GR:MER

17th April, 1963.

Dr. K. A. Longman,
University College of Wales,
Aberystwyth,
WALES....U.K.

Dear Dr. Longman,

Recently I have found a short article giving a synopsis of your experiments on growth of trees relative to gravity. This appeared on page 417 of Discovery, October 1960. There is very small literature about mechanical handling of plants. Please send to me reprints for references about your scientific papers on such matters.

Enclosed is a short article of mine entitled "Reversed Beam Vines".

Yours faithfully,

Grete Reber.

2 reprints
arrived on 23/9/63 from Sierra Leone
No return address.

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The objections to the use of a cellulose column are that cellulose has a low capacity and the column is very slow-running. Thus considerable labour and time is needed to obtain even a small quantity of tannin. These difficulties have been overcome in an apparatus of Swedish manufacture in which a cellulose column of large diameter and hence high capacity is employed. A reasonable rate of elution is obtained by applying pressure to the top of the column.

Polycaprylamide has a higher capacity than cellulose and was tried as an absorbent. The *Calluna* extract was injected and eluted first with water. A brown band remained at the top of the column. When the eluate seemed to be free of phenols, as indicated by testing with diazotised sulphanilic acid, the column was eluted with 70% aqueous formamide. The brown band moved down the column, the area behind it being brownish purple. The brown band was eluted. It did not give a precipitate with gelatine. The whole of the column was then purplish.

The column was then eluted with 50% aqueous acetone, which washed out the purple substance. The eluate gave a faint turbidity with gelatine, and appeared to be a very dilute solution of the tannin.

Polycaprylamide seems to be superior to cellulose as an absorbent. It is at present only available in pellet form, and is prepared for use in a column by solution in hot phenol and precipitation with methanol. The powder obtained is extracted with methanol to remove traces of phenol, the whole operation being very time-consuming. Unless it can be obtained in powder form it is not intended to follow up the use of polycaprylamide as a means of obtaining tannins.

We thank Dr. W. R. C. Handley for helpful advice and discussions.

STUDIES ON THE PHYSIOLOGY OF FLOWERING IN FOREST TREES

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The main scope of this project was outlined in the *Research Report* for 1957, and details of some of the results obtained were given in the 1958 *Report*. The following further results have been obtained.

Effects of Photoperiodic Treatment on Flowering and Growth

Grafted material has been used in order to determine the effect of day-length conditions on flower initiation. In Scots pine, female cone formation has been shown to be dependent on long-day conditions, no cones being initiated under short-days, either in 1957 or 1958. The same appears to be true of birch. On the other hand, 4-5-year-old seedlings of lodgepole pine initiated female cones under short-days under outdoor conditions, and in fact there appears to be an actual stimulation, as compared with long-days. It is of further interest that if the short-days are given in a greenhouse at 15°-25°C, no female cones at all are formed.

In beech and Japanese larch no effects of day-length on flowering have yet been detected.

The growth of trees is also greatly affected by day-length, and it is possible by appropriate manipulation of the day-length and temperature to build up the size of grafts and seedlings at a considerable rate. For example, beech grafts have grown up to five feet in one season. In another experiment, seedling birch reached a height of 17 feet after two years under long-day conditions in a greenhouse. As was reported last year, several of these trees have borne numbers of catkins, whereas under natural conditions this would not occur for five to ten years. In addition to its value as a technique for tree-breeding, this experiment has thrown some light on the fundamental problem of the existence of juvenile and mature stages in trees. (Longman and Wareing.)

Effects of Gravity on Flowering

Further experiments have been set up to investigate the effect of tying branches of Japanese larch into different positions relative to gravity. Few flowers were initiated in 1958, due to the unfavourable weather conditions, but it is hoped that further information will be obtained in 1959. In birch, flowering is not stimulated by tying branches down; the position in *Pinus* is being further investigated.

Effect of Other Treatments on Flowering

Complete girdling of branches of 10-year-old birch has produced large numbers of female and male catkins, compared with few or none on the control branches. A similar effect has been obtained with potted seedlings in their third year. Partial breaking of the stem did not, in most cases, increase flowering, which suggests that the interruption of phloem transport is more important in this flowering effect than is the checking of the transport in the xylem.

On the other hand, Japanese larch (about 12 years old) responded to partial breaking provided the branch was also tied down. An average of 62 male flowers was formed, while only one flower was formed on all the control branches. It is also noteworthy that partial breaking and tying down had produced this result in a poor year for flower initiation, when tying down alone had little effect. Moreover, flowering was greatly increased by this treatment in a tree which was already flowering regularly, nearly 900 male and 8 female cones being formed on a single 8-year-old branch.

