvement. The tropical forests of the world are being exploited at an ever-increasing rate, for timber and paper pulp, and for farming and building land (17). Consequently their genetic diversity is diminishing rapidly, and in some instances species may soon become lost from a whole region. In addition to conserving blocks of forest in each area, it is also important to retain examples of the full geographical range of valuable species by planting them in research collections or "banks." So thinly scattered are the representatives of any one species in these mixed forests that it would require an unreasonably large area to conserve all the diversity *in situ*.

In *Triplochiton scleroxylon*, the West African tree producing the important timber "Obeche," a shortage of viable seed restricts attempts at conservation, and indeed limits ordinary reafforestation. Seed cannot be stored for very long, and there is also evidence of inbreeding depression, particularly from small seed lots. Projects at Ibadan, Nigeria, and at the Bush, Edinburgh, have recently shown that large numbers of well-rooted plants can be raised under mist, using leafy cuttings taken from young trees. Vegetative propagation thus offers the triple possibility of increasing the numbers of available plants, preserving some of the many natural combinations of genes, and multiplying those most suitable for forestry. These projects are sponsored by the United Kingdom Overseas Development Ministry and the Nigerian Government to look at the potential and the problems of this approach.

Work of this kind is beset by the basic and most difficult problem of forest genetics: how to identify the outstanding genotypes and then to produce thousands of superior trees from them (15). By the time that one can be reasonably sure that a tree is desirable, its mature shoots are usually very difficult to root. If cuttings can be produced, they may exhibit growth patterns typical of mature trees, and therefore not be suitable as planting stock. Conversely, a young tree is an unknown quantity when it is used as a vegetative stockplant, although this is, of course, also true of seedlings without prior progeny testing.

The group in Nigeria have made the important discovery that cuttings can be rooted easily from coppice shoots growing from stumps of 8 year old trees which had been felled. Moreover, similar shoots can be induced, by such methods as ringing and scoring of the bark, without cutting the tree down. Because coppice shoots have a juvenile growth habit, a single rooted cutting could start a clone of "young" trees from an outstanding older tree. With 25 or 50 such clones, the likelihood of an improved plantation would be high, and it would soon become clear which were those with inherently good stem form and branching habit. It has still to be shown, however, whether old trees lose the ability to form juvenile coppice shoots.

The team in Edinburgh, investigating the physiology of root formation, has shown that bed temperatures around 30°C appear to be optimal for most clones of *Triplochiton* cuttings. A mixture of 0.1% IBA and 0.1% NAA (given as an alcoholic "quick dip") stimulates rooting, again in most though not all clones (11). Further topics under consideration include the role played by the leaf in root initiation, and the possibilities of tissue and organ culture. Meanwhile, other tropical species have been rooted at the Bush (see Table 1), an interesting example being *Shorea albida*, a dipterocarp tree producing seed once every 8 to 10 years, which will remain viable for 14 days. Rooting cuttings from "wildings" may be the only chance of re-afforesting the hundreds of square miles of peat-swamp forest of *S. albida* in S. E. Asia which are due to be felled shortly for paper pulp.

When undertaking a programme of propagation by cuttings, a major consideration is the production of large numbers of uniform shoots from vegetative stockplants. Involved here is the outgrowth of buds which are normally inactive due to dormancy or to apical dominance, for in a number of tropical species, particularly members of the mahogany family (Meliaceae), young trees can grow to a height of 2 to 10 metres with only one active shoot tip. Decapitation may produce a flush of lateral shoots, but in *Cedrela odorata*, for example, one lateral usually re-establishes dominance within a few weeks or months. Such a growth habit obviously tends to lead to non-uniform cuttings.

If *T. scleroxylon* plants about 1½ metres tall are decapitated and planted at about 45° from the vertical, this causes a greater number of laterals to sprout and continue growing (11). Similar gravimorphic effects on apical dominance are known for temperate fruit and forest trees (22, 23, 27). In the "angled" decapitated *T. scleroxylon* plants, the developing laterals rather surprisingly are of two different types: basal sprouts near the roots, which grow vertically and have a spiral leaf arrangement resembling a seedling main stem; and apical shoots near the point of decapitation, which have a distichous or two-ranked arrangement of the leaves and a non-vertical habit of growth more reminiscent of branches (Fig. 4).

Cuttings of the apical type generally root less easily than the basal, and continue to grow (for a time at least) at an oblique angle. Thus cuttings originating from a single plant can show quite wide differences, and it is obviously important to know whether these are temporary "carry-over" effects from the stockplant, or whether they involve permanent phase-change. Planting the main stem horizontally, coppicing or "hedging" (8) may perhaps be found to produce more uniform shoots.

