SILVA FENNICA VOL. 14, 1980, *N:o* 1: 95—105

FLOWER INDUCTION BY EXOGENOUS PLANT HORMONES IN SCOTS PINE AND NORWAY SPRUCE GRAFTS

OLAVI LUUKKANEN and STIG JOHANSSON

University of Helsinki, Department of Silviculture

SELOSTE:

HORMONIKÄSITTELYN VAIKUTUS MÄNNYN JA KUUSEN VARTTEIDEN KUKINTAAN

1. INTRODUCTION

The Finnish tree breeding programme (cf. Anonymous 1966, 1975, 1978) aims at the creation of about 3 700 ha of clonal coniferous seed orchards. The initial establishment of these first-generation seed orchards has already been completed through the planting of about 1.5 million grafts originating from phenotypically selected plus trees. Scots pine, *Pinus sylvestris* L., is the main tree species used in this seed orchard programme, corresponding to 85 % of the seed orchard area. Norway spruce, *Picea abies* (L). Karst., is the second most important species (15 % of the seed orchard area). Other tree species such as larch *(Larix* spp.) will be of minor importance as far as the total effort is concerned.

As shown in a recent investigation (Bhumibhamon 1978), Scots pine grafts will not flower abundantly until they reach the age of about 20 years, under the conditions prevailing in southern and central Finland, where most of the seed orchards are located. The grafts tend to flower irregularly, particularly at a young age, and the production of male flowers, in particular, is poor during the early development of seed orchards. This leads to pollination of grafts by local tree populations surrounding the seed orchards. Consequently, the utilization of Scots pine seed originating from hybridization between northern plus tree clones in seed orchards and local southern Finnish populations poses a difficult problem, since no investigations are available concerning the genetic value of such seed. Observations on Norway spruce seed orchards in Finland also indicate very low or irregular flowering patterns.

All methods which improve or accelerate flower production in seed orchards will thus have a considerable immediate impact on tree seed procurement in Finland. Owing to the large investments associated with the Finnish seed orchard programme this also has considerable economical importance. It is conceivable that many different methods for improving flowering and seed production can be used simultaneously in seed orchards. Thus, for instance, soil cultivation and fertilization, which are known to have a favourable effect on the development of seed orchard grafts, can be successful (PHARIS 1976, BHUMIBHAMON 1978).

Of the plant hormones which have been used for promotion of flowering in conifers, gibberellins (GA's)[1] seem to be the most promising. Although auxins undoubtedly contribute to the development and differentiation of various organs in conifers, treatments with exogenous auxins (such as IAA or NAA) have generally had significant flower-promoting effects only when applied together with GA (PHARIS 1976). Growth inhibitors (such as CCC) also seem to be effective in promoting flowering of conifer species only when used after a GA application (BLEYMÜLLER 1978). Thus the main emphasis in studies on the hormonal treatments of conifers lies in finding optimum methods of GA application.

The role of gibberellins in regulating vegetative and reproductive growth in conifers has been reviewed in considerable detail by PHARIS and KUO (1977). These authors concluded that endogenous gibberellins definitely control shoot growth in all the conifers so far investigated. Exogenous GA's are also known to affect cambial growth, but no exact relationships have been established between levels of endogenous GA's and cambial activity.

At least 50 different GA's have been identified chemically. Effects of exogenous GA's have been most thoroughly studied in conifer species representing the Cupressaceae and Taxodiaceae families. In such species GA treatments have readily induced abundant and precocious flowering even in juvenile seedlings (KATO 1959, PHARIS *et al.* 1965, OHBA *et al.* 1971, PHARIS 1976). It is already known that GA treatments are not as successful in Pinaceae conifers. However, considerable information about the response of *Pseudotsuga*, *Pinus*, *Picea*, and *Larix* species to GA treatments and the occurrence of endogenous GA's in these genera has accumulated during recent years (cf. OWENS 1969, HASHIZUME 1973, DUNBERG 1973, 1974, 1976; OWENS and MOLDER 1975, PHARIS *et al.* 1976, ROSS and PHARIS 1976, PHARIS 1976, CHALUPKA 1978, ROSS and GREENWOOD 1979).

The review by PHARIS and KUO (1977) lists a total of 47 conifer species in which the effects of GA's or GA-like substances has been tested by bioassay or gas chromatography. As regards Scots pine, very few earlier studies are available: effects of exogenous GA on flowering in this species have been reported by CHALUPKA (1978) only. Endogenous GA's or GA-like substances have, however, been identified from various organs and tissues of *Pinus sylvestris* (IVONIS 1970, MICHNIEWICZ 1970).

As concluded in the review by PHARIS and KUO (1977), the general result obtained in experiments with various GA's on Pinaceae has been that the most commonly available gibberellin GA_3 is relatively inefficient at inducing flowering in these species. This result is in striking contrast to the abundant flowering which can be achieved using GA_3 in mature trees or even juvenile seedlings of Cupressaceae or Taxodiaceae species (KATO 1959, PHARIS *et al.* 1965, OHBA *et al.* 1971, PHARIS 1976). In the Pinaceae conifers, GA_3 seems to be effective only when the application is followed by treatment with the growth retardant CCC, as shown by BLEYMÜLLER (1978) in *Picea abies*.

