

SYMPOSIUM PAPER

Status of flowering in conifers:
A constraint to tree improvement?

S.D. Ross and R.P. Pharis

634.909
711
BCMF
RES
1985
MR 7

STATUS OF FLOWERING IN CONIFERS: A CONSTRAINT TO TREE IMPROVEMENT?

Stephen D. Ross

Research Laboratory, British Columbia
Ministry of Forests, Victoria
British Columbia, CANADA V8Z 5J3

Richard P. Pharis

Plant Physiology Research Group
Department of Biology, University of
Calgary, Alberta, CANADA T2N 1N4

Abstract.--For Pinaceae family conifers we now have the ability to circumvent by appropriate hormonal (gibberellin A_{4/7} mixture) and cultural (girdling, modest water stress, root-pruning, NO₃-N fertilization, high temperature) treatments the biological constraints posed by sexual juvenility. Problems of flowering potential and periodicity also no longer need constitute a major obstacle to the breeding and production of genetically improved seed. Realization of this potential, however, requires a change in our traditional approach to seed production-- i.e., in soil-based orchards comprised of large, widely spaced trees, with little control over climatic and treatment factors, or pollen parentage. Alternative seed production systems are considered. Of these, indoor-potted orchards at present appear to provide the best opportunity for rapidly, completely and economically realizing the benefits of tree improvement in reforestation.

INTRODUCTION

Much has been written in recent years about the inefficiencies of propagating conifers by sexual means (e.g., seed), especially in relation to the potential of clonal forestry (e.g. Libby, 1985). The future role of sexual propagation in tree improvement is increasingly being questioned. For most conifers, however, the "potential of clonal forestry" is simply that-- a potential whose possible realization will require many additional years of further research, testing and validation. Additionally, unless there are breakthroughs in the economics of tissue culture propagation, or somatic embryogenesis propagation can be shown to be truly clonal (and feasible), the number of propagules produced from any one 'superior' genotype will probably remain limited, especially if those propagules are derived from tested mature genotypes and families. Furthermore, propagules derived from such mature

Invited paper presented at the 20th meeting of the Canadian Tree Improvement association, Laval University, Quebec, 19-22 August, 1985.

genotypes (as opposed to young seedlings) will have many of the characteristics of mature/maturing trees, including slower growth (Sweet and Wills, 1974; Greenwood, 1984). Sexual reproduction will still probably be the most efficient way to create the new variation upon which future genetic improvement must depend. And, if the economics and dependability of seed production are improved, it may remain the most viable option for reforestation with superior genotypes. This does not preclude, however, a vegetative propagation program (traditional or tissue culture) being combined with an economically improved seed production program (Smith *et al.*, 1981), especially if early progeny testing becomes feasible (Pharis and Ross, 1985a,b).

Rather than waiting for the new 'biotechnology of vegetative propagation' to replace propagation of our forests by seed/seedlings, we should be considering what can, in fact, be done now to improve the efficiency of seed production. The biological and practical constraints to flowering in forest trees have been the subject of numerous reviews (Jackson and Sweet, 1972; Puritch, 1972; Lee, 1979; Ross and Pharis, 1982, 1985; Owens and Blake, 1985) and several recent symposia (Bonner, 1979; Krugman and Katsuta, 1981), including two in 1985 (see Pharis and Ross, 1985c and Ross *et al.*, 1985b). Here we will only attempt to briefly summarize the progress to date in overcoming these constraints to breeding and seed production in conifers.

BIOLOGICAL CONSTRAINTS

Juvenility, The Problem

Hackett (1985) has defined juvenility as that period during the early ontogeny of most woody perennial plants grown from seed when flowering does not occur naturally and cannot be induced by the normal floral-initiating treatments. Using age to first flowering in natural stands as a criterion, the juvenile phase may last from only a few years (e.g. *Pinus contorta* Dougl. and *P. banksiana* Lamb) to 30 or more years (e.g. some species of *Abies* and *Picea*). Typically, though, the so-called juvenile phase is 10 to 20 years for most north temperate conifers (Puritch, 1972; Hackett, 1985; Zimmerman *et al.*, 1985).

However, as trees may not flower for some years after sexual maturity is attained, presumably because climatic and site conditions are not favorable, this age to first flowering can be misleading. Ross *et al.* (1983) cite the example of seedling seed orchards of *Pseudotsuga menziesii* (Mirb.) Franco established on southern Vancouver Island, both on cool, wet locations and also in the relatively sunny rain shadow of the Saanich Peninsula, near Victoria. Flowering in any one family at the latter location may begin (and continue) after only 3 to 5 years of age, 5 to 10 years earlier than flowering in the cool, wet location. Is then 'sexual maturity' of *P. menziesii* reached by age 3 years, as evidenced by this early flowering on this one rather unique site within its normal range? A survey over the vast majority of sites throughout its normal

range would set the age of 'sexual maturity' in excess of 10 to 15 years (Puritch, 1972). Because of anomalies such as this, Zimmerman et al. (1985) have produced a somewhat modified version of when phase change occurs:

"Phase change has occurred (1) if a plant flowers, no matter how flowering is induced, and (2) if the said plant will then continue to flower in its natural environment without application of any artificial stimulator that may have originally induced flowering."

This latter definition seems to us to best fit our current knowledge of natural controls over flowering, and just how those controls can be circumvented.

Juvenility is a concern that has yet to be faced and dealt with by most tree improvement programs here in Canada, or elsewhere. For the most part, breeding and seed production activities are still being carried out with ramets of phenotypically 'superior' adult trees whose sexual maturity is maintained, more or less, in vegetative propagation. There may be a temporary suspension of flowering in these 'mature' scions following rooting or grafting onto seedling rootstock and this may superficially resemble the juvenile condition of young seedlings. However, the former can often be readily stimulated to flower by the usual floral-initiating cultural treatments (water stress, girdling, root-pruning, high temperature, N fertilization), whereas very young seedlings normally will not (see Puritch, 1972; Hackett, 1985; Ross and Pharis, 1985).

Juvenility, furthermore, should not become a practical problem so long as forest geneticists retain a conservative approach to progeny testing, waiting 10 to 15 years before selecting the next-generation's breeding and seed production populations. By that age the selected ortets (and their vegetatively propagated ramets) should have already attained a significant degree of sexual maturity, although the vagaries of climate and poor choice of site may still limit the practical production of seed, even from so-called 'sexually mature' orchards (more on this latter). However, the future should see a substantial shortening of the testing period. Lambeth (1980) has demonstrated the reliability of early selection for growth traits in Pinus taeda L. and some other conifers based on 4- to 6-year progeny performance in well designed field tests. New approaches to physiological testing under controlled-environment glasshouse conditions (see examples cited in Pharis and Ross, 1985b) may some day enable identification of superior individuals and families at less than a year of age.

To better comprehend the possible impact of juvenility on future breeding and seed production programs, it is necessary to consider the phenomenon called 'phase change' in more detail. Some workers (Borchert, 1976; Pharis, 1977; Greenwood, 1981; Ross et al., 1983) question whether conifers exhibit a true juvenile phase with regard to flowering, suggesting that the normal reproductive incompetence of young seedlings is associated with other endogenous causes that are themselves under phase-change control.

As a tree matures its growth rate declines, in part due to increasing morphological complexity and competition among meristems (i.e. ageing), but also reflecting a nonreversible maturation effect that is retained in vegetative propagation (Sweet and Wills, 1974; Greenwood, 1984). Greenwood (1981) concluded that young *P. taeda* seedlings normally do not flower because, relative to older trees, their shoots continue growing too long into autumn to set a terminal bud capable of differentiating reproductively prior to the onset of winter dormancy. Such seedlings can be induced to set bud early by a treatment known as 'out-of-phase dormancy', and this treatment often also causes precocious flowering (Greenwood, 1981).

Most of the cultural practices which promote flowering in conifers (drought, girdling, root-pruning, etc.) also retard shoot elongation (see Ross and Pharis, 1985). Several of these floral-inducing treatments have been shown to retard the metabolism of the less polar [³H]GA₄, and to increase the level of less polar GAs which are relatively low in nonflowering control trees (see references cited in Ross *et al.*, 1983; Pharis and Ross, 1985a). Applied exogenously, certain of these less polar GAs (GA₄, GA₇, GA₉) are highly effective in promoting flowering in Pinaceae family conifers, where they also stimulate shoot elongation especially in younger individuals. A working hypothesis is that young, vigorously growing trees utilize endogenous GAs preferentially for vegetative growth. Only when maturation, environmental or cultural treatment factors restrict vegetative growth do endogenous less polar GAs become available for a long enough time (during the cone bud differentiation period) at sufficiently high concentrations for sexual differentiation to occur.

The traditional concept of phase change based on herbaceous and woody angiosperms may no longer be strictly applicable with respect to flowering in conifers. The definition put forward by Zimmerman *et al.* (1985) appears more likely, as does the maxim, 'the older the tree, the greater its ability to flower'. However, it does seem that there is no true age constraint to flowering in conifers, provided the appropriate stimulus is applied at the proper time of shoot ontogeny. For most conifers it appears that the appropriate stimulus includes GAs.

Overcoming the Strictures of Juvenility

It is well known that for many conifers of the Cupressaceae and Taxodiaceae families, a variety of GAs when applied exogenously will cause profuse flowering even in very young seedlings (see ref. cited in Pharis and Kuo, 1977). Conifers of the Pinaceae family also respond, but generally only to certain of the less polar GAs, most notably a mixture of GA₄ and GA₇ (GA_{4/7}). Pharis and Ross (1985b) cite nearly 80 referenced reports which demonstrate the effectiveness of exogenously applied GA_{4/7} for promoting flowering in at least 16 species representing 5 of the 6 genera of this commercially important family.

For reasons that are not completely clear, seedling members of the Pinaceae family as a group are not as responsive to applied GAs as

are those of the Cupressaceae and Taxodiaceae (Pharis and Ross, 1985a). Also, the GA_{4/7}-induced flowering in Pinaceae family conifers is much more dependent upon the use of adjunct cultural treatments (e.g. root-pruning, water stress, girdling, N fertilization, etc.), which may be ineffective by themselves but can often enhance synergistically the flowering response to GAs (see Ross and Pharis, 1982, 1985). Although these cultural and GA_{4/7} treatments do work best on more mature individuals they can still be highly effective on young, presumably still 'juvenile', seedlings.

Tsuga heterophylla (Raf.) Sarg. is a good illustration of this. Within its natural range this species has one of the longer 'juvenile' phases of any conifer (20-25 years). Yet, it is possible to induce profuse flowering in container-grown seedlings only 2 years old from seed when GA_{4/7} is applied in conjunction with nitrate-N fertilization, high temperatures and(or) water stress (Pollard and Portlock, 1981; Brix and Portlock, 1982). Pseudotsuga menziesii is another Pinaceae family conifer with a relatively long juvenile phase in nature (10-20 years) for which similar treatments will cause precocious flowering, the earliest thus far being three years of age (S.D. Ross, unpublished results). Thus, when GA_{4/7} is used in conjunction with the appropriate cultural conditions (which appear to often be species dependant) there is every reason to believe that flowering in most conifers can be promoted at a very early age.

Hastening Sexual Maturation--Is It Possible?

It is important to emphasize that even though applied GAs can be used to induce precocious flowering in conifers, they only over-ride and do not permanently terminate the juvenile condition associated with young seedlings (see Zimmerman et al., 1985). Without subsequent retreatment a seedling thus induced might not again flower until sexual maturity was naturally attained several years later. Fortunately, we have at our disposal a practical method which appears, for all practical purposes, to accelerate the sexual maturation process.

It is now well established that for many woody angiosperms the attainment of the adult condition is primarily a function of tree size rather than age per se (see Hackett, 1985). It seems that an angiosperm seedling must first attain a certain minimum size before it can flower, and it makes little difference whether this size is achieved through continuous growth or the normal succession of annual growth increments. In conifers as well we find that growing seedlings under extended photoperiods in a heated greenhouse prior to outplanting in the seed orchard can considerably shorten the age to first flowering (Young and Hanover, 1976; Wheeler et al., 1982; Hackett, 1985).

This may seem paradoxical, given our assumption that the normal reproductive incompetence of young conifer seedlings is associated with their inherently vigorous vegetative growth. However, J.E. Webber (personal communications) has found some caveats for Picea glauca (Moench) Voss. In comparison with 'non-accelerated' control plants,

accelerated-grown seedlings only flowered earlier if they were then exposed to appropriate stress conditions, such as drought, which restrict vegetative growth. A similar stress situation may be occurring under the field conditions cited by Young and Hanover (1976) and Wheeler et al. (1982).

Growth acceleration of conifer seedlings may hasten the sexual maturation of individual apical meristems as appears to be the case for some woody angiosperms (Hackett, 1985). Or, as previously discussed, the effect of maturation may be indirect through a reduction in the shoot's growth potential. The growth-acceleration treatment also promotes branchiness (Wheeler et al., 1982), so that more shoots presumably also will be 'maturing' in a given period. In the study of Wheeler et al. (1985), *P. contorta* seedlings grown under continuous light for 6 months in a heated greenhouse prior to outplanting differentiated seed and pollen cones, respectively, at 2 and 4 years of age. This was one year in advance of nonaccelerated-grown seedlings on the same site. By age 5 years, the accelerated seedlings were 61% taller and had 79% more branches than the controls. And, the following year they initiated, on average, 6.1 and 5.5 times as many seed- and pollen-cone buds, respectively. Hence, their increased flowering response may reflect both direct 'maturation' effects as well as indirect 'having more branches' effects. Or, the larger, branchier, accelerated-grown seedlings may be under greater water stress from the mere logistics of supplying a larger shoot from approximately the same volume of soil. If this were the case, then the flowering response to accelerated growth would not involve increased 'maturation' at all.

To reiterate Hackett (1985), "the best formula which can be given to obtain rapid flowering in many tree species is to grow the seedlings as rapidly as possible to a certain species dependent size and then apply the flower-inducing treatment which is appropriate for the species." This strategy of early growth acceleration followed by GA_{4/7} plus an appropriate cultural treatment has now been successfully used to promote very precocious flowering in several Pinaceae family conifers (Ross, 1978; Greenwood, 1981; Brix and Portlock, 1982; Cecich, 1983).

Limitations Placed on Flowering by the Number of Potential Conebud Differentiation Sites

The concern is frequently expressed that seed yields per tree and per hectare will necessarily be lower for future advanced-generation orchards comprised of younger, sexually immature selections. However, to a large extent the age-dependent increase in flowering probably has less to do with age or maturation than with the number of potential flowering sites. Thus, we observe for *Pseudotsuga menziesii* what is probably a characteristic of conifers in general. A clonal seed orchard may come into flowering (naturally or after cultural and GA_{4/7} treatment) earlier, but the seedling seed orchard rapidly catches up and soon becomes much more productive (Konishi, 1985). The fact is that seedlings develop potential flowering sites much more rapidly than do vegetative propagules of mature trees. This is reflected not only in the inherently

faster growth rate of seedling-origin trees, but also their greater branchiness as measured by number of lateral shoots per unit length of stem (Sweet and Wills, 1974; Wheeler et al., 1982; Greenwood, 1984).

It would be a mistake, however, to equate flowering potential with simply number of shoots. Even for mature trees, and even in years conducive to abundant flowering, only a relatively small proportion of the total shoots may be contributing to female or male flowering. When one considers also the number of axillary and(or) terminal apices per shoot that are potentially capable of differentiating reproductively, we find that the realized potential for flowering in most Pinaceae family conifers is very low indeed (Owens and Blake, 1985).

Conifers generally exhibit a pattern of sexual zonation whereby seed cones are concentrated in the upper crown and pollen cones in the lower crown, with a transition zone inbetween where cones of both sex may be produced, often on the same shoot (Pharis and Morf, 1968; Marquard and Hanover, 1984). These zones may be extended but the pattern still holds even under conditions (natural and artificially induced) highly favorable for flowering (Chalupka, 1981; Ross et al., 1981; Marquard and Hanover, 1984). However, whether a shoot differentiates mainly seed cones, mainly pollen cones, or both, appears to depend relatively more on its vegetative vigor than its position per se within the crown. The following relationship between increasing shoot vigor and probable bud developed described by Tompsett (1978) for Picea sitchensis (Bong.) Carr. seems to hold but with slight modification for many Pinaceae family conifers: weak vigor=vegetative < pollen cone < intermediate vigor=vegetative < seed cone < strong vigor=vegetative.

Sweet and Krugman (1978) proposed crown pruning as a means not only of making cones more accessible from the ground, but also for redirecting the otherwise rapid height growth into increased production of lateral shoots with high flowering potentials. Ross and Pharis (1982) review a number of studies on conifers which demonstrate the practicality of top pruning for achieving both of these objectives. Here, increased cone production frequently resulted, even though the method of pruning was not designed to specifically favor those types of shoots most predisposed to differentiate conebuds. Also, top pruning in these studies was usually delayed until the seed orchard trees became too tall for efficient management. From the experience with fruit tree orchards (Jackson, 1985), pruning beginning at a relatively young age would seem to provide the best opportunity for manipulating crown architecture to maximize potential flowering sites, especially if at the same time trees are optimally cultured for rapid vegetative development.

Flowering Periodicity

In well-managed seed orchards, as in nature, even mature trees exhibit considerable periodicity in flowering. Thus, most trees initiate few if any conebuds for one or possibly several years following a heavy cone crop, and, depending on the site and species, the interval between years of abundant flowering is generally much longer.

Studies correlating seed crops in conifers with weather data (e.g. Rehfeldt et al., 1971; Eis, 1973) indicate that the proper sequence of optimal environmental conditions (e.g., dry or even droughtly, with high solar insolation, during the late spring or summer prior to initiation/differentiation of cone buds) for flowering may occur but infrequently in nature. However, for a variety of reasons (see Rehfeldt et al., 1971; Owens and Blake, 1985), such studies do but a poor job of quantifying the optimal environmental conditions for any given stage of reproductive bud development. This information is now slowly becoming available through growth-chamber and greenhouse studies using container-grown trees (Pollard and Portlock, 1981; Longman, 1982; Philipson, 1983; Ross, 1985).

This information on optimal environmental conditions for cone bud initiation/differentiation can be profitably used to select field seed orchard sites with a high probability of consistently providing abundant flowering and subsequent good cone development. Cultural practices can also be used to moderate, though not totally eliminate, the natural periodicity in flowering (see Wheeler et al., 1985). Even the most effective of these practices, even when applied together with GAs, will not compensate for an otherwise unfavorable (usually wet and cool, with low solar insolation) environment (Dunberg, 1980; Ross and Pharis, 1982).

Owens and Blake (1985) emphasize that there is also an endogenous component to the periodicity in flowering in sexually mature trees which determines how frequently the tree should be given cultural and(or) GA_{4/7} treatments for best results. Wheeler et al. (1985) recently reported the successful promotion of flowering in 4 consecutive years from annual stem girdling in grafted Pseudotsuga menziesii seed orchards. However, it was only in the last year of their study that the cone crop induced could be considered heavy in relation to tree size. It is doubtful that the girdling or other treatments would have been effective in overcoming the bienniality of flowering which normally follows such a heavy cone crop year. Developing cones and seeds constitute a strong sink for nutrients (Dickmann and Kozlowski, 1970), and their period of maximum growth in many conifers coincides with the differentiation of lateral primordia, a weak sink, into reproductive cone buds (Owens and Blake (1985). Also, because cone buds differentiate at the expense of vegetative buds, prolific flowering one year may significantly reduce the number of shoots with lateral primordia that are capable of differentiating reproductively the following year (Owens and Blake, 1985). This was particularly apparent with potted Picea engelmannii grafts that had been induced to flower profusely by the highly effective combination of properly timed heat, drought and GA_{4/7} treatments (Ross, 1985 and unpublished results).

Furthermore, it must again be emphasized that most of the cultural practices used to promote flowering are also stress treatments (Ross and Pharis, 1985). Consequently, their repeat application in consecutive years will further retard vegetative development and the recovery of flowering potential, as well as adversely affect the development of existing pollinated cone buds and their seeds (S.D. Ross, unpublished results). Our results for T. heterophylla and P. engelmannii

(Ross et al., 1985b) indicate that the optimal strategy for maximizing cone production in the long term is to apply promotion treatments every other year (and then no longer nor more severely than absolutely necessary), keeping trees well watered and fertilized inbetween to ensure rapid recovery of vegetative tissues and normal cone and seed development in the off-treatment year.

Clonal differences

The so-called "20/80" rule was coined by one southern pine tree improvement cooperative (Anon., 1976) to reflect the fact that 80% of its orchard seed were produced by only 20% of the clones. The ratio can be much more disproportionate than this, especially in young orchards and on sites and years unfavorable for flowering (Eriksson, 1978; Wheeler et al., 1985). To our knowledge, a strong negative genetic correlation between fecundity and vegetative growth rate has not been shown (see Libby, 1985), although this does not mean it does not exist. Of more serious concern are the negative impacts of these clonal differences in fecundity on seed orchard yield and genetic efficiency (Eriksson, 1978; Smith and Adams, 1983; Wheeler et al., 1985).

Although our cone-enhancement treatments are almost always most effective on those clones and families that are inherently predisposed to flower, they still may be profitably used to increase the proportion of genotypes flowering and to dampen the differences in fecundity among them (Pharis et al., 1980; Ross et al. 1981, 1985b). Wheeler et al. (1985) reported that stem girdling in a grafted Pseudotsuga menziesii seed orchard doubled both the proportion of ramets and clones producing seed cones, and that pollen density was 4 times as heavy in the girdled as in the ungirdled portion of the orchard.

Ross et al. (1985a) compared 10 each of previously good- and poor-flowering, half-sibling P. menziesii seed orchard families for their response to GA_{4/7} and root-pruning. Treatments were compared alone and together. In combination, the two treatments had a highly synergistic effect on flowering, and the magnitude of this synergism was significantly greater for the poor- than good-flowering families. Without treatment, 50% of the poor-flowering families flowered (1 seed-cone bud per tree, on average), compared to 80% of the good-flowering families (an average of 24 seed-cone buds per tree). When GA_{4/7} and root-pruning were given together, all 10 families in each group of trees flowered. And, the difference in mean seed-cone buds per tree between the poor- and good-flowering families (413 and 928 each, respectively), although still significant, was also much reduced. A similar 'treatment by clone interaction' was also noted for T. heterophylla in response to the combined application of GA_{4/7} + calcium nitrate fertilizer (Ross et al., 1981). Probably most clones and families, regardless of their inherent fecundity, are susceptible to flowering promotion if given the appropriate stimulus.

PRACTICAL CONSTRAINTS TO SEED PRODUCTION

The message we have tried to convey in the preceding sections is:

'treatments are presently available that can be used to overcome many of the biological constraints to flowering, at least to the extent where the lack of flowering no longer need constitute the major obstacle to breeding and seed production programs.

However, there are other constraints, including economic ones, with regard to the continued use of the traditional soil-based seed orchards.

Much effort has been devoted to the development and implementation of new technology to overcome the well known production, genetic and management inefficiencies of conventional seed orchards (see Sweet and Krugman, 1978; Ross and Pharis, 1982; Ross et al., 1985b). This includes various methods already discussed to ensure earlier, more reliable flowering and top pruning for size control; supplemental mass pollination for improved seed set and genetic gains (see Wheeler and Jech in this volume); and installation of costly overhead-misting systems for avoidance of contaminating foreign pollen and for protection against frost (El Kassaby et al., 1984). However, it is time that we begin to question the effectiveness, operational practicality, and economics of such remedial actions and consider instead those alternative seed production systems that might be employed which circumvent the inherent limitations of conventional seed orchards.

Miniaturized Field Seed Orchards

There is much we can learn from the experience of fruit tree orchardists. Jackson (1985) points out that they too started out with large, spreading trees similar to our seed orchards today, but found it was far more efficient to diffuse fruit production among many small, closely spaced trees, using crown pruning both to control size for easy management and to maximize potential flowering sites. Sweet and Krugman (1978) adapted this concept to Pinus radiata D. Don seed orchards, as have Longman and Dick (1981) for Thuja plicata Donn. The approach differs somewhat for the two species, however. With T. plicata, Longman and Dick (1981) essentially miniaturized a conventional orchard, with trees planted at very close spacing but with clone members still separated to favor random mating through wind pollination. On the other hand, what Sweet and Krugman proposed for P. radiata was in essence a group of 2-clone orchards wherein ramets are grown in low clonal hedges, and in which pollen parentage is controlled through artificial pollination rather than juxtaposition of clones.

Each proponent described the demonstrated advantages of their approach for their particular species and program. Breeding of P. radiata in New Zealand is sufficiently advanced so as to be able to capitalize on specific-combining as well as general-combining effects of superior clones through artificial pollination. This, however, was not

the case for T. plicata in Scotland. Another major difference relates to size control, which again is determined by species characteristics. With T. plicata, trees are induced to flower profusely while still quite small by treatment with GA₃, and severe top pruning then follows as a means also for conveniently harvesting the seed cones, which are concentrated in the upper crown (Longman, personal communications). As with most species of the Cupressaceae, T. plicata does not lack for potential flowering sites; however, this plethora of potential conebud differentiation sites is not the case for most Pinaceae family conifers. In Sweet and Krugman's approach with P. radiata, hedge development begins at a young age and has as a major objective increasing the number of potential conebud differentiation sites, after which GA_{4/7} and other treatments may be used to promote early flowering.

Miniaturization of soil-based field orchards by either approach represents an advance over our present approach to seed production. We feel that further testing with other species is definitely warranted. As discussed in the current Members' Report by Ross, preliminary results with early crown pruning of P. menziesii and T. heterophylla are quite encouraging. Seed yields per tree may be less, but many more trees will be contributing to a higher overall production on a per-hectare basis. Conebud enhancement by GA_{4/7} and cultural treatments can also begin earlier in the miniaturized orchard owing to its much shorter period required for early vegetative development, during which induction treatments of a stressful nature are not recommended (see Ross and Pharis, 1982). We have furthermore found that many stimulation treatments, GA_{4/7} in particular, are much more effectively and efficiently applied with smaller trees.

Indoor-Potted Seed Orchards

Whatever the approach to soil-based orchards, seed production will still be subject to a significant degree to the vagaries of climate and the whims of nature. And, regardless of tree size or clonal arrangement, there remain serious practical difficulties in attempting to control pollen parentage in field-grown trees. Since 1980, the British Columbia Ministry of Forests has been actively involved in the development and evaluation of indoor-potted orchards as a practical alternative to conventional soil-based seed orchards for T. heterophylla and the interior spruces, P. engelmannii and P. glauca. Our progress to date is summarized by Ross in recent Members' Reports, and Ross et al. (1985b) provide a detailed discussion of the many identified (and demonstrated) advantages of working with small, potted trees, subject to intensive management and strict environmental control. These advantages include:

- (a) earlier, more reliably abundant flowering, with a greater proportion of clones contributing to seed production;
- (b) ease of conebud induction, pollen management, seedcone collection and virtually all other management practices;

- (c) an increased ability to protect cones and seeds from adverse climatic conditions and fungal and insect pests that could otherwise, in some years, result in total crop failure;
- (d) strict control over pollen parentage for maximum genetic gains;
- (e) clonal composition is not fixed but can be rapidly upgraded to include new 'progeny-tested' selections as soon as they become available;
- (f) more efficient site utilization and the flexibility to rapidly scale production capacity upward or downward to meet changing planting requirements; and
- (g) absolute flexibility of siting as, for example, in conjunction with a container nursery where facilities and labor may be shared for increased efficiency, or on inexpensive nonagricultural land not otherwise suitable for cone production.

Ross *et al.* (1985b) point out that these advantages of indoor-potted orchards can probably be achieved at a cost equal to or even less than that of conventionally produced seed. They give as a hypothetical example two B.C. interior spruce seed orchards, one potted and the other soil-based, each with an annual production capacity of five million viable seeds. The latter field seed orchard would, conservatively occupy 3.5 ha of expensive agricultural land and then not attain full production for 15 years after establishment. The potted seed orchard would only require 1400m² of land, half of that space in relatively inexpensive plastic-covered houses, with full seed production reached in only 7 years. Operating costs promise to be lower as well owing to the greater ease of management and increased efficiency of production brought about by the use of small potted trees.

CONCLUSIONS

We now have at our disposal the knowledge and techniques to largely overcome those biological constraints to flowering in conifers that have long been considered as the major obstacle to the breeding and production of genetically improved trees. This is not to say that further research on the mechanism of flowering and its efficient control is no longer necessary (see Owens and Blake, 1985 for discussion of future research needs). However, what is now needed is a change in the way that we now go about producing our improved seeds (e.g., currently in soil-based orchards comprised of large, widely spaced trees with wind as the agent for pollination). Serious consideration must be given, we think, to alternative seed-production systems which can circumvent many of the well known limitations (production, genetic and management) of such field seed orchards. Miniaturization of soil-based orchards, possibly coupled with artificial pollination, is one such system that may work well for some species and programs if an appropriate climatic

location exists. For many other species and regions, however, we believe that the indoor container-grown seed orchards will offer the best potential for rapidly and efficiently realizing the full benefits of tree improvement possible through sexual propagation.

LITERATURE CITED

- Anon. 1976. Twentieth annual report on cooperative tree improvement and hardwood research program. North Carolina State Univ., Raleigh, N.C.
- Bonner, F.T. 1979. Editor. Proc. Symposium on flowering and seed development in trees. Mississippi State Univ., 15-18 May 1979. U.S. Gov. Printing Office, Washington, D.C. 380 p.
- Borchert. 1976. The concept of juvenility in woody plants. Acta. Hort. 56:21-33.
- Brix, H., and F.T. Portlock. 1982. Flowering response of western hemlock seedlings to gibberellin and water-stress treatments. Can. J. For. Res. 12:76-82.
- Cecich, R.A. 1983. Flowering in a jack pine seedling seed orchard increased by spraying with gibberellin A₄/7. Can. J. For. Res. 13:1056-1062.
- Chalupka, W. 1981. Influence of growth regulators and polythene covers on flowering of Scots pine and Norway spruce grafts. Silvae Genet. 30:142-146.
- Dickmann, D.I. and T.T. Kozlowski. 1970. Mobilization and incorporation of photoassimilated ¹⁴C by growing vegetative and reproductive tissues of adult Pinus resinosa Ait. trees. Plant Physiol. 45:284-288.
- Dunberg, A. 1980. Stimulation of flowering in Picea abies by gibberellins. Silvae Genet. 29:51-53.
- Eis, S. 1973. Cone production of Douglas-fir and grand fir and its climatic requirements. Can. J. For. Res. 3:61-70.
- El-Kassaby, Y.A., A.M.K. Fashler, and O. Sziklai. 1984. Reproductive phenology and its impact on genetically improved seed production in a Douglas-fir seed Orchard. Silvae Genet. 33:120-125.
- Eriksson, G. 1978. Do flowering characteristics constitute a constraint for forest tree breeding in Sweden? In Proc. 3rd World Consultation on forest tree breeding, Vol. 2. CSIRO, Canberra, Australia. pp. 883-893.

- Greenwood, M.S. 1981. Reproductive development in loblolly pine. II. The effect of age, gibberellin plus water stress and out-of-phase dormancy on long shoot growth behaviour. *Amer. J. Bot.* 68:1184-1190.
- Greenwood, M.S. 1984. Phase change in loblolly pine shoot development as a function of age. *Physiol. Plant.* 61:518-522.
- Hackett, W.P. 1985. Juvenility, phase change and rejuvenation in woody plants. *Hortic. Abstr.* 7:109-155.
- Jackson J.E. 1985. Future fruit orchard design. In *Attributes of Trees as Crop Plants*. Edited by M.G.R. Cannel, J.E. Jackson, and J.C. Gordon. Institute of Terrestrial Ecology, Monks Wood Exp. Sta., Abbots Ripton, Huntingdon, England. In press.
- Jackson, D.I. and G.B. Sweet. 1972. Flower initiation in temperate woody plants. *Hortic. Abstr.* 42:9-24.
- Konishi, J. 1985. Review of seed production area and seed orchard management in the Inland Mountain West. In *Proc. Symposium on conifer tree seed in the Inland Mountain West*. Univ. of Montana, 5-6 August 1985. In press.
- Krugman, S.L. and M. Katsuta. 1981. Editors. *Proc. Symposium on flowering physiology, XVII IUFRO World Congress, Kyoto, Japan*. The Japan Forest Tree Breeding Assoc, Tokyo, Japan. 140 p.
- Lambeth, C.C. 1980. Juvenile-mature correlations in Pinaceae and implications for early selection. *For. Sci.* 26:71-580.
- Lee, K.J. 1979. Factors affecting cone initiation in Pines: a review. *Res. Rep. Inst. Forest Genet. Korea*, no. 15, pp. 45-85.
- Libby, W.J. 1985. Potential of clonal forestry. In *Proc. 19th Meeting Can. Tree Improv. Assoc.* Edited by L. Zsuffa, R.M. Rauter, and C.W. Yeatman. Part 2, pp. 1-11.
- Longman, K.A. 1982. Effects of gibberellin, clone and environment on cone initiation, shoot growth and branching in Pinus contorta. *Ann. Bot.* 50-247-257.
- Longman, K.A. and J. McP. Dick. 1981. Can seed-orchards be miniaturized? In *Proc. Symposium on flowering physiology, XVII IUFRO World Congress, Kyoto, Japan*. Edited by S.L. Krugman and M. Katsuda. The Japan Forest Tree Breeding Assoc., Tokyo. pp. 98-102.
- Marquard, R.D. and J.W. Hanover. 1984. Sexual zonation in the crown of Picea glauca and flowering response to exogenous GA_{4/7}. *Can. J. For Res.* 14:27-30.

- Owens, J.N. and M.D. Blake. 1985. Forest tree seed production: a review of literature and recommendations for future research. Petawawa Nat. For. Inst., Can For. Serv., Petawawa, Ontario. In press.
- Pharis, R.P. 1977. Interaction of native or exogenous plant hormones in the flowering of woody plants. In Proc. Regulation of developmental processes in plants. Edited by H.R. Schutte and D. Gross. Academy of Sciences of the GDR, Halle. pp. 343-360.
- Pharis, R.P. and W. Morf. 1968. Physiology of gibberellin-induced flowering in conifers. In Biochemistry and physiology of plant growth substances. Edited by F. Wightman and G. Setterfield. Runge Press, Ottawa. pp. 1341-1356.
- Pharis, R.P. and C.C. Kuo. 1977. Physiology of gibberellins in conifers. Can. J. For. Res. 7:299-325.
- Pharis, R.P. and S.D. Ross. 1985a. Hormonal promotion of flowering in the Pinaceae. In Handbook on Flowering, Vol. 5. Edited by A. Halevy. CRC Press, Boca Raton, FL. In press.
- Pharis, R.P. and S.D. Ross. 1985b. Gibberellin A_{4/7} mixture and the promotion of flowering in Pinaceae family conifers: An update on successes. In Symposium on conifer tree seed in the Inland Mountain West. Univ. of Montana, 5-6 August 1985. In press.
- Pharis, R.P. and S.D. Ross. 1985c. A morphogenic role for gibberellins in the flowering of conifers. In Symposium on flowering and seed bearing in forest seed orchards. Inst. of Dendrology, 1-8 September 1985, Kornik, Poland. In press.
- Pharis, R.P., S.D. Ross, and E.E. McMullan. 1980. Promotion of flowering in the Pinaceae by gibberellins. III. Seedlings of Douglas-fir. Physiol. Plant. 50:119-126.
- Philipson, J.J. 1983. The role of gibberellin A_{4/7}, heat and drought in the induction of flowering in Sitka spruce. J. Exp. Bot. 34:291-302.
- Pollard, D.F.W. and F.T. Portlock. 1981. Effect of temperature on strobilus production in gibberellin-treated seedlings of western hemlock. Can. For. Serv. Res. Notes. 1:21-22.
- Puritch, G.S. 1972. Cone production in conifers. Can. For. Serv, Pac. For. Res. Ctr. Inf. Rep. BC-X-65. 94p.
- Rehfeldt, G.E., A.R. Stage and R.T. Bingham. 1971. Strobili development in western white pine: periodicity, prediction and association with weather. For. Sci. 17:454-461.

- Ross, S.D. 1978. Influences of gibberellins and cultural practices on early flowering of Douglas-fir seedlings and grafts. In Proc. 3rd World Consultation on Forest Tree Breeding, Vol. 2. CSIRO, Canberra. pp. 997-1007.
- Ross, S.D. 1985. Promotion of flowering in potted *Picea engelmannii* (Perry) grafts: effects of heat, drought, gibberellin A_{4/7}, and their timing. Can. J. For. Res. 15:618-624.
- Ross, S.D. and R.P. Pharis. 1982. Recent developments in enhancement of seed production in conifers. In Proc. 18th Meet. Can. Tree Improvement Assoc., Part 2. Edited by D.F.W. Pollard, D.G. Edwards, and C.W. Yeatman. pp. 26-38.
- Ross, S.D. and R.P. Pharis. 1985. Promotion of flowering in crop trees: different mechanisms and techniques, with special reference to conifers. In Attributes of Trees as Crop Plants. Edited by M.G.R. Cannell, J.E. Jackson, and J.C. Gordon. Institute of Terrestrial Ecology, Monks Wood Exp. Sta., Abbots Ripton, Huntingdon, England. In Press.
- Ross, S.D., R.F. Piesch, and F.T. Portlock. 1981. Promotion of cone and seed production in rooted ramets and seedlings of western hemlock by gibberellins and adjunct cultural treatments. Can. J. For. Res. 11:90-989.
- Ross, S.D., R.P. Pharis, and W.D. Binder. 1983. Growth regulators and conifers: their physiology and potential uses in forestry. In Plant Growth Regulating Chemicals, Vol. II. Edited by L.G. Nickell. CRC Press, Boca Raton, FL. pp. 35-78.
- Ross, S.D., J.E. Webber, R.P. Pharis, and J.N. Owens. 1985a. Interaction between gibberellin A_{4/7} and root-pruning on the reproductive and vegetative process in Douglas-fir. I. Effects on flowering. Can. J. For. Res. 15:341-347.
- Ross, S.D., A.M. Eastham, and R.C. Bower. 1985b. Potential for indoor-potted seed orchards. In Symposium on conifer tree seed in the Inland Mountain west. Univ. of Montana, 5-6 August 1985. In press.
- Smith, D.B. and W.T. Adams. 1983. Measuring pollen contamination in clonal seed orchards with the aid of genetic markers. Proc. South. For. Tree Improv. Conf. 17:69-77.
- Smith, D.R., J. Aitken, and G.B. Sweet. 1981. Vegetative amplification - an aid to optimizing the attainment of genetic gains from *Pinus radiata*? In Proc. Symposium on flowering physiology, XVII World Forestry Congress, Kyoto, Japan. Edited by S.L. Krugman, and M. Katsuta. Japan Forest Tree Breeding Assoc., Tokyo. pp. 117-123.

- Sweet, G.B. and L.G. Wills. 1974. Comparison of the growth of vegetative propagules and seedlings of *Pinus radiata*. N.Z.J. For. Sci. 4:399-409.
- Sweet, G.B. and S.L. Krugman. 1978. Flowering and seed production problems - and a new concept of seed orchards. In Proc. 3rd World Consultation on Forest Tree Breeding, Vol. 2. CSIRO, Canberra, Australia. pp 749-759.
- Tompsett, P.B. 1978. Studies of growth and flowering in *Picea sitchensis* (Bong.) Carr. 2. Initiation and development of male, female and vegetative buds. Ann. Bot. 42:889-900.
- Wheeler, N.C., C.C. Ying, and J.C. Murphy. 1982. Effect of growth on flowering in lodgepole pine seedlings and grafts. Can. J. For. Res. 12:533-537.
- Wheeler, N.C., C.J. Masters, S.C. Cade, S.D. Ross, J.W. Keeley, and L.Y. Hsin. 1985. Girdling: a effective and practical treatment for enhancing seed yields in Douglas-fir seed orchards. Can. J. For. Res. 15:505-510.
- Young, E. and J.W. Hanover. 1976. Accelerating maturity in *Picea* seedlings. Acta Hort. 56:105-114.
- Zimmerman, R.H., W.P. Hackett, and R.P. Pharis. 1985. 3 hormonal aspects of phase change and precocious flowering. Ency. of Plant Physiology (NS) 11:79-115.