Figure 4. Effects of ontogeny and environment. Obeche cutting 2½ yr. old showing the stimulation of many branches by decapitation and growing at an oblique angle. Note that the strong "basal" laterals grow more or less vertically, but the vigorous "apical" laterals tend to grow in the direction that the bud was pointing.

These results pose interesting problems in morphogenesis, and have also suggested a possible way of testing forest trees early in their life for their later characteristics. Some clones respond to treatment by producing one or a few lateral shoots, while in others a large number grow out. Can these differences be used to predict the later branchiness of the tree, or the persistence of its main stem? Clearly there may be many other factors involved, and the hypothesis requires full testing in the field.

Flower Induction. Although some trees flower regularly, and produce ample supplies of viable seed, it is common for flowers or cones to occur so irregularly that breeding is difficult or impossible. Even in a good flowering year, some of the selected parent trees may remain vegetative, or produce too few male flowers to form an effective pollen cloud. In most temperate-zone trees, flowers are initiated in spring or summer of the year before the one in which they open and are pollinated, so any flower-inducing treatments have to be applied sufficiently early.

Considerable progress has been made recently in identifying factors affecting the initiation of flowers, and in some cases techniques are now being developed for the reliable stimulation of heavy flowering in field conditions. One of the most striking of these is the response to gibberellic acid (GA_3), and in this project it has been found that a single dose of a fifth of a gram, injected in June to mature *Thuja plicata* cuttings about 15-20 feet tall, increased the number of cones formed in the same year by around 100,000 female and about half a million male cones. These very large numbers are possible because nearly all the many vegetative shoot tips in this species are capable of becoming reproductive. There were slight differences in response from tree to tree, but all

17 clones used over a four year period of study have shown a *pronounced increase in both sexes.*

Large numbers of male and female cones can also be induced by GA_3 in *X. Cupressocyparis leylandii* and other members of the *Cupressaceae* and *Taxodiaceae*. In the *Pinaceae*, however, there appears to be no such general response to GA_3, although recent evidence suggests that combinations of other gibberellins may promote flower formation (21). Before long it may perhaps become *possible to influence the two sexes differentially*, by using different concentrations of gibberellin, or mixing it with other growth substances.

In broadleaved species, on the other hand, it is likely that gibberellins may be found to inhibit rather than promote flowering. In birch (Table 3), both sexes of catkins were decreased by applying GA_3, especially the female.

Table 3. Effects of gibberellic acid[1] on flower initiation in birch.

	Percentage of branches forming catkins			
	Female Injected with		Male Injected with	
	H_2O	GA_3	H_2O	GA_3
Unringed branches	47	6	71	50
Ringed branches	88	43	76	64

[1]100 mg GA_3 in 200 ml H_2O injected on May 15-17 into 17 trees of *Betula pubescens* and *B. pendula (B. verrucosa,)* about 1 m above a fork. The other limb injected with 200 ml H_2O. Assessment of sample branches in autumn of same season (female by dissection, normally of 30-50 buds).

Table 4. Forest tree species flowering in response to complete bark-ringing.

Species	Type of shoot ringed[1]	Year of response[2]	Sexes induced
Betula pubescens	SB, SMS	1	F, M
	LMS*	2	F, M
B. pendula (B. verrucosa)	SB, SMS	1	F, M
	LMS*	2	F, M
X. Cupressocyparis leylandii	SMS	1	M
	SMS	2	F, M
Larix decidua	SB	1	F, M
L. kaempferi	SB	1	F, M
L. x. eurolepis	SMS*	1,2	F, M
Metasequoia glyptostroboides	SMS	1	F, M
Picea abies	SB*	1	M
Pinus sylvestris	SB	1	F, M
Pseudotsuga menziesii	SB	2	F, M
	LMS*	3,4	F, M

Table 4. continued

Species	Type of shoot ringed[2]	Year of response[2]	Sexes induced
Thuja plicata	SB, SMS	1,2	F, M
	LMS	1, 2*, 3	F, M

[1] Type of shoot ringed: SB - small branch; SMS - main stem of small plant; LMS - strong limb or main stem of large plant.

[2] Year of response indicates the year(s) in which substantial enhancement of flower initiation was detected. Year 1 means later in the same season that the shoots were ringed.

* - Observational trial, not yet confirmed by replicated experiment.

Inhibition of flowering also occurs, for example, in apple trees, where it is possible to promote flowering with growth retardants such as Alar, which suppress natural gibberellin production (9). These results should not however be taken to imply that treatments which retard vegetative growth necessarily promote flower initiation (26).