The effect of girdling and partial breaking is also being studied in beech and Scots pine, where the indications are that similar results may be expected.

A full-scale manurial trial was set up in 1956-7 to investigate the effects of N, P and K fertilizers on female cone production of young Scots pine. Statistical analysis of the data is still proceeding, but the main effect on female cones appears to be that potash increases both the number of cones and the proportion of trees coning. Male cones were also formed, possibly due in part to a severe drought in May and June, 1957. Nitrate and phosphate combined appear to increase considerably the proportion of trees bearing cones.

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5. FACTORS AFFECTING FLOWER INITIATION IN CERTAIN CONIFERS

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THE factors which affect flowering in coniferous trees have received little attention until recent years, and there is not yet a great deal more known about the morphological changes which occur at the apex when reproductive organs are formed. It must therefore be made clear at the outset that the investigations described here are in an early, exploratory phase.

It is in some ways rather surprising that so little is known about the flowering of conifers, and some explanation may not therefore be out of place. In a number of ways experimentation with coniferous trees is difficult. For instance, the material is genetically very variable, there having been practically no systematic breeding of conifers in this country until the last decade. A second more important point is the existence of a juvenile or non-flowering period in the life of the tree, in some conifers as long as 25–30 years. Investigation of flowering is therefore complicated, since a factor which affects flowering in a mature tree need not necessarily affect the change from the juvenile to the mature phase, and *vice versa*. Furthermore, by the time that flowering commences most conifers are too large to grow under controlled environments, and it may even be necessary to climb the tree to reach the flowers. Moreover, the shoot system has by this time become complex, imparting a certain lack of precision to experiments.

Previous studies on the initiation of flowering in other groups of plants, such as fruit trees and ornamental shrubs, suggested that such factors as temperature, day-length and manurial status might be involved. Effects on flowering have, in fact, been found with several different treatments, but attention will be concentrated here on the effect of gravity. That the force of gravity might influence flowering in woody species was suggested in the first place by horticultural practice, rather than by previous experimentation. For example, techniques of training fruit trees in France and Germany involving the pulling over or 'arching' of vertical shoots are claimed to reduce vegetative growth and increase flowering. Wareing & Nasr (1958) have shown experimentally that to grow varieties of apple horizontally leads to a great increase in flowering, and they were able to demonstrate that the important factor was the orientation of the shoot relative to gravity.

A further interest in gravity was stimulated by a study of the morphological position of flower buds in Japanese larch (*Larix leptolepis* (Sieb. & Zucc.) Gordon). These are initiated in the early summer, and then emerge in February or March of the following year. It was noticed that the male flower buds occurred mainly on twigs orientated horizontally or below; and that their arrangement on these twigs was rather striking. The majority of flower buds were to be found on the *lower* sides of more or less horizontal twigs, and on *all* sides of the trailing twigs which are common in this genus. In general, therefore, the flower buds themselves may be expected to point downwards on the horizontal twigs, and horizontally on the trailing twigs.

An assessment of more than 300 male flower buds showed that 98 per cent

of them pointed either horizontally or below. None was found pointing directly upwards. These measurements abundantly confirmed the observations on the morphological position of the male flower buds in larch, and this distribution in fact appears to be a regular feature of this genus. It was not yet clear, however, whether these results indicated an effect of gravity, or whether the flower buds occupied the lower side of horizontal shoots because of some inner, ' fixed ' feature of the abaxial side of the shoot.

In a preliminary experiment it was found that male flower buds could be induced on the upper or adaxial side of a shoot simply by inverting the whole top of the tree. A more precise experiment was carried out in a subsequent year, using material in which flower buds were already detectable macroscopically, though sporophyll primordia had not yet been initiated. Horizontal twigs, bearing presumptive flower buds on their lower sides, were bent and fixed in such a position that the distal part was completely inverted, while still remaining in a horizontal plane.

In each of six such twigs, flower buds subsequently developed on the original upper side, now situated below; while on the original lower side some at least of the presumptive flower buds developed as vegetative buds. In the corresponding control pairs, flower bud distribution was normal. It is evident that, during the early stages of bud initiation, it is possible to convert a developing vegetative bud into a flower bud, and *vice versa*. More important, this experiment indicates that a direct gravitational stimulus is involved in the determination of floral structures in larch.

Certain observations suggested that gravity might also be one of the factors concerned in the attainment of the mature condition in larch. Young trees of this genus frequently have branches which curve strongly upwards, on which flowering has generally not started. As the branches become older, they frequently come to lie more horizontally, and the first appreciable flowering occurs. Later, branches may even come to point downwards, although at the top of the tree the new branches are often upswept for many years.