In contrast to the polar GA_3, non-polar gibberellins such as GA_4, GA_5, GA_7, GA_9 and GA_{14} clearly seem to promote flowering in the Pinaceae conifers. A mixture of two of these effective gibberellins, $GA_{4/7}$, significantly increased flowering in *Pseudotsuga menziesii* grafts and seedlings when used alone or in combination with GA_5, GA_9, or NAA (ROSS and PHARIS 1976, PHARIS *et al.* 1974, 1976). These and later studies with *Pseudotsuga* (*e.g.* ROSS 1976) have indicated that the GA treatments are more effective when applied to grafts of mature clones than to seedlings. Positive results using $GA_{4/7}$ treatments (either $GA_{4/7}$ alone or in combination with GA_9 or NAA) have since been obtained with *Pinus contorta* seedlings (PHARIS *et al.* 1975), and *P. contorta* or *P. taeda* grafts, as well as in *Picea abies*, *P. glauca*, and *P. sitchensis* grafts, as reported by PHARIS and KUO (1977) with reference to studies of several authors.

[1]) Abbreviations: CCC, (2-chloroethyl) trimethyl -ammonium chloride; GA, gibberellin; IAA, indolyl acetic acid; NAA, naphtyl acetic acid.

As regards *Pinus sylvestris*, the results of a recent investigation by CHALUPKA (1978) were also in good agreement with these observations, showing that $GA_{4/7}$, in particular, increased the number of shoots bearing male inflorescences in 15-year-old grafts of this species (from 23% in control trees to 38 % in treated individuals). There was only a slight effect on female flowering, the control level initially being very low. The effect of $GA_{4/7}$ treatments on female or male flowering varied considerably among the five clones included in this study.

The amounts of gibberellins needed to induce flowering in conifers have varied between 10 and 600 μg per shoot; smaller amounts being used in injections and larger ones in foliar sprays. Ethanolic solutions containing 100 to 600 ppm of GA in 50–80 % ethanol are widely used; if gibberellin sprays are applied as aqueous solutions, surfactants are needed to achieve deeper penetration (cf. PHARIS 1976, PHARIS and KUO 1977). Several authors, for instance CHALUPKA (1978) when referring to *Pinus sylvestris*, emphasize the importance of proper timing of the treatments. It is generally agreed that the most effective time for GA treatments in Pinaceae conifers is during shoot elongation one year prior to flowering, when the flower buds are being differentiated. Most investigators use repeated treatments, for instance weekly of biweekly applications during the shoot elongation period.

A wide variety of application methods has been recommended. In addition to foliar sprays and shoot injections, lanolin paste application, hanging bottle injection, or root drench has been used (PHARIS 1976). It is obvious, however, that for practical purposes in large-scale seed orchard management only simple methods such as the spraying of whole grafts or shoots are feasible.

The aim of the present study was to establish whether hormonal treatments would promote flowering in Scots pine or Norway spruce grafts under Finnish conditions. Furthermore, an attempt was made to test the efficiency of different hormones as well as the variation in response among different clones.

The authors are greatly indebted to Professor Richard P. Pharis, University of Calgary, Canada; to Dr. W. Chalupka, Institute of Dendrology, Kórnik, Poland; and to Dr. Arne Dunberg, Umeå University, Sweden, for suggestions and comments concerning our choice of methods and for reporting their own results. The Central Board of Private Forests in Finland (TAPIO) has, through Mr. Antti Pasanen and Mr. Esko Niittylä, provided us with the experimental material as well as with financial aid and assistance during the field work. Financial support has also been obtained from the foundations Niemi-Säätiö and Metsätalouden Edistämisrahasto. Imperial Chemical Industries Ltd. (ICI), Surrey, England, has through Mr. G. W. Elson, kindly supplied the gibberellins used in our study.

2. MATERIAL AND METHODS

In 1976, six Scots pine clones were selected from among the material grown in the clone archive managed by TAPIO and located in Oitti, southern Finland. The grafted trees were 12 years old (about 3–4 m in height) and planted in rows, each row containing one clone, with a spacing of 5.5 m. The selection of the experimental clones was based on an earlier report on flowering intensity and cone production in this clonal collection (TORMILAINEN 1972). Of the six clones, three were among the best and three among the poorest cone producers.

In a Norway spruce collection, managed by the same organization in Hartola, Jääsjärvi (also in southern Finland), six clones were similarly selected and the treatments were carried out with this material following approximately the same methods applied to the pine material. However, no information was available about the previous flowering characteristics of the individual spruce clones, except that most of the grafts had not yet reached flowering stage. The spruce grafts were considerably smaller than the pine grafts mentioned above. The age of the spruce collection was only six years (calculated from the date when the grafts were transferred to the field) and the height of trees only about 2 m.

Table 1 shows the reference numbers of the pine clones used in the present study as well as the origin of these clones. Both experimental sites received the type of maintenance treatments which are normally used in actual seed orchards as far as fertilization (with a compound NPK fertilizer) was concerned. In the pine collection (which was established on alluvial soil with a high clay and slit content, weeding was done by repeated soil cultivation, whereas on the site of the spruce collection (on varying moraine soil) no weeding was carried out.