A method of inducing flowering, known even in Roman times, is that of bark-ringing or girdling the stem, and this is effective in a number of unrelated genera (Tables 3 and 4).

Stimulation is greatest when a complete "ring" of bark is removed in spring, well before the time at which the flower initials for the next year are laid down. This varies between May and September in Britain, but, as a general rule, ringing should be done as soon as the new leaves are appearing and the bark will "slip" on the wood. The cut surfaces should be protected with a suitable bitumastic compound, and the ringed shoots may need extra support. They may survive and flower and fruit heavily for a number of years, even though the phloem has been completely severed, provided that the ring is not made in a position which leads to mechanical failure, or to the death of a portion of cambium or of the entire root system (Fig. 5).

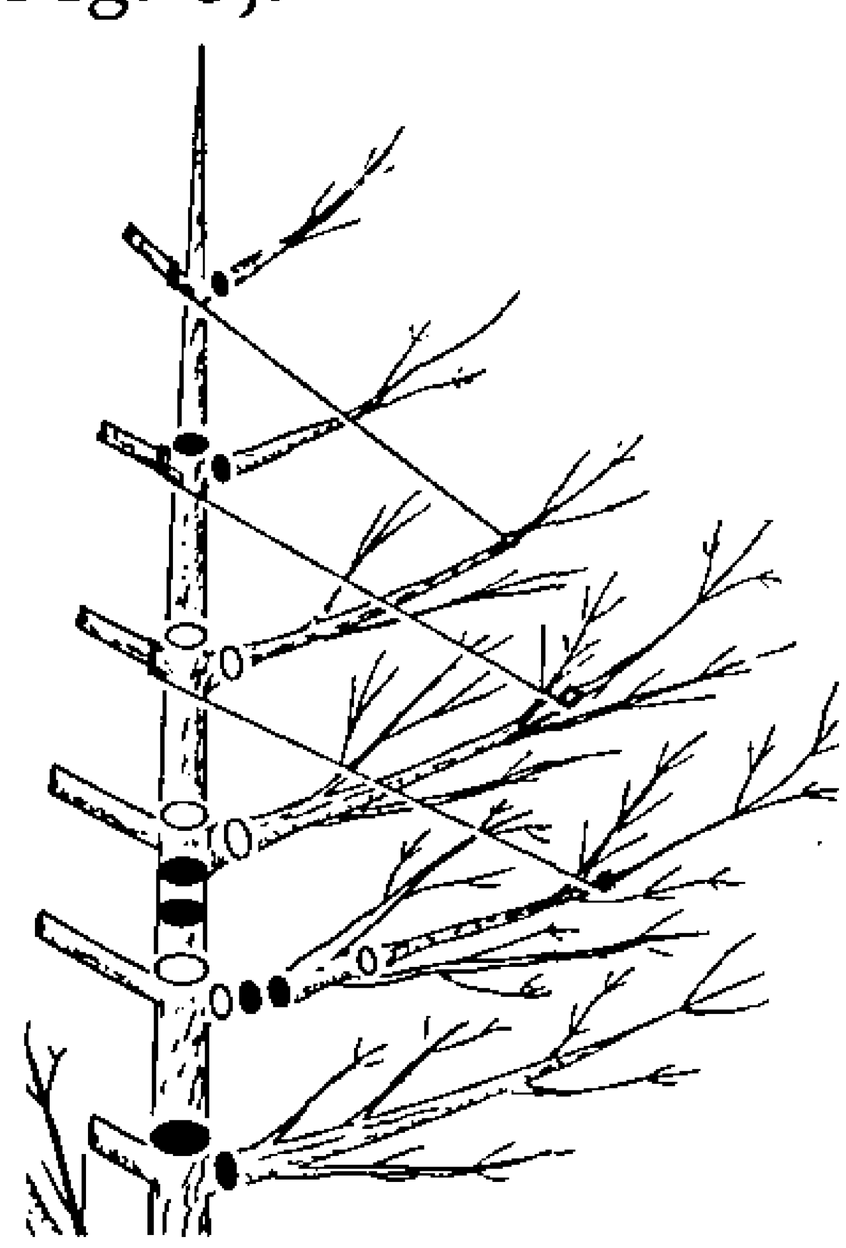

Figure 5. Suitable (o) and unsuitable (•) positions for complete bark-ringing to induce heavy flowering.

In *T. plicata*, which has been used as a test plant for flowering studies, ringing of branches or the main stem of small plants stimulates male and particularly female cone formation in the year of treatment and especially the second year (Fig. 6). Small ringed shoots are liable to break off after a while, but larger trunks and limbs can be treated with less risk, and here the effect occurs less rapidly, reaching a peak in the third year. These methods are also very effective in birch, for example, where small ringed shoots initiate catkins in the current year, whereas flower formation is delayed to the second year when large limbs are ringed.

