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Sisällys Contents

| OLAVI LUUKKANEN: Effects of gibberellins GA, and GA, on flowering in Scots pine grafts | 359 |
|--|-----|
| Seloste: Havaintoja gibberellinien GA, ja GA, vaikutuksesta männynvartteiden kukintaan | 365 |
| MARTTI SAARILAHTI: Mikroaaltotutka jään paksuuden mittauk- seen | |
| | 366 |
| Summary: Radar measurement of ice thickness on ice roads and landings | 376 |
| RISTO JALKANEN, SATU HUTTUNEN and SEIJA VÄISÄNEN: The wax structure of the developing needles of <i>Pinus sylvestris</i> progenies infected by <i>Lophodermella sulcigena</i> | 377 |
| Seloste: Nuorten neulasten vaharakenne harmaakaristeisissa mäntyjälkeläistöissä | |
| This was a superior of the sup | 381 |
| SATU HUTTUNEN (ed.): Proceedings of the symposium: "Air pollutants as additional stress factors under northern conditions." Novem- | |
| ber 11-13, 1980, Oulu, Finland | 382 |
| Ilman epäpuhtaudet kasvien stressitekijöinä pohjoisessa. Oulussa 11.–13. 11. | |
| 1980 pidetyn symposiumin esitelmät | 504 |
| | |

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EFFECTS OF GIBBERELLINS GA4 AND GA7 ON FLOWERING IN SCOTS PINE GRAFTS

OLAVI LUUKKANEN

SELOSTE:

HAVAINTOJA GIBBERELLIINIEN GA, JA GA, VAIKUTUKSESTA MÄNNYNVARTTEIDEN KUKINTAAN

Saapunut toimitukselle 1981-05-28

Ethanolic sprays of GA4 or GA7 on 9-year-old Scots pine grafts, repeated four times during the shoot elongation period, resulted in a statistically significant increase in female flowering one year after the treatment. Of the two compounds, GA4 seemed to be somewhat more efficient, yielding 47 female strobili/100 shoots vs. 36 and 6 strobili/100 shoots in GA, and control treatments respectively. The mixture GA_{4/7} was also applied and seemed to have an effect intermediary to those of the purified compounds. However, due to the limited amount of material, none of the differences between the gibberellins could be statistically confirmed. Male flowering frequencies were also too low to allow any firm conclusions, but the numerical results suggested that the purified gibberellins may promote male and female flowering in different ways.

INTRODUCTION

The potential advantage of an increase in nutrients) are available and commonly used the flowering frequency and seed crop of in seed orchards. Thus any new method conifers has become evident in both practical aimed at promotion of flowering will seed procurement and forest tree breeding. Earlier Finnish investigations have shown that lowering the age at which seed orchard grafts begin to flower abundantly would definitely facilitate the national seed orchard programme. Apart from seed crops, the genetic gain would also be increased as a result of such a measure, as shown for Scots pine — by far the most important species used in Finnish seed orchards – by BHUMIBHAMON (1978).

mostly carried out under nursery or greenhouse conditions, a great variety of flowerpromoting methods can be used, whereas only cheap and less intensive management

probably find its first application as a tool of tree breeders, for instance in provenance or plus-tree hybridization work.

Obviously, no method used to increase the flowering frequency and seed crop in Scots pine (whether in seed orchards or in breeding nurseries and greenhouses) can alone solve the problem of poor flowering and long breeding rotation in this species. The best possible results will, instead, most probably In advanced tree breeding work, which is be achieved by combining various flowerpromoting methods.

The effect of plant hormones, particularly gibberellins (GAs), on flowering in conifers has been frequently discussed in the literature methods (such as fertilization with mineral (cf. PHARIS and KUO 1977, LUUKKANEN

and JOHANSSON 1980a). Of the large number of naturally-occurring GAs (more than 50 have already been separated and identified), only one, GA3, is commercially available in sufficiently large quantities and cheap enough to be widely used in artificial control of plant growth and development. This gibberellin represents the group of more-polar GAs, higher polarity being associated with a more oxidized form of the GA HO molecule and a stronger affinity for such materials as silicic acid in partition chromatography (PHARIS and KUO 1977).

Of the less-polar gibberellins, GA4 and GA7 are among the most commonly available ones. They have also been used on an experimental scale in connection with flower-promotion work on conifers. Since the molecular structures of GA4 and GA7 are very similar (Figure 1), these GAs are not easily separable by chromatographic methods and are therefore usually applied as a mixture, GA_{4/7}. The first attempts to promote flowering in conifers by means of KANEN and JOHANSSON 1980 a, b). No gibberellins were made using GA3, positive results being obtained in a number of conifers representing the Taxodiaceae and Cupressaceae families (such genera as Cryptomeria, Cupressus, Juniperus and Thuja; KATO et al. 1959). In Pinaceae conifers, however, GA, (alone or in combination with other gibberellins, auxins or growth retardants) seems to have a marginal effect only, as discussed in the review by PHARIS and KUO (1977).

According to recent summaries on earlier investigations (PHARIS et al. 1980, WHEEL-ER et al. 1980), the mixture GA_{4/7} has been shown to possess a flower-promoting effect in 13 species of the Pinaceae family (including Pinus sylvestris and six other pine species). In earlier Finnish studies on P. sylvestris, only hormonal treatments which include GA_{4/7} have distinctly increased the flowering frequency. On the other hand, a combination of GA_{4/7} with GA₃ in a ratio of 3:1 or, in the case of male flowering, 1:3, did not result in significantly lower flowering

COOH CH₃ COOH CH₃ COOH

Fig. 1. The chemical structure of the polar gibberellin GA₃ and some less-polar gibberellins (GA₄, GA₇, and

Kuva 1. Polaarisen gibberelliinin GA3 ("gibberelliinihappo") sekä eräiden vähemmän polaaristen gibberelliinien (GA4, GA7 ja GAo) kemiallinen rakenne. Hydrofiilisten ryhmien -COOH -OH määrä on suorassa suhteessa polaarisuu-

frequencies than with GA_{4/7} alone (LUUKdistinct effects on flowering have been obtained in small-scale experiments with GA3 or GAo alone (the latter being a less-polar gibberellin) on Finnish P. sylvestris grafts.

Since it is obviously possible to alter the ratio between GA, and GA, (as well as the ratio between these and other GAs) in the final GA product available for practical use, a more comprehensive knowledge of the separate physiological effects of GA4 and GA7 would be of great interest. With this consideration in mind, the present experiment was conducted in order to clarify whether there are any differences in the flower-promoting effects of GA4 and GA7.

Acknowledgement: The author wishes to express his gratitude to Imperial Chemical Industries (ICI) Ltd., Plant Protection Division, Haslemere, Surrey, England, and personally to Mr. G. W. Elson of the above company, for providing the purified GA samples and for kind advice concerning the present study. Financial support was obtained from Suomen Luonnonvarain Tutkimussäätiö.

VINABILITA TEL OUIX LA CELLA LA CONTRA L

MATERIAL AND METHODS

A total of 14 nine-year-old Pinus sylvestris L. grafts, originating from a northern Finnish plus tree (located at Ylitornio, 66° 40' N., 24° 50' E., elevation 150 m; register No. P-244), were transplanted in the nursery of the Hyytiälä Forestry Field Station of the University of Helsinki (60° 50' N., 24° 20' E., elev. 150 m) on 1 June 1979. These grafts had previously been grown at the Ruotsinkylä Forest Tree Breeding Station (the Finnish Forest Research Institute) where they were lifted one week before being transported to Hyytiälä. Prior to transplanting the grafts were stored in a cool cellar. Soil preparation at the transplanting site included ploughing and harrowing, but no nutrients were added to the soil. The only maintenance measure (in addition to watering at transplanting) was manual weeding during the course of the experiment.

The grafts were approximately 1.5 m high at transplanting and produced, on an average, 55 new vegetative shoots each in 1980, when the experiment was terminated. Hormonal treatments in 1979 were randomized within the single row (with 3 m spacings) containing the experimental ma-

In order to study the separate effects of GA4 and GA7 three groups of grafts from the transplanted material were randomly selected, each consisting of four grafts. These groups were used to test the effects of the two hormones, as well as to show the control level of flowering, respectively. The control group consisted of two completely untreated grafts and two grafts sprayed with the solvent only.

Apart from these 12 grafts, the material also included two grafts treated with a GA4/2 mixture (the approximate ratio between the different components GA4, GA7, and GA9 being 53:41:6 according to analysis data kindly provided by Professor R. P. Pharis, Calgary, Canada).

The hormones were applied in an ethanolic solution (50 % ethanol v/v), which also contained 0.01 % (100 ppm) of the cationic surfactant AROMOX C12. The GA concentration was 200 mg 1⁻¹ (200 ppm) in all hormonal treatments.

Spraying applications were carried out four times (12, 19 and 26 June, and 17 July 1979). Sprays were applied to all the elongating shoots in the treated grafts until complete wetting of the shoots was achieved. On an average, 53 ml of the spray solution was needed for each graft during each of the four application rounds.

In 1979, the experimental grafts had flowered approximately one week prior to the first applications of hormones; phenological observations indicated that the current year's female strobili reached the stage at which they bend to take up a horizontal position between the first and the second application round.

One year after the treatments with hormonal sprays, in 1980, the number of male and female inflorescences as well as the number of new (current year's in 1980) vegetative shoots was checked in all grafts. The main results were expressed in terms of flowering frequency (the number of male or female inflorescences/100 vegetative shoots).

RESULTS

All hormonal treatments caused a distinct increase in the female flowering frequency of Scots pine grafts, as illustrated by Table 1. In contrast to female flowering, no clear effects on the number of male flowers were observed. As a whole, the number of male

was relatively much larger than the corresponding variation in female flowering.

Based on the flowering frequencies, the treatments with GA₄, GA₇, and GA₄/₇ all increased the number of female inflorescences/100 shoots by six or seven times as flowers was very low and also the variation in compared to the inflorescences on the control male flowering within each treatment group grafts. A t-test also confirmed this variation

| Treatment | No. of grafts | Number of inflorescences $\pm s_{\bar{X}}$ | | | |
|---------------------------------------|---------------|--|-------------------------------------|--------------------------------------|----------------------------------|
| | | Female flowering | | Male flowering | |
| | | Per 100 shoots | Per graft | Per 100 shoots | Per graft |
| No spraying Solvent only Control mean | 2 4 | 5.1± 1.25 6.7± 1.10 5.9± 0.83 | 4.0±1.00 4.0±1.00 4.0±0.58 | 0.7± 0.65 5.6± 5.55 3.1± 2.68 | 0.5±0.50 3.0±3.00 1.8±1.44 |
| GA ₄ GA ₇ | 4 2 | 46.8±12.87 35.9±10.04 40.6±16.85 | 24.0±4.15 19.5±7.73 22.0±9.19 | 2.2± 0.83 4.6± 1.63 25.0±17.68 | 1.0±0.41 2.3±0.75 9.5±6.72 |

as statistically significant (P>0.05) as far as the pure compounds or the mixture GA_{4/7} were concerned. The same trend was observed in the number of female flowers per graft, although this variation could not be confirmed statistically, due to the limited amount of material and the considerably large variation within each treatment group.

The largest number of female flowers was produced in grafts treated with GA4 alone (on an average, 46.8 female inflorescences/100 shoots vs. 5.9 inflorescences/100 shoots in control grafts). Somewhat smaller frequencies were obtained using GA, or the mixture GA_{4/7} (35.9 and 40.6 female inflorescenes/100 shoots respectively). Thus the mixture GA_{4/7} produced a number of female flowers which was almost exactly intermediary to the effects of the purified compounds. However, due to the limited material, none of these differences between the effects of the three compounds could be statistically confirmed.

The increase in the female flowering frequency obtained using GA4 instead of GA7 was, in terms of relative units somewhat larger (31 %) when the number of flowers per graft was used as the measure, as compared to the relative difference in flowering frequencies expressed per 100 shoots (23 %). Such a discrepancy between the two ways of expressing relative increases was caused by the variation in graft size within and between treatment groups. Not unexpectedly, the range of variation in female flowering was larger when the number of flowers per graft

instead of the number per 100 shoots was

The number of male flowers in the experimental grafts was generally very low. Only zero to three male inflorescences per graft (0 to 7.5 inflorescences/100 shoots) was found in the grafts sprayed with the GA4 or GA, solutions (one graft out of four being without any male flowers in both of these groups).

Although the limited size of the material rendered firm conclusions concerning male flowering difficult, the numerical results indicated that the male flowering frequency in grafts treated with GA, was somewhat higher than in those treated with GA4. Thus the comparison between these two gibberellins suggested that the effect on male flowering was opposite to the case for female flowering after these treatments. Since only two grafts were sprayed with the mixture GA_{4/7}, and one of them produced no male flowers, the effect of GA_{4/7} on male flowering in the present material remainded obscure, although a seemingly high male flowering frequency after this treatment is presented in Table 1.

As far as the effect of the ethanolic solvent (50 % ethanol with 0.01 % AROMOX C12) was concerned, the results suggested that the solvent alone had a slight promoting effect on the number of female flowers/100 shoots (Table 1). The limited amount of material did not, however, allow any statistical confirmation of this result.

It is not known in detail which structural properties of the gibberellin molecules are associated with their known physiological action in trees. Nevertheless, distinct effects of several different gibberellins have been found in Scots pine and other Pinaceae conifers by a number of investigators. Earlier studies indicate that less-polar GAs, such as the enhance the effect of GA_{4/7} on female mixture GA_{4/7} or GA₉, promote flowering in flowering in Pseudotsuga (PHARIS et al. 1980) these tree species, whereas the polar GA_3 , at or be at least as effective as $GA_{4/7}$, as shown in least when applied alone, seldom causes an Pseudotsuga (ROSS et al. 1980) and Picea increase in flowering frequency (PHARIS and KUO 1977).

GAs has led to the ranking of these compounds, in the order of their decreasing efficiency: $GA_{4/7}>GA_{9}>GA_{14}>GA_{5}$ (PHA-RIS and ROSS 1976). Investigations have also shown that, at least in Pseudotsuga, both GA₅ and the polar GA₃ are generally ineffective 1976; cf. PHARIS and KUO 1977) or (ROSS et al. 1980). Experiments carried out synergistic increases in flowering frequency on Scots pine have not indicated positive using the combination of GA₅ and GA_{4/7} results from applications of GA, or GA, in cases where GA_{4/7} distinctly promotes flowering (LUUKKANEN and JOHANSSON 1980 b). The general picture of the effects of different less-polar GAs is further complicated by the results which show that the GA_{4/2} mixture can be partly substituted for by the polar GA₃, without any significant loss of efficiency, as demonstrated in Pseudotsuga (ROSS and PHARIS 1976, PHARIS et al. 1980), Picea sitchensis (TOMPSETT and FLETCHER 1979), Pinus taeda (ROSS and GREENWOOD 1979), and Pinus sylvestris (LUUKKANEN and JOHANSSON 1980 a,

Thus the varying degree of success obtained in connection with applications of various less-polar GAs, does not suggest that there is a straightforward relationship between the degree of polarity (or other characteristics associated with the molecular structure of GAs) and the physiological effects of GAs in conifers. Further evidence for this inference is shown in experiments in which GA₀ was included. GA9 has no hydroxyl groups contrast, both GA4 and GA7 seem to possess a attached to the gibbane skeleton of the molecule and thus chemically represents an extreme case among the less-polar GAs (one hydroxyl groups is present in GA4, GA5, and GA₂, whereas the polar GA₁ and GA₃ contain

two hydroxyl groups). Various investigations have shown that GA₉, when applied alone, is less efficient in promoting flowering than the mixture GA_{4/7}, at least as far as flowering in Pseudotsuga is concerned (PHARIS and ROSS 1976, ROSS and PHARIS 1976). However, GAo may, under certain circumstances, sitchensis (TOMPSETT 1977).

Of the GAs with one hydroxyl group only, Comparison between various less-polar GA₅ generally shows smaller flower-promoting effects than the GA_{4/7} mixture (PHARIS and ROSS 1976, PHARIS et al. 1980). Nevertheless, a few studies on Pseudotsuga also indicate a positive effect of GA₅ on male flowering (ROSS and PHARIS (ROSS et al. 1980).

> A most intriguing result was presented by TOMPSETT (1977), who found that GA, did not affect the flowering frequency in Picea sitchensis under conditions which resulted in distinct positive effects with GA4/7 (when the latter compound was applied either alone or in combination with GA₃ and GA₅). Similar conclusions about the effect of GA_{4/7} as compared to that of purified GA4 have also been presented for Pseudotsuga (PHARIS and ROSS 1976). These results have led to the suggestion that flowering frequencies in Pinaceae conifers are not affected by the less-polar GAs in general, but by the mixture GA_{4/2} only (cf. ROSS and GREENWOOD 1979). Accordingly, the positive results often obtained with GA_{4/7} applications would be caused by the synergistic effect of GA4 and GA, together, implying a less distinct effect when either component is applied alone (PHARIS and ROSS 1976).

The present results for Pinus sylvestris are not in agreement with such considerations. In statistically significant flower-promoting effect. In addition, the increase in female flowering frequency using GA4 in the present investigation, was larger than that obtained using GA₁, and the efficiency of GA_{4/1} seemed

material, differences between the GAs (purified compounds and their mixture) could not be confirmed statistically, however. Further studies are also warranted to clarify the separate effects of GA4 and GA7 on male flowering in Pinus sylvestris.

Interconversions of various endogenous or exogenously applied GAs appear to be a factor which may explain the variation in the flower-promoting effects of these hormones in conifers. For instance, it is known that the less-polar GA₄ is converted to GA₂, GA₃₄, and other more polar GAs through addition of a hydroxyl group to the gibbane skeleton in metabolic pathways in Pseudotsuga seedlings PHARIS and KUO 1977, WAMPLE et al. 1975). Similar processes have also been demonstrated in Pseudotsuga shoots, in which tritiated GA4, when applied exogenously, was converted into a number of more polar metabolites, such as GA₃₄ and GA₃₉ (WAMPLE et al. 1975).

Radioactively labelled GA, has also been used in studies on germinating Pinus attenuata pollen; during pollen germination an increased level of more polar GAs was observed (KAMIENSKA et al. 1976). A mechanism based on varying degrees of efficiency of the GA conversion pathways could thus also explain the difference between the results of GA₄ application in earlier investigations and in the present work. However, the clarification of such a fact that the amount of exogenous GA may affect the direction and efficiency of the GA interconversion pathways (cf. PHARIS and KUO 1977, p. 318).

Manipulation of the ratio between male and female flowers by means of GA treatment is of considerable practical importance, as discussed in the literature (e. g. PHARIS and ROSS 1976, PHARIS and KUO 1977). Most

to be intermediate to the purified compo- of the earlier investigations show that nents. Owing to the limited size of the hormonal treatments frequently promote female flowering, whereas the effect on male flowering is often less distinct. However, Finnish investigations have earlier demonstrated distinct increases in male flowering in (12 to 14-year-old) Pinus sylvestris grafts after GA_{4/2} treatment (LUUKKANEN and JOHANSSON 1980 a, b). Further work is needed to clarify whether increases in the number of flowers of one sex are associated with a decrease in the number of flowers of the other, following hormonal treatments. Studies on Pinus sylvestris grafts in Poland suggest that such relationships are possible and may be associated with different effects of exogenous hormones during different stages of the seasonal development of flower initials (CHALUPKA 1980).

The present results give some support to the possibility that applications of GA4 and GA₂, when used during the same period of time, yield a different male/female ratio, GA4 having a more distinct increasing effect on female flowering. The extremely small number of male flowers in the young grafts of the present study did not allow, however, definite conclusions to be made.

The relatively small difference between the overall effects of GA4 and GA7 on flowering in Pinus sylvestris and especially between the effects of pure compounds and the GA_{4/2} mixture, as observed in the present study, suggest that factors other than the proportions of the two components of the mixture GA_{4/2} mechanism must also take into account the will determine whether or not this mixture can be used as a tool in breeding programmes or seed orchard management. In particular, the proper timing of GA applications may become more important instead, especially if a change in the ratio between GA4 and GA7 in this mixture or the manufacture of these components in purified form is associated with significant increase in the cost of GA treatments.

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SELOSTE:

HAVAINTOJA GIBBERELLIINIEN GA, JA GA, VAIKUTUKSESTA MÄNNYNVARTTEIDEN KUKINTAAN

Aikaisemmat tutkimukset ovat osoittaneet hormonikäsittelyn lisäävän männynvartteiden emi- ja hedekukintaa avomaalla myös Suomen olosuhteissa. Nimenomaan perusteella jo käytettäväksi ainakin pienimittakaavaisessa sensijaan vielä tarkempia tutkimuksia mahdollisimman halvan ja tehokkaan hormonikäsittelyn löytämiseksi.

Näiden tietojen pohjalta pyrittiin käsilläolevassa työssä erikseen tutkimaan havupuiden hormonikäsittelyissä yleisimmin käytössä olevan gibberelliinisekoituksen GA_{4/7} osakomponenttien GA₄ ja GA₇ vaikutusta vartteiden kukintaan. Materiaalina olivat Helsingin todeta tilastollisesti merkitseviksi; hormonien keskinäisyliopiston metsäasemalla Hyytiälässä taimitarhaolo- ten erojen merkitsevyyttä ei sensijaan vielä pystytty tilassuhteissa kasvavat, pienikokoiset, kokeen aloitushetkellä yhdeksänvuotiaat (pohjoissuomalaisen pluspuukloonin P 244) vartteet. Hormonit (sekä kumpikin gibberelliini erikseen että näiden sekoitus) ruiskutettiin 50 % etanoliin liuotettuna vartteiden saman vuoden kasvaimiin neljästi viitteitä siihen suuntaan, että puhtaat gibberelliinit GA4 12. 6.-17. 7. 1979 välisenä aikana. Liuokset sisälsivät ja GA, eivät ehkä samassa suhteessa lisää sekä emi- että lisäksi 0.01 % kationista pintajännitystä alentavaa ainetta hedekukintaa.

AROMOX C12. Gibberelliinien pitoisuus oli kaikissa tapauksissa 200 ppm (200 mg 1⁻¹). Kontrollina olivat pelkällä liuottimella (50 % etanoli + AROMOX) ruiskutegibberelliinisekoitus GA4/7 sopii nykyisen tietämyksen tut sekä kokonaan käsittelemättömät vartteet. Puhdistetut gibberelliinit GA4 ja GA7 samoin kuin niiden sekoitus ja intensiivisessä jalostustoiminnassa, jossa hormonikus- GA_{4/2} lisäsivät kaikki selvästi emikukintaa v. 1980. Suurin tannusten merkitys on suhteellisen vähäinen. Siemenvil- emikukintamäärä todettiin GA4:llä ruiskutetuissa vartjelysvartteiden hormonikäsittelyn aloittaminen vaatii teissa, joissa oli keskimäärin 47 emikukintoa/100 kasvainta. GA₇:llä saavutettu tulos ja kontrollitaso olivat vastaavasti 36 ja 6 emikukintoa/100 kasvainta. Sekoitus GA_{4/7} aikaansai emikukkamäärän, joka vastasi puhtaiden hormonien avulla saavutettujen tulosten keskiarvoa. Suhteellisen pienestä materiaalista johtuen vain vertailutason ja muiden käsittelyjen väliset kukintaerot voitiin tollisesti varmistamaan.

Hedekukinta oli koko aineistossa erittäin vähäistä, mihin oli ilmeisesti syynä vartteiden pieni koko ja alhainen ikä. Hedekukintomäärien vaihtelu antoi kuitenkin