The main hormonal treatments were spray applications of gibberellins (with 50 % ethanol as the solvent) on the developing shoots. The hormone mixtures applied were as follows: Treatment 1, 400 ppm of $GA_{4/7}$; Treatment 2, 400 ppm $GA_{4/7}$ + 10 ppm NAA; Treatment 3, 300 ppm GA_3 + 100 ppm GA_3; Treatment 4, 100 ppm $GA_{4/7}$ + 300 ppm GA_3; and the control with no spraying (Treatment 0) or spraying with the ethanolic solvent only (Treatment 9).

Table 1. Reference numbers used in the present study, register numbers, and origins of the experimental Scots pine clones. Symbols for cone production category indicate abundant (+) and poor (−) cone producers, according to previous observations.

Reference No. and cone production category	Plus tree register No.	Origin
I −	E 79	Heinola
II +	E 708	Ruokolahti
III −	E 710 D	Ruokolahti
IV +	E 724	Sulkava
V +	E 726 A	Sulkava
VI −	E 732	Sulkava

A gas chromatographic analysis[1] carried out on the gibberellin mixture $GA_{4/7}$ indicated that it contained gibberellins GA_4, GA_7, and GA_9 in the proportions 53: 41 : 6.

In the case of Scots pine, sprayings were applied to 40 whorls of developing new shoots in the upper and to 20 whorls in the lower part of the individual grafts, so as to study possible varying effects in different parts of the tree crown. At the same time the selection of the shoots was aimed at standardizing the shoot material consisting of different grafts and clones — the proportions of upper and lower branches fixed in the present study were selected so as to reflect the actual situation in pine grafts where most branches represent the upper-crown morphology associated with predominantly female flowering (cf. Bhumibhamon 1978). In the case of Norway spruce, no such stratification of the shoot material was possible; consequently an equal number of shoots (40 developing whorls) was selected from the middle part of each spruce graft and treated with gibberellic solutions in the same way as for the pine grafts.

Only one test solution was applied to each graft. Four grafts in each clone received the same treatment. Among the controls, however, two grafts were not sprayed and two were sprayed with the solvent only within each clone; thus the material consisted of 20 grafts per clone, or a total of 120 grafts in the pine and spruce clone archives respectively.

The four replications (blocks) were arranged linearly within each particular clone row. Each block contained one graft per treatment, the same order of treatments being systematically repeated within the block.

Between 1 and 2 ml of the spray solution was required to achieve complete wetting of each of the selected new shoots (smaller amounts were applied at the beginning of the experiments, whereas more was needed to achieve the same degree of wetting at the end of the experimental period). However, all clones received approximately the same amount of solution at any particular round of application. The spraying device was a SPRAYMIST plastic bottle, equipped with a nozzle which gave about 1 ml of fine aerosol droplets each time the handle was depressed. The GA solutions were prepared immediately prior to the experiment and once during the experimental period using 96 % ethanol and were diluted to the final concentration (double volume) when the spray bottles were filled, by adding an equal amount of distilled water. Spray bottles and containers with the concentrated solutions were kept at about 4° C in darkness when not in use.

Hormonal treatments were carried out four times (at intervals of 10 to 16 days) on the selected shoots during the period 24 May to 14 July, 1976.

Air temperature and relative humidity were recorded at both experimental sites using shielded thermohygrographs placed in the middle of the clonal collections (at a height of 2 m in the pine collection and on the ground in the spruce sollection). Shoot elongation of the pine grafts was followed through daily shoot length measurements. Temperature and shoot growth data were collected in order to make quantitative phenological comparisons among the experimental clones and to synchronize the hormonal applications with the annual development cycle of the trees. This was primarily done because earlier investigations have shown that the temperature sum (Sarvas 1972) or the internal stage of development (Hari 1972, 1976; Hari *et al.* 1970) are useful variables for explaining genetic differences in trees. Flowering phenology was also recorded so as to gain more information about the variation among the clones.

[1]) We are indebted to Professor Richard P. Pharis, Calgary, Canada, for the analysis of our $GA_{4/7}$ mixture.

In 1977, one year after the GA treatments, the numbers of male and female flowers on the selected shoots in treated and control trees were counted in the Scots pine collection. Flowering characteristics of the Scots pine grafts were also analysed on the basis of flowering frequency and the size of cone crops in 1969 and 1970 (Tormilainen 1972) and 1975–1976.

The variation in flowering intensity among different treatments and clones was studied using analyses of variance. The basic unit used for expressing the results on flowering intensity of Scots pine was *flowering frequency*, or the number of flowers (female strobili or male inflorescences) per 100 shoots; the shoot being defined as the annual shoot of the flowering year (bearing one or several female strobili at the apex or a male inflorescence at the basal portion of the shoot).

Details of the method used in the present study have been separately presented by Johansson (1979). Results on flowering in 1978, following a replication of the present treatments on Scots pine, are also being published elsewhere (Luukkanen and Johansson 1980).

3. RESULTS

31. General observations

None of the treated or untreated spruce grafts flowered. No male or female flowers were found in the whole spruce clone archive. In 1977, extremely few flowers were also found in natural spruce stands, which indicated that the environmental conditions during the previous years had not favoured flower induction in spruce.

A distinct increase in flowering in Scots pine was observed as a result of spraying with hormone solution. The effect of various treatments on male and female flowering in pine is shown in Figs. 1 and 2. These figures illustrate the effect of different compounds in each clone as well as the average effects in the whole material including six clones. Table 2 summarizes the results for flowering characteristics in the whole Scots pine material and shows the average values for the flowering frequency percentages and relative flowering indices (control = 100).

The results show that treatments with gibberellin had a distinct promoting effect

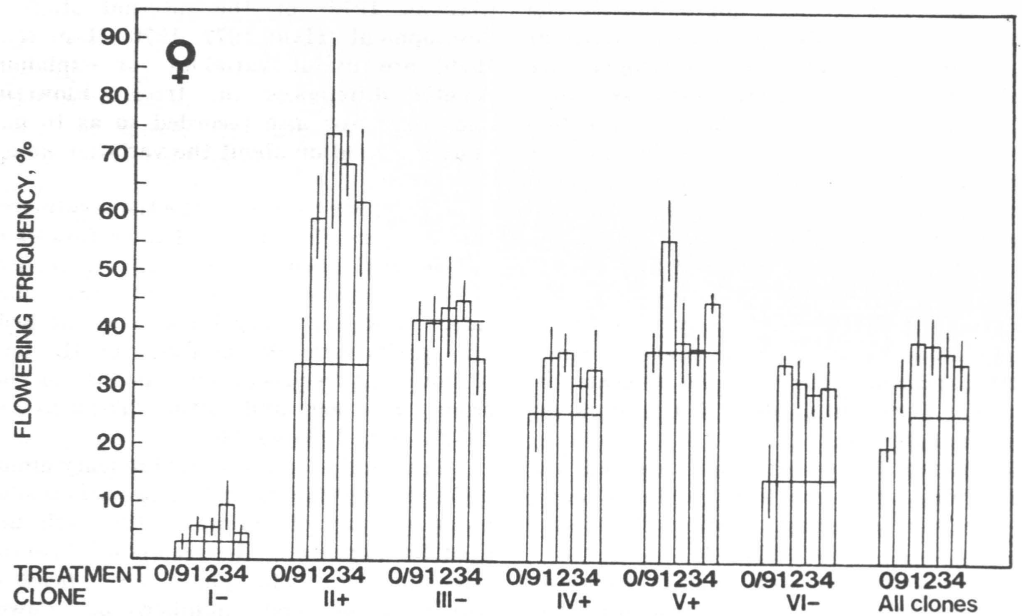

Figure 1. Female flowering in 12-year-old Scots pine grafts after five biweekly treatments with 400 ppm of GA in 50 % ethanol during the shoot elongation period. Treatments: (0) and (9) control (with no treatment or ethanol only, respectively); (1) $GA_{4/7}$; (2) the same with 10 ppm of NAA; (3) $GA_{4/7}$ and GA_3 in a ratio of 3 : 1; (4) the same in a ratio of 1 : 3. The six clones include those with abundant (+) and those with poor (—) cone crops according to previous observations. Flowering frequency equals the number of inflorescences /100 shoots, vertical bars correspond to $\pm s_{\bar{x}}$.

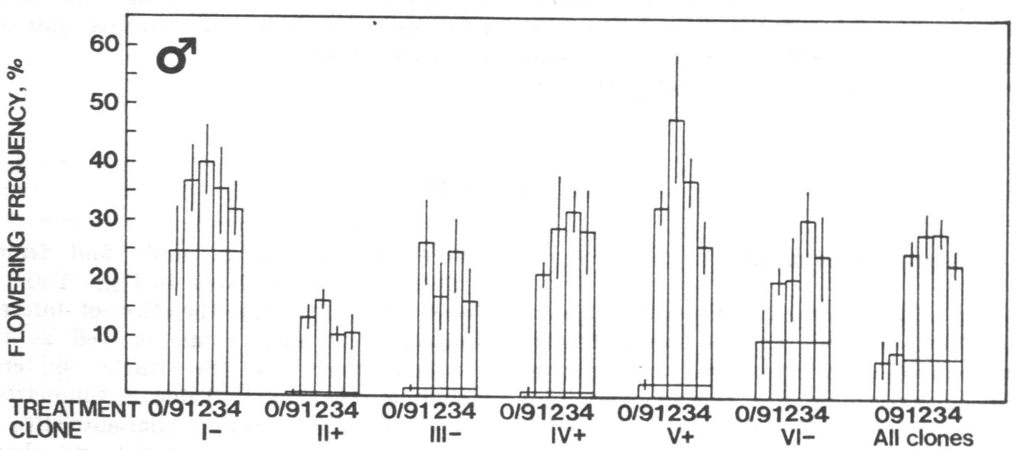

Figure 2. Male flowering in 12-year-old Scots pine grafts after five biweekly treatments with 400 ppm of GA in 50 % ethanol during the shoot elongation period. Treatments and clone symbols as those in Fig. 1.

Table 2. Summary of average values for flowering characteristics of six Scots pine clones. Percentages of flowering frequency equal the number of inflorescences/100 shoots; flowering indices are calculated as compared to mean frequencies in control grafts, including those with no treatment (0) and those sprayed with 50 % ethanol only (9).