Figure 6. Prolific female coning induced during the year following treatment in mature cuttings of western red cedar. Left — portion of completely ringed branch; Right — part of control branch.

The stage is now being reached when these discoveries can be developed into practical techniques for tree improvement. Thus gibberellin injection has been used to stimulate approximately 10 million cones on the best selections in a seed orchard which is shortly to be lost through a road widening scheme, and it has also been suggested for other trees which are due to be felled the following year. Where it is desirable to obtain a continuing supply of seed, it may be appropriate to develop "renewal" methods of shaping forest seed-trees. In some species the majority of potential flowering sites tend to be utilised in a single year of heavy initiation, and so a multi-stemmed tree may be needed (see Fig. 5), one or two limbs of which would be treated each year, and then removed when the seeds were almost ripe.

A further important development is that small mature cuttings have been induced to flower in glasshouses and growth chambers. This allows the research worker greater control, and also enables experiments to be done on the effects of climatic factors on flower initiation. It has been appreciated for many years that there is a correlation between fine summers and heavy flowering the following year (18). It is now possible to test the effects of separate components of climate, keeping the others constant. In one such experiment, a combination of warm temperatures (25^{0}C) and very long days (about 20 hours) stimulated female and male coning in *T. plicata*. This did not happen when cooler temperatures and/or shorter days were given. The Forestry Commission Genetics Branch has recently been successful in stimulating copious flower formation on 5-year-old grafts of selected mature trees of *Picea sitchensis*, kept in a polythene tunnel for the whole of the growing season..

A long growing season in a controlled environment has also stimulated flowering in the Dawn cypress (*Metasequoia glyptostroboides*), which never produces male cones out of doors in our latitudes (14). Pollination of female cones of the same clone has resulted in the first home produced seedlings of this species to be raised in Britain. In addition it also responds to ringing and to gibberellin injection by marked changes in shoot growth as well as by forming cones.

As mentioned at the beginning of this article, one of the greatest barriers to tree breeding is the scarcity of flowers during the juvenile period. Stimulating flower formation is more difficult in seedling material, but is evidently not impossible (16), for several species have now been induced during the first three years of life (Table 5). These developments are being used in Finland for large-scale crossing to produce improved seed of birch (12). It is estimated that by 1985 birch cultivars will be producing 100% more timber than the unimproved species. Selection and breeding for improved yield and form would be particularly relevant in Britain, where many sites are suited to birch, but the natural populations have been subjected to centuries of intense negative selection since they have been regarded as weed species (4).

Hopes for improving tropical trees were increased recently by the occurrence at the Bush of more than 30 flower buds on a cutting originating from a seedling of *Triplochiton scleroxylon*. In the tropical forest, this tree opens its flowers towards dusk, perhaps 50 to 150 feet above the ground, and pollination probably has to occur within the next few hours. By contrast, the flower buds shown in Fig. 7 were 3 feet from the ground, on a cutting 2 years old. If this can be achieved on a regular basis, controlled pollinations and repeated crossing would become feasible as well as easy seed collection and study of the reproductive biology of this species.

Table 5. Forest tree species induced to form flowers during the first three years from seed germination.

Species	Treatment	Approximate age at first flower initiation (months)	Sexes induced
Betula pubescens	Complete ringing of mainstem	27	F, M
	Rapid growth, then complete ringing of main stem	15	F, M
B. pendula (B. verrucosa)	Complete ringing of mainstem	27	F, M
	Rapid growth, then complete ringing of main stem	15	F, M
	Rapid, continuous growth	8-30	F, M
Larix x. eurolepis	Rapid growth, then complete ringing of main stem plus horizontal orientation	26*	F, M
Thuja plicata	Complete ringing of mainstem, grown at 20^{0} - 28^{0}C	24	F, M
Triplochiton scleroxylon	Plant decapitated and grown at oblique orientation	35*	F

* - Observational trial, not yet confirmed by replicated experiment.
See also: Jackson and Sweet (9); Zimmerman (28); Pharis and Kuo (21).

Figure 7. Flowering branch of Obeche, produced in Edinburgh on the plant shown in Fig. 4, at 35 months from germination.

Clearly there is still a great deal of work to be done before all these possibilities have been fully investigated. However, forest and ornamental tree breeding may soon start catching up with other crops, whose rate of improvement must presumably slow down. Spectacular advances can be expected in some tree species, now that the knowledge is being gained and the barriers overcome. One day the grower may get the set of trees for the purpose, instead of plants so variable that there is no way of finding out why some of them are unsuitable.

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