Clearly, any such ' sagging ' of the branches will result in more and more twigs and buds pointing horizontally and below: that is, in a potentially flowering position, and a correlation between changing branch orientation and the onset of flowering is therefore suggested. Accordingly, a series of experiments was started in which branches were experimentally pulled down and tied either horizontally or in a downwardly pointing position. Young trees were chosen which had borne few or no flowers to date, and the treatments were applied in March and April to branches two to five years old.

A marked effect was produced by both the training treatments in eight out of twelve trees, and a smaller effect in two more. An average of 90 flowers in the tied down branches and 50 in the horizontal compare with few or none in the equivalent control branches. There was considerable variation in the material, but significant differences were shown from the controls in both cases. Moreover, since in several cases the whole of the rest of the treated trees bore no flowers, pulling the branches down has undoubtedly advanced the onset of appreciable flowering by one to two years at least. It therefore appears probable that in nature the gradual ' sagging ' of branches will favour the onset of flowering. Other factors are doubtless involved as well, and may modify the response to gravity. For instance, the weather of the early summer of 1957, in which year this experiment was carried out, was warm and sunny, which is apparently favourable for flower initiation. 1958, on the other hand, was a cool, wet summer, and there were only a few flowers induced in a second experiment. In 1959, however, there was again a large effect of tying down.

It is clear that these effects of gravity on flowering cannot aptly be described under the heading of geotropism. Moreover, although there were marked

reductions in shoot growth in all treatments involving horizontal and downwardly directed branches, this was not necessarily associated with any growth curvatures. The term ' gravimorphism ' has been proposed (Wareing & Nasr, 1958) to cover all such morphological rather than tropic responses. One may then speak of 'gravimorphic treatments' with the same implication as, for example, ' photoperiodic treatments '.

As regards a possible mechanism for these gravimorphic effects in larch, it is too early to do more than make certain observations. It is widely held that both geotropic curvature and apical dominance are brought about by differential distribution of growth hormones, and in some herbaceous plants flowering is thought to be similarly controlled. In this connection, the work of Nečesaný (1958) is of considerable interest. He has reported finding a preponderance of growth-promoting substances in extracts of cambium and young xylem elements of the lower side of horizontal pine shoots. The upper side of these horizontal shoots contained more inhibitors.

A similar technique is to be tested with larch, and an attempt made to relate the findings with the flowering effects. Meanwhile, some circumstantial evidence was provided by the experiment in which horizontal shoots were inverted. When twigs were sectioned it was found that there had been an effect on the position of compression wood, an abnormal type of xylem which is very commonly found on the lower sides of coniferous branches. Compression wood had evidently commenced before the twigs in question were inverted, but it ceased abruptly upon treatment and recommenced on the new lower side. There is thus a possibility that the floral stimulus and the compression wood stimulus were similar, or even the same, since both ' migrated ' round the twig within a few days or a week when the twig was inverted. Nečesaný's claim that he could stimulate compression wood formation by applying synthetic indoleacetic acid lends some further weight to this hypothesis.

To sum up, therefore, gravity has been shown in a number of experiments to influence the flowering and shoot growth of Japanese larch, and it may be that natural changes in branch orientation have similar effects. It appears likely that effects of gravity will also be found with other genera of conifers. Amongst Angiosperms marked effects of gravimorphic treatment on flowering have been found with apple, and smaller effects with cherry (Wareing & Nasr, 1958). On the other hand, birch and plum trees showed no such effects on flowering, though shoot growth was reduced as in larch.

In conclusion, some mention may be made of studies on the effects of other environmental factors. Temperature and day-length have been clearly shown to affect flower initiation of *Pinus contorta*. Young potted trees of this species formed substantially more female cones under short-days than under natural day-lengths, provided that the plants were grown out-of-doors. Under greenhouse conditions, no female cones at all were initiated under short-days over a period of three years.

Another technique which has often been used with success is the old horticultural practice of girdling branches. In one experiment, for instance, an average of nearly 1300 flowers were initiated in branches of larch which were girdled and tied down, compared with 400 in branches merely tied down. These results, and others, suggest that nutritional levels are important in respect to flowering.

There are thus a number of external or environmental factors which affect flowering of conifers. But even when external conditions are favourable to flower initiation, there remains the question of how it is that, for example, a 15-year-old larch tree initiates flowers but a five-year-old tree generally does not. It is clear that there must be internal factors influencing the onset of the reproductive phase in addition to environmental factors. In view of this, it is perhaps

not surprising that, although two-year-old larch were in one experiment grown upside-down for a number of years, they did not form a single flower.

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