Flowering characteristic	Control			GA treatment			
	0	9	Mean	1	2	3	4
Female flowering							
Frequency, %	20.2	31.2	25.7	38.5	38.0	36.5	34.9
Index (control mean = 100)	—	—	100	150	148	142	136
Male flowering							
Frequency, %	6.7	6.8	6.7	25.1	28.4	28.5	23.1
Index (control mean = 100)	—	—	100	376	426	426	345

both on male and female flowering in the Scots pine grafts, although the responses varied as far as different hormones or different clones were concerned. The relative promoting effect was also generally more distinct in male flowering as compared to the induction of female flowers. In general, levels of male and female flowering also varied in that a very small number of male flowers was initially found in the grafts as compared to the number of female flowers.

32. Effect of different hormonal treatments on female flowering

As indicated by Fig. 1 and Table 2, all GA treatments increased the female flowering frequency considerably in the Scots pine grafts. The difference between the mean control level and any one of the GA treatments was also statistically confirmed.

No statistically confirmed differences were found among the GA treatments. The highest flowering frequency was reached, however, using $GA_{4/7}$ alone (Treatment No. 1), and successively smaller frequencies were obtained when 10 ppm of NAA was added to this hormone (No. 2), when a 3 : 1 ratio of $GA_{4/7}$ and GA_3 was used (No. 3), or when this ratio was 1 : 3 (No. 4). The mean flowering frequency in the control grafts (Treatments 0 and 9 combined) reached a value of 25.7 % and the most effective treatment (No. 1, $GA_{4/7}$ alone) increased this value to 38.5 %. Consequently, the flowering index in the most effective treatment showed a 50 % increase in female flower production. The solvent used in GA applications, 50 % ethanol, also increased the female flowering frequency from 20.2 % in untreated grafts to 31.2 % in treated ones. This increase was not statistically significant.

33. Effect of different hormonal treatments on male flowering

All hormonal treatments caused a distinct increase in the male flowering of the Scots pine grafts. This variation was also statistically confirmed in all cases, as far as the whole Scots pine material or individual clones were concerned. On the other hand, no statistically confirmed differences were obtained among the hormonal treatments when average effects in the six clones were analysed.

The highest flowering frequencies were reached in treatments with a mixture of $GA_{4/7}$ and GA_3 in a ratio of 3 : 1 or with $GA_{4/7}$ combined with 10 ppm of NAA (the flowering frequencies being 28.5 % and 28.4 % respectively). The smallest increase in flowering frequency (from 6.7 % in control trees to 23.1 %) was achieved using the mixture of $GA_{4/7}$ and GA_3 in a ratio of 1 : 3.

The control level of male flowering was very low (6.7 %), with practically no difference between untreated grafts and those sprayed with 50 % ethanol only. Consequently, the flowering index (control = 100) reached as high a value as 426 in the two most effective treatments and the value 345 in the treatment with the smallest response, on an average over six clones (Table 2).

34. Variation of hormonal effects among clones

Both male and female flowering varied considerably among the six individual Scots pine clones as far as responses to GA applications were concerned. The promoting effect clearly caused by gibberellins on female flowering in the material as a whole was not statistically significant in every clone (cf. Fig. 1). This variation among clones did not depend on clonal characteristics, *i.e.* the tendency to produce high or low cone crops or the ratio between male and female flowering in control grafts. One clone, identified as Clone I in Figs. 1 and 2, seemed to produce predominantly male flowers. The control level of female flowering was only 3 % in this clone, and the most effective hormonal treatment ($GA_{4/7}$ and GA_3 in a ratio of 3 : 1) caused a large relative increase in flowering (up to about 9 %). A very distict increase in female flowering after GA treatment (both in terms of absolute and relative units) was also found in Clone II, in which the most effective treatment ($GA_{4/7}$ + NAA) produced 74 female strobili/100 shoots, *vs.* the control level of 34 %.

In contrast, male flowering also increased statistically significantly in each individual clone. The largest relative increases were found in clones which had almost no male flowers without the GA treatment but nevertheless produced 10 to 30 male inflorescences per 100 shoots after GA treatment. In Clone I, the male flowering frequency in control grafts was about 25 % and the increase caused by GA (up to about 40 %) remained small in terms of relative units. The highest average male flowering frequency after GA treatment was found in Clone V, in which the treatment with $GA_{4/7}$ + NAA resulted in 48 male inflorescences/ 100 shoots *vs.* the control level of 2.5 % in this clone. Curiously enough, this particular clone did not show any clear responses to the GA treatment as far as female flowering was concerned (cf. Figs. 1 and 2).

4. DISCUSSION

The positive results obtained in flower induction of *Pinus sylvestris* in the present study are also in accordance with earlier conclusions concerning the possibilities of GA applications in the Pinaceae conifers (cf. PHARIS and KUO 1977). The negative result obtained for *Picea abies* in the present work can be interpreted as indicating that a certain flowering tendency has to be brought about by ontogenic factors or the environment before a hormonal treatment will increase the number of flowers. The *Picea abies* grafts probably had not reached the size necessary for flowering, although they were made using scions from sexually mature trees. Earlier observations on the *Picea abies* clonal archive in question had confirmed that virtually no flowers had been produced prior to the present experiments.

Recent results have shown that such *Picea abies* grafts which do not react to GA treatment may show a positive response to hormones when grown in a plastic greenhouse (LUUKKANEN 1980). Earlier studies also indicate that GA applications may increase flowering in this species under field conditions (BLEYMÜLLER 1978, CHALUPKA 1979).

A combination of the auxin NAA with GA did not result in any clear differences in flowering when compared to the use of GA alone. However, a slight (nonsignificant) increase in male flowering was found, when the whole material was analysed (Fig. 2), to be due to NAA. Earlier investigations suggest that NAA alone or at least in combination with GA promotes flowering of Pinaceae conifers and generally tends to enhance maleness (PHARIS 1976, PHARIS and KUO 1977).

The GA concentration used in the present study (400 ppm in 50 % ethanol) was chosen on the basis of earlier experiments. Since this concentration proved to be effective, studies should be carried out in the future to determine whether lower concentrations could be used under similar conditions. Ethanol is, perhaps, not the best solvent for large-scale applications owing to handling problems and health hazards (*e.g.* if commercially available denaturated ethanol is to be used). Ethanolic solutions also seem to damage young shoots; this was especially apparent in spruce grafts and thin shade shoots of the pine grafts in the present study. If aqueous solutions are to be used, surfactants should obviously be added in order to improve the penetration of the solution into the shoots.

The present study suggests that at least a part of the $GA_{4/7}$ found to promote flowering can be substituted by GA_3. In the present work the combined results for six *Pinus sylvestris* clones showed that a mixture of $GA_{4/7}$ and GA_3 in a ratio of 1 : 3 still significantly increased both male and female flowering, although the effect was smaller than when using a ratio of 3 : 1 or $GA_{4/7}$ alone. The highest male flowering frequency was in fact obtained with the mixture of $GA_{4/7}$ and GA_3 in a ratio of 3 : 1, but this variation (as well as all differences between treatments including $GA_{4/7}$ alone or $GA_{4/7}$ in combination with GA_3) was statistically nonsignificant.

The possibility of a partial substitution of $GA_{4/7}$ by GA_3 has a considerable economical inpact as far as large-scale treatments of Scots pine seed orchards are concerned. In the present study, about 400 μg of GA/ shoot was sprayed at each application, which corresponded to 2.0 mg/shoot for a total of five applications during shoot elongation. The treatment of a whole 12-year-old pine graft would require at least 0.4 l of the GA solution at each application, or 2 l/graft during the whole season. This would equal 800 mg of GA/graft, corresponding to an estimated cost of about 40 Fmk/graft during the season.

Many factors in this calculation are only rough estimates. For instance, the production costs of $GA_{4/7}$ can obviously be lowered if large amounts are to be produced by the microbiological process used in the GA manufacturing industry. Development of the application technique alone will substantially reduce the costs. With proper timing, only one or two applications will be needed each year, and also lower concentrations may be used as discussed above. Finally it has to be emphasized that the economic feasibility of GA applications depends on the total genetic and economic gain which can be achieved by using improved seed from treated seed orchards. The total gain is not dependent on the increase in female flowering only but is also affected by the significant increase in male flowering shown to be one of the main results of hormonal treatments in Scots pine by the present work. Economic considerations which still render hormonal treatments in seed orchard management rather difficult do not, however, prevent an immediate application of hormonal treatments to shorten the breeding rotation in conifer breeding programmes.

LITERATURE

ANONYMOUS 1966. Valtakunnallinen metsänjalostuksen kehittämisohjelma vuosiksi 1967—1976. Metsäntutkimuslaitos, metsänjalostuksen tutkimusosasto.

— » — 1975. Metsänjalostustoimikunnan mietintö. Metsänjalostusohjelma vuosiksi 1976—85. Komiteamietintö 25/1975.

— » — 1978. Suomen metsänjalostuksen yleistilastoa. Metsäntutkimuslaitos, metsänjalostuksen tutkimusosasto.

BHUMIBHAMON, S. 1978. Studies on Scots pine seed orchards in Finland with special emphasis on the genetic composition of the seed. Commun. Inst. For. Fenn. 94.4.

BLEYMÜLLER, H. 1978. Versuche mit Fichtenpropflingen zur Blühinduktion durch

Wirkstoffbehandlung. Silvae Genet. 27: 117–122.
CHALUPKA, W. 1978. Effect of growth regulators on the flowering of Scots pine (*Pinus sylvestris* L.) grafts. Silvae Genet. 27: 62–65.
— » — 1979. Effect of growth regulators on flowering of Norway spruce (*Picea abies* (L.) Karst.) grafts. Silvae Genet. 28 (in print).
DUNBERG, A. 1973. Gibberellin-like substances from Norway spruce (*Picea abies*). Physiol. Plant. 28: 358–360.
— » — 1974. Occurrence of gibberellin-like substances in Norway spruce (*Picea abies* (L.) Karst.) and their possible relation to growth and flowering. Stud. For. Suec. 111: 1–62.
— » — 1976. Changes in gibberellin-like substances and indole-3-acetic acid in *Picea abies* during the period of shoot elongation. Physiol. Plant. 38: 186–190.
HARI, P. 1972. Physiological stage of development in biological models of growth and maturation. Ann. Bot. Fenn. 9: 107–115.
— » — 1976. An approach to the use of differential and integral calculus in plant autecology. Univ. Helsinki Dept. Silvic. Res. Notes 13.
— » — , LEIKOLA, M. & RÄSÄNEN, P. K. 1970. A dynamic model of daily height growth of plants. Ann. Bot. Fenn. 7: 375–378.
HASHIZUME, H. 1973. Studies on flower bud formation and flower sex differentiation and their control in conifers. Bull. Tottori Univ. For. 7: 1–139.
IVONIS, I. Yu. 1970. Gibberellinopodobnye veshchestva v pochkakh i generativnykh organakh sosny obyknovennoi. Fiziol. Rast. 16: 937–939.
JOHANSSON, S. 1979. Tutkimuksia gibberelliinien vaikutuksesta männyn vartteiden kukintaan. Pro gradu -työ, Helsingin yliopisto, metsänhoitotieteen laitos. 65 s.
KATO, Y. 1959. Stimulation of differentiation of flower buds in sugi (*Cryptomeria japonica*). J. Jap. For. Soc. 41: 138–141.
LUUKKANEN, O. 1980. Hormonal treatment increases flowering of Norway spruce grafts grown in a plastic greenhouse. Foundation for Forest Tree Breeding Annu. Rep. 1979, pp. 20–26.
— » — & JOHANSSON, S. 1980. Effect of exogenous gibberellins on flowering in *Pinus sylvestris* L. grafts. (In prep.).
MICHNIEWICZ, M. 1970. Growth regulators. *In* Outline of Physiology of Scots pine (*Ed.* BIALOBOK, S. & ZELAWSKI, W.), pp. 269–301. Foreign Scient. Publ. Dept., Warsaw.
OHBA, K., OKADA, Y. & MURAI, M. 1971. Advancing the generation of sugi (*Cryptomeria japonica* D.) done by greenhouse cultivation. J. Jap. For. Soc. 53: 133–137.
OWENS, J. N. 1969. The relative importance of initiation and early development in cone production in Douglas-fir. Can. J. Bot. 47: 1039–1049.
— » — & MOLDER, M. 1975. Development of long-shoot terminal buds of *Pinus contorta* *In* Management of Lodgepole Pine Ecosystems (*Ed.* BAUMGARTNER, D. M.), pp. 86–105. Washington State Univ., Pullman, Washington.
PHARIS, R. P. 1976. Manipulation of flowering in conifers through the use of plant hormones. *In* Modern Methods in Forest Genetics (*Ed.* MIKSCHE, J. P.), pp. 265–282. Springer-Verlag, Berlin.
— » — & KUO, C. G. 1977. Physiology of gibberellins in conifers. Can. J. For. Res. 7: 299–325.
— » — , ROSS, S. D. & WAMPLE, R. L. 1974. Promotion of flowering in seedling Douglas-fir and lodgepole pine by certain of the gibberellins, alone and in combination with each other and with an auxin. *In* Proc. 3rd N. Am. For. Biol. Workshop (*Ed.* REID, C. P. & FECHNER, G. H.), p. 372. Colorado State Univ., Ft. Collins, Colorado.
— » — , ROSS, S. D., WAMPLE, R. L. & OWENS, J. N. 1976. Promotion of flowering in conifers of the Pinaceae by certain of the gibberellins. Acta Hortic. 56: 155–162.
— » — , RUDDAT, M., PHILLIPS, C. C. & HEFTMANN, E. 1965. Precocious flowering of Arizona cypress with gibberellins. Can. J. Bot. 43: 923–927.
— » — , WAMPLE, R. L. & KAMIENSKA, A. 1975. Growth, development and sexual differentiation in *Pinus*, with emphasis on the role of the plant hormone gibberellin. *In* Management of Lodgepole Pine Ecosystems (*Ed.* BAUMGARTNER, D. M.), pp. 106–134. Washington State Univ., Pullman, Washington.
ROSS, S. D. 1976. Differential flowering responses by four-year-old Douglas-fir seedlings and equi-sized two-year-old grafts to gibberellins and auxin. Acta Hortic. 56: 163–167.
— » — & GREENWOOD, M. S. 1979. Promotion of flowering in the Pinaceae by gibberellins. II. Grafts of mature and immature *Pinus taeda*. Physiol. Plant. 45: 207–210.
— » — & PHARIS, R. P. 1976. Promotion of flowering in the Pinaceae by gibberellins. I. Sexually mature, nonflowering grafts of Douglas-fir. Physiol. Plant. 36: 182–186.
SARVAS, R. 1972. Investigations on the annual cycle of development of forest trees. Active period. Commun. Inst. For. Fenn. 76.
TORMILAINEN, M. 1972. Havaintoja Oitin siemenviljelyksen mäntykloonien kukinnasta ja käpysadosta. *Summary* Studies of flowering and cone crop in a seed orchard of Scots pine. Silva Fenn. 6: 147–156.

SELOSTE:

HORMONIKÄSITTELYN VAIKUTUS MÄNNYN JA KUUSEN VARTTEIDEN KUKINTAAN

Keskusmetsälautakunta Tapion Oitin männynvartekokoelmassa ruiskutettiin kuutta (käpysatotutkimuksissa erityyppiseksi todettua) kloonia edustavien 12-vuotisten vartteiden oksia hormoniliuoksilla n. kahden viikon välein verson pituuskasvuvaiheen aikana touko-heinäkuussa v. 1976. Käsittelyihin sisältyi kontrollin lisäksi gibberelliinisekoituksia ($GA_{4/7}$ yksinään sekä GA_3:n kanssa eri suhteissa yhdistettynä). Lisäksi kokeiltiin yhtä auksiinia ($GA_{4/7}$-liuokseen lisättiin 10 ppm NAA:ta). Gibberelliinien kokonaisväkevyys oli kaikissa hormoniliuoksissa 400 ppm. Liuottimena oli 50 % etanoli.

Vuoden kuluttua ruiskutuksista, kesällä 1977, tutkittiin käsiteltyjen männynvartteiden emi- ja hedekukinta. Kaikki hormonikäsittelyt lisäsivät selvästi sekä emi- että hedekukkien määrää, joskin vaikutus hedekukintaan oli huomattavasti voimakkaampi. Tehokkain hormoniyhdistelmä lisäsi emikukintaa 50 %:lla kontrolliin (käsittelemättömien vartteiden ja pelkällä etanolilla ruiskutettujen vartteiden keskiarvoon) verrattuna. Heikoimmallakin hormoniyhdistelmällä ($GA_{4/7}$ ja GA_3 suhteessa 1 : 3) saavutettiin 36 %:n lisäys. Eri hormonikäsittelyllä aikaansaatu hedekukinta oli 3.5–4.3-kertainen käsittelemättömiin ja pelkällä etanolilla ruiskutettuihin vartteisiin verrattuna. Myös pelkkä 50 % etanoli lisäsi emikukintaa täysin käsittelemättömiin vartteisiin verrattuna noin puolitoistakertaiseksi; hedekukintaan ei liuottimella sen sijaan ollut vaikutusta.

Vaikka eri hormoniyhdistelmien väliset vaikutuserot olivat vähäisiä, näytti ilmeiseltä, että $GA_{4/7}$ on tehokkaampi männyn kukinnan lisääjänä kuin kaupallisesti saatavissa oleva GA_3. Osa ensinmainitusta, toistaiseksi vielä kalliista ja rajoitetusti saatavissa olevasta hormonista voitaneen korvata jälkimmäisellä halvemmalla aineella ilman että kukintaa lisäävä vaikutus oleellisesti pienenee. Auksiinin lisävaikutuksesta pelkkään gibberelliinikäsittelyyn verrattuna kokeet eivät antaneet selvää vastausta.

Samanaikaisesti edelläkuvatun mäntyä koskevan tutkimuksen kanssa kokeiltiin hormonien vaikutusta Kml Tapion Hartolassa sijaitsevassa kuusen vartekokoelmassa. Periaatteessa Oitissa männyllä suoritettuihin kokeisiin verrattuna täysin samanlaiset käsittelyt eivät aikaansaaneet kuusen vartteissa minkäänlaista näkyvää vaikutusta. Kyseiset (vasta 6-vuotiaat) kuusen vartteet eivät kuitenkaan vielä ilmeisesti olleet kukkimisiässä, ja ylipäätään v. 1977 ei havaittu kyseisessä kokoelmassa lainkaan kuusen kukkia. Tämä vuosi oli myös heikko kukintavuosi luontaisissa kuusikoissa. Tämän johdosta pääteltiin, että hormonikäsittelyillä voidaan edistää havupuiden vartteiden kukintaa ilmeisesti vain silloin kun sisäiset ja ulkoiset säätelytekijät muutoin luovat edellytykset vartteiden kukkimiselle. Männyn siemenviljelyksissä nämä edellytykset lienevät yleisesti olemassa; sensijaan kuusen vartteiden kukinnan lisääminen saattaa vaatia ympäristöolosuhteiden säätelyä esimerkiksi muovihuoneiden avulla.

Näyttää ilmeiseltä, että jo nyt voidaan gibberelliinikäsittelyjä käyttää hyväksi havupuiden vartteiden sukupolviajan lyhentämisessä käytännön jalostustyössä. Tehokkaan hormonin korkeat valmistuskustannukset estävät vielä menetelmän käytön männyn siemenviljelyksillä. Mikäli menetelmää onnistutaan vielä kehittämään, esimerkiksi vähentämään tarvittavan hormonin määrää ja ajoittamaan käsittely täsmälleen oikeaan ajankohtaan, voidaan kustannuksia ehkä alentaa niin paljon, että laaja-alaiset siemenviljelysten käsittelyt tulevat kannattaviksi. Nyt saadut tulokset osoittavat joka tapauksessa, että hormoneilla pystytään lisäämään vartteiden kukintaa. Huomionarvoista on myös, että hormonikäsittely lisää männyn vartteissa kaikkein selvimmin hedekukintaa. Tuloksia arvosteltaessa on siten otettava huomioon kukinnan ja siemensadon määrällisen lisääntymisen ohella siemenviljelyksen pölytyssuhteiden parantumisen kautta saavutettava jalostushyöty.