Cone Production in Conifers

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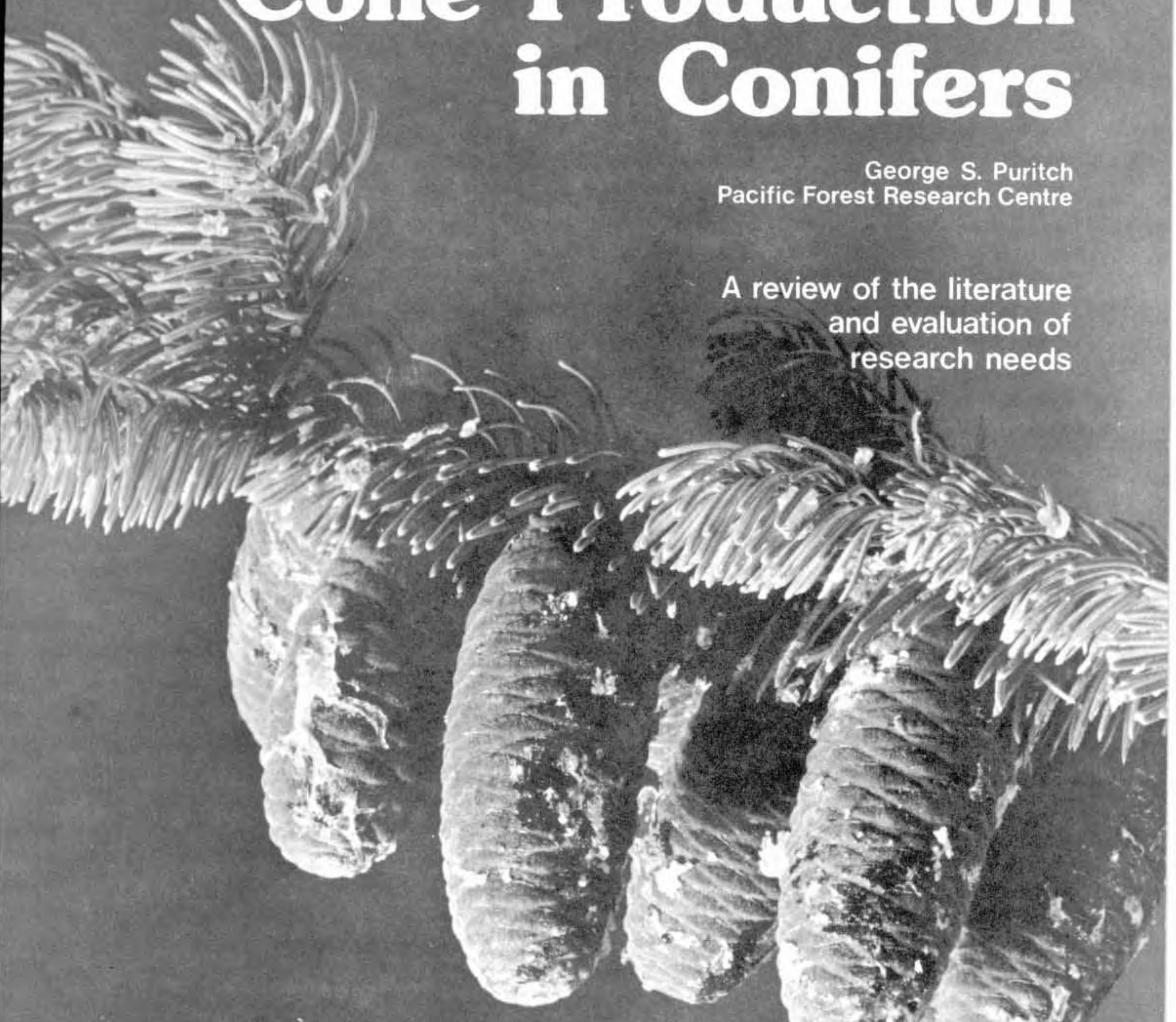
A review of the literature and evaluation of research needs



With an economic analysis
by A.H. Vyse

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INTRODUCTION

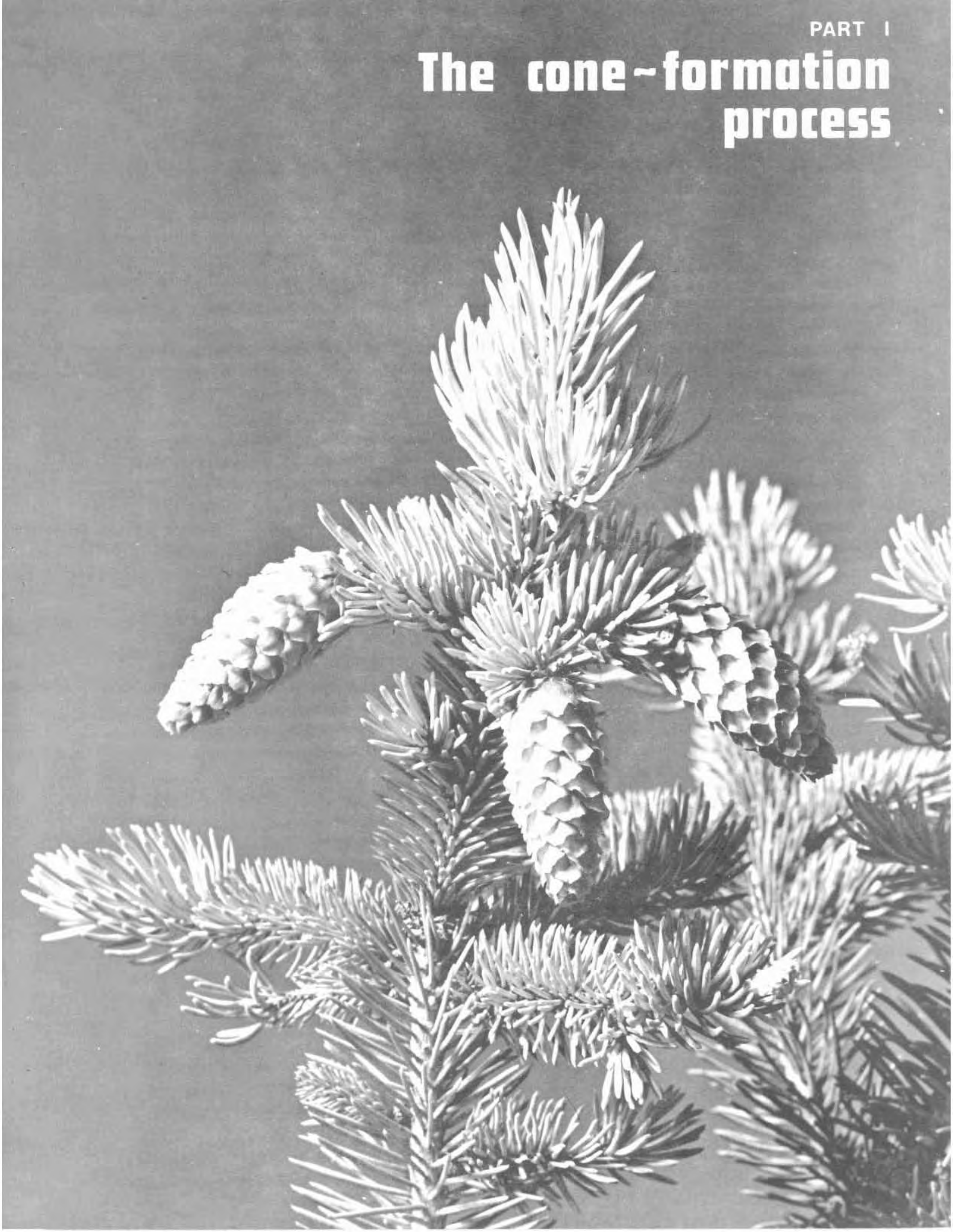
In recent years, forest industries have found it economically advantageous to reforest land with genetically superior stock, consequently, they have embarked upon extensive tree improvement programs. Superior quality trees have been selected and vegetatively propagated for seed production in compact breeding arboreta or seed orchards. Controlled genetic crossings have also been undertaken to develop progenies that have improved growth characteristics and are resistant to insects or disease. The success of these programs is dependent upon the continuous production of abundant seed. Unfortunately, this demand for seed cannot be met solely through natural processes and must be supplemented by cone-induction treatments.

The Canadian Forestry Service was requested by the forest industry in British Columbia and the British Columbia Forest Service to undertake further research on cone production. Current and past research was fairly extensive and involved a wide variety of approaches. It was therefore decided to establish the extent of current knowledge on cone production and the success that had been achieved in controlling cone crops. This would lead to a consideration of whether additional investigations should be undertaken and in what areas they should be carried out. This report records the results of the review and contains recommendations based on it.

The report is confined to the cone-production process and does not deal with factors which reduce cone numbers and seed quality after the cones have formed e.g. cone and seed insects, pollination, cone harvesting, seed extraction, etc. It was reasoned that the primary obstacle in obtaining seed was the lack of cones and unless this aspect was resolved then seed shortages would occur regardless of how the seed was protected and processed. It should be stressed, however, that the factors which decrease seed yields may in certain cases become a major problem and should not be neglected.

PART I

The cone-formation process



PART I

THE CONE-FORMATION PROCESS

A. NATURAL PROCESS OF CONE FORMATION IN WESTERN CONIFERS

Before embarking on a study of cone production, the normal reproductive patterns of conifers must be established. Different species of conifers vary in their cycle of reproduction, although the process is still broadly similar throughout the Pinaceae. Recently, Allen and Owens (1972) completed an extensive history of the life cycle of Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco., outlining the entire process of reproduction from bud initiation to seed drop. In view of this report and since Douglas-fir is the main commercial species on the West Coast, it is used as an example of the reproductive cycle of a typical west coast conifer.

(1) Reproductive Cycle of Douglas-fir

The cones of Douglas-fir are initiated as microscopic primordia in the axils of some leaves within the vegetative buds. The initiation is first evident as increased metabolic activity in the leaf axils around the end of March (Owens, 1969). By early April, the primordia undergo active division and appear swollen when viewed microscopically (Owens and Smith, 1964). The lateral buds all appear at the same time and are indistinguishable as vegetative or reproductive. However, the buds nearest the shoot apex tend to become vegetative or seed cones, while those nearest the base become pollen cones (Allen and Owens, 1972).

Throughout April, the lateral bud primordia enlarge but, in some cases, certain buds stop dividing and cease to develop. These buds do not appear on the mature shoot and have been termed "aborted" (Owens, 1969). Other buds develop further and form bud scales but also cease growing. These buds, termed latent (Owens, 1969), are potentially active and can develop after forcing treatments (Silen, 1967). Figure 1 shows the pathways of bud development, according to Owens (1969).

The buds continue to undergo development during April and May. Sometime during this period, transition occurs in certain buds from undetermined primordia to reproductive forms (Allen and Owens, 1972). The cause of this change is still obscure, although the transformation is perhaps one of the main physiological processes controlling cone production. It is during this time that seed-induction techniques are commonly applied, as will be discussed later. Owens (1969) and Ebell (1971) have reported that these alternate pathways of development, abortion and latency are a major cause of the periodicity of cone production.

By the end of May, vegetative and reproductive buds can be distinguished on the basis of cytochemical tests and by early July, they can be distinguished anatomically (Owens, 1969). The reproductive buds undergo further development during the summer and enter dormancy in mid-December (Allen and Owens, 1972).

Although the dates of these differentiation stages are well established for certain localities, e.g. Victoria (Allen and Owens, 1972), they can vary with geographic location, environment and between trees. Silen (1967) reported that as elevation increased, the times of bud initiation and development occurred progressively later. Owens (personal communication) found a similar relationship with latitude; the more northern the latitude, the later in the year bud initiation occurred. As environment has a major role in controlling the growth of plants, it can similarly affect the times of development of the vegetative and reproductive buds (Matthews, 1963). A late spring will invariably cause a delay in bud break and growth. Even under similar environmental conditions, variations in the phenotype of the tree can cause variation in bud differentiation. Kiss and Sziklai (1965) found that bud break could vary up to 4 weeks on trees in the same location in the Haney forest of British Columbia. Despite these variations in timing, differentiation of vegetative and reproductive buds still occurs before, during and after the period of vegetative bud break, and the time of bud break thus can be used as a valid index for timing cone-induction treatments.

On southern Vancouver Island, the reproductive buds remain dormant throughout the winter period until March of the following year, when they begin to expand. Bud burst occurs about the first week in April, when both pollen-cone and seed-cone

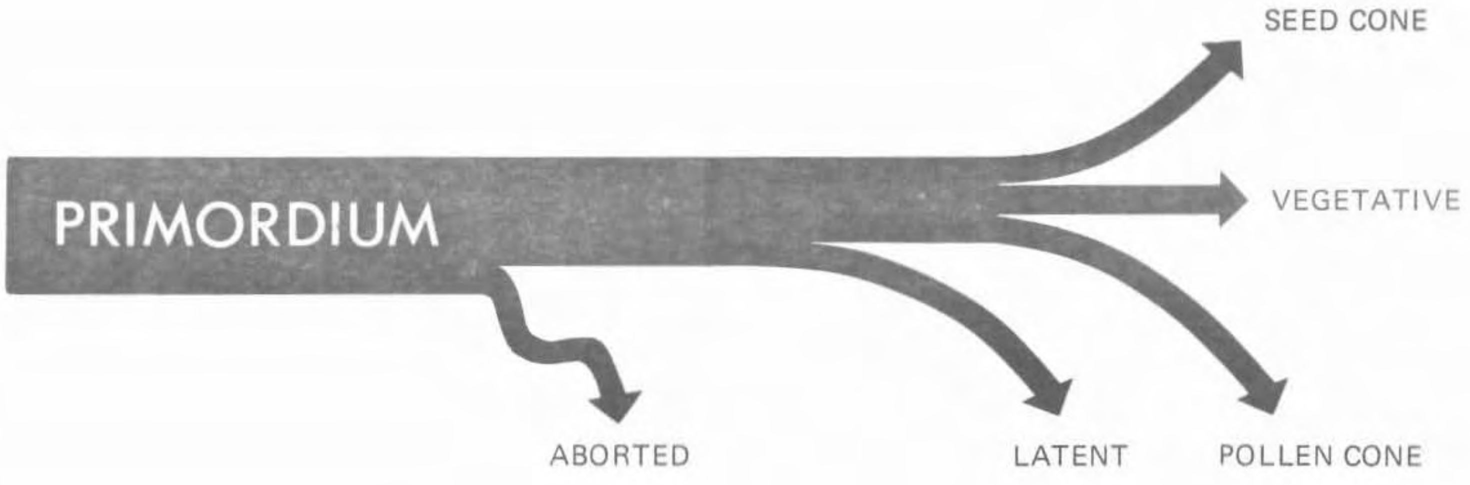


Figure 1 Diagramatic representation of pathways along which lateral primordia may develop (Reproduced by permission of the Research Council of Canada from Owens, J.N. 1969. Canadian Journal of Botany, 47: 1040.).

primordia expand through the bud scales. The pollen from the male cones is subsequently blown to the receptive female cones which are upright on the twigs. After pollination, the pollen grain produces a long tube which grows through the nucellar tissue of the female gametophyte. Two sperm nuclei are released from this tube and one fuses with the egg to complete fertilization, usually between June 1 and June 20 at lower elevations in British Columbia (Allen and Owens, 1972). The embryo grows at the expense of the female gametophyte tissue throughout the months of June, July and August and reaches maturity by early September. During late August, the cones begin to dry and turn brown. As drying continues, the cones open and the seed is released in September.

The release of seed thus completes the Douglas-fir reproductive cycle, which covers about 17 months, from cone initiation during late March and early April until seed release in September of the following year (Allen and Owens, 1972). Figure 2 shows the entire reproductive cycle.

(2) Reproductive Cycles of Other West Coast Conifers.

Although other members of the Pinaceae follow basically the same pattern as Douglas-fir, some show important differences especially in times of differentiation. In view of the importance of correctly timing cone-induction techniques with the period of reproductive differentiation, it is important to understand just when this period occurs in different conifer species.

(a) Western hemlock

Preliminary work on the reproductive cycle of western hemlock Tsuga heterophylla (Raf.) Sarg., has been undertaken by Owens (1971) and is diagrammatically represented in Figure 3. Perhaps the most important variation in the hemlock reproductive cycle is that seed cones and most pollen cones form by the transition of a previously vegetative bud to a reproductive bud after the bud scales have been formed about mid-June. Hence mid-June to mid-July is probably the crucial time for reproductive bud differentiation in hemlock.

(b) True fir

Abies grandis (Dougl.) Lindl. and A. lasiocarpa (Hook.) Nutt. appear to be similar to Douglas-fir in their life cycle (Eis, 1970) and undergo sexual differentiation during the April-May period.

(c) Spruce

Fraser (1966) reported that the lateral buds of black spruce (Picea mariana (Mill.) B.S.P.) are initiated around the beginning of June at Chalk River, Ontario, and are distinguishable as reproductive or vegetative by the end of July. Eis (1967), in a similar study on white (Picea glauca (Moench) Voss) and black spruce in the Interior British Columbia Region, observed that reproductive buds were distinguishable with a hand lens by late July. Fechner (1964) first located reproductive buds by mid-July in blue spruce (Picea pungens Engelmann) in North Colorado. The reproductive cycle of spruce thus appears to besimilar to that of hemlock with reproductive bud differentiation between June and July.

(d) Western red cedar

The pattern of bud development in cedar (Thuja plicata Donn) varies from the conifers mentioned previously. In this species, pollen cones are differentiated about the beginning of June, whereas seed cones are differentiated one month later (Owens and Pharis, 1971). The sequence of development, shown in Figure 4, is taken from Owens and Pharis (1971).

(e) Pine

The reproductive cycle and seasonal development of the shoot apices of the pines are the most completely documented of all conifers (Ferguson, 1904; Doak, 1935; Mergen and Koerting, 1957; Wareing, 1958; Duff and Nolan, 1958; Sacher, 1954; Owston, 1969; Eggler, 1961; Gifford and Mirov, 1960). The reproductive structures in the "hard pines", which includes lodgepole, are laid down within the terminal bud during July, August and September. Pollen- and seed-cone primordia are usually produced on separate shoots although occasionally both appear on the same shoot (Duff and Nolan, 1958). On the pollen-

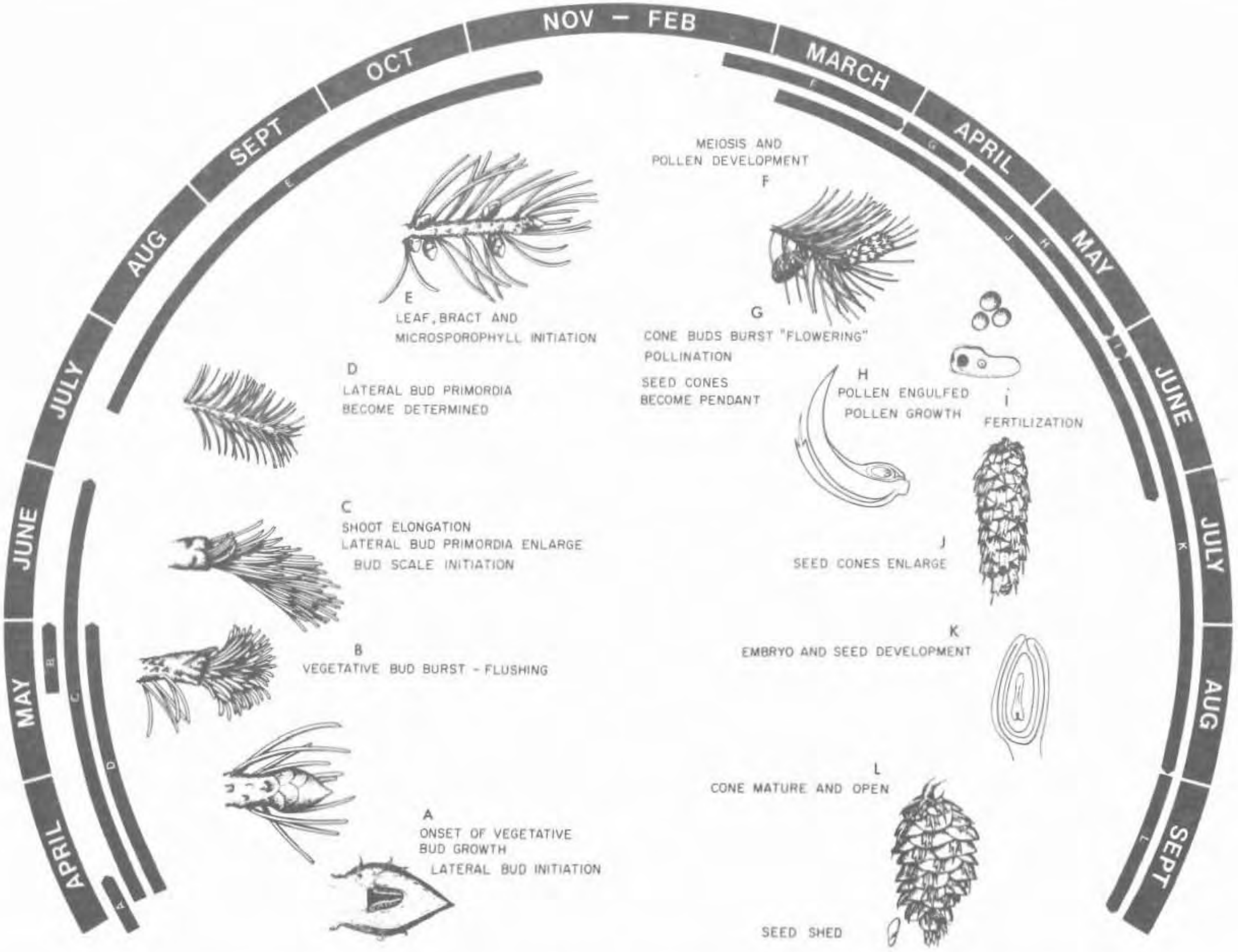


Figure 2 The reproductive cycle of Douglas-fir. Cones are initiated in April, pollination of these cones occurs the following April and the mature seed is shed in September of the second year. Letters A-L represent various stages and arrows represent the approximate time each stage occupies in the reproductive cycle. (From Allen and Owens, 1972).

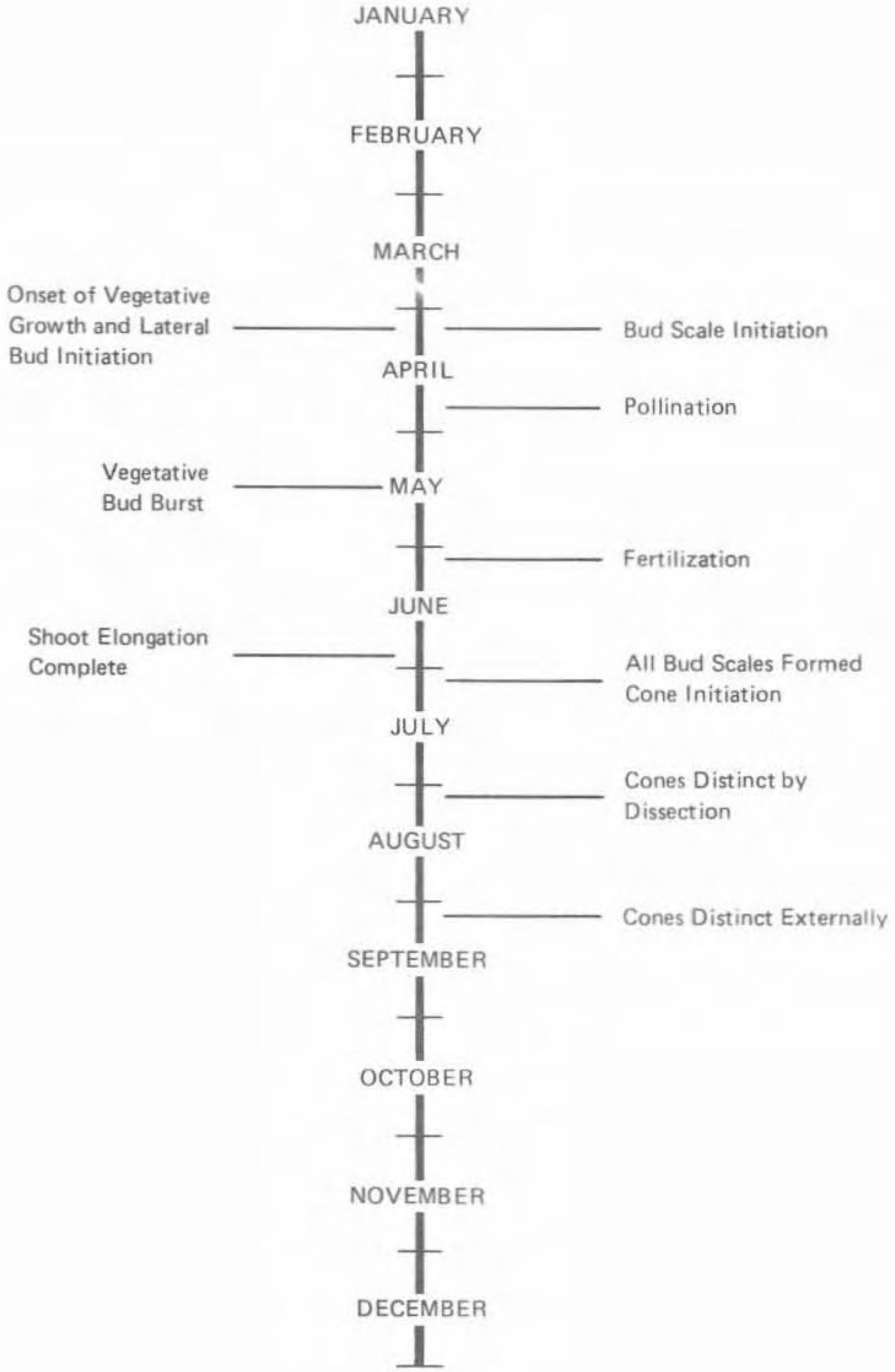


Figure 3. Tentative Phenology for Western Hemlock
on Southern Vancouver Island
(From Owens, 1971)

DATE		PHOTOPERIOD	STAGE IN GROWTH CYCLE	
		HR MIN	POLLEN CONES	SEED CONES
MAY	21	1526	VEGETATIVE APICES	VEGETATIVE APICES
	25	1534		
	29	1543		
JUNE	2	1549	FIRST APICES TO UNDERGO TRANSITION	
	6	1555	INITIATION OF POLLEN CONES	
	10	1559		
	14	1602		
	18	1604		
	22	1605	LAST APICES TO UNDERGO TRANSITION	
	26	1603	DEVELOPMENT OF POLLEN CONES	
	30	1601		
JULY	2	1600		FIRST APICES TO UNDERGO TRANSITION
	6	1555		INITIATION OF SEED CONES
	10	1550		
	14	1543		
	18	1536	ALL MICROSPOROPHYLLS AND MICROSPORANGIA INITIATED	
	22	1527		LAST APICES TO UNDERGO TRANSITION
	26	1518		DEVELOPMENT OF SEED CONES
	30	1508	MATURATION OF POLLEN CONES	
AUGUST	3	1457		
	7	1445		
	11	1434		
	15	1420		ALL BRACTS AND OVULES INITIATED
	19	1408		MATURATION OF SEED CONES
	23	1355		
	27	1342		
	31	1329		

Figure 4. Phenological summary of stages inccone initiation and development in Thuja plicata as they relate to the natural photoperiod. (Reproduced by permission of the National Research Council of Canada from Owens, J.N., and Pharis, R.P., Canadian Journal of Botany 49: 1165-1175 (p. 1171). 1971.

cone-bearing shoot, the primordia are initiated in the order of pollen-cone primordia, leaf fascicle branches and lateral branches. However, in the seed-cone-bearing shoot, leaf fascicle and lateral branches are initiated before seed-cone primordia. Thus the pollen cones are produced earlier in the season than the seed cones. The time sequence of cone formation is variable, depending upon the species of pine studied. Pollen cones have been observed microscopically as early as late May in lodgepole pine (Owens, 1971) to as late as mid-August in Scots pine (Wareing, 1958). Seed-cone development shows a similar variation, varying from July in longleaf to mid-October in loblolly (Eggler, 1961). Probably a certain amount of variation in time of morphogenesis could be due to differences in investigational techniques and habitat. Generally, it would appear that in the hard pines, pollen cones are initiated from the beginning of June to mid-August, while seed cones are initiated from mid-August until late September. In "soft pines", potential seed-cone primordia are initiated in the fall but do not differentiate until the following spring (Owston, 1969).

The different conifer species thus show a wide diversity in their time and mode of development of the reproductive structures (Figure 5).

(3) Juvenility Phase and Maturation

There is a minimum period after germination in which the conifers do not form reproductive structures. This period of the life cycle, the juvenile phase of growth, is common to all conifers and lasts for varying periods, depending upon the species (Baker, 1950). Table 1 shows the approximate duration of the juvenile period for West Coast conifers.

After a certain time period, juvenile plants undergo a phase change (Robinson and Wareing, 1969) and enter the adult or reproductive phase. During this phase, the trees are capable of producing cones and undergo the reproductive cycles mentioned above. Attainment of the adult phase does not necessarily mean that plants will produce cones, and they may retain the vegetative state indefinitely. In other words, although the tree is potentially capable of cone production, the formation of reproductive structures is dependent upon suitable conditions both within the plant and in the environment. Like the juvenile state, the adult condition is relatively stable (Schaffalitzky de Muckadell, 1959) and is maintained even if the mature scion is grafted onto a juvenile rootstock.

(4) Periodicity

Conifers in the adult stage do not produce similar amounts of cones year after year but show considerable fluctuation or periodicity (Matthews, 1963; Lowry, 1966; Eis, 1967; Daubenmire, 1960). Good cone crops are invariably followed either by crop failures or very light production and it is rare to have two heavy cone crops in succession (Eis et al., 1965). Table 2 shows a 48-year record of Douglas-fir cone crops for Washington and Oregon compiled by Lowry (1966). The time between abundant cone crops varies from 2 to 11 years, with an average around 5. Eis et al. (1965) showed the same periodicity for Douglas-fir on Vancouver Island, B.C. and found that grand fir followed a similar pattern. Eis (1967) reported that bountiful seed crops in spruce occurred once in about every six years in the interior of B.C. However, Zasada and Viereck (1970) observed that for white spruce growing in Alaska, very good seed years may be separated by 10 to 20 years. Unlike the firs, western white pine generally shows consistent cone production from year to year (Bingham and Rehfeldt, 1970; Franklin, 1968). Cone-crop periodicity is dependent not only upon species, but also upon many additional factors. Climatic conditions (Lowry, 1966), squirrel damage (Shearer and Schmidt, 1971), insect damage (Baldwin, 1942), and tree metabolism (Brondbo, 1970) all interact to alter the pattern of cone production and give rise to periodicity of cone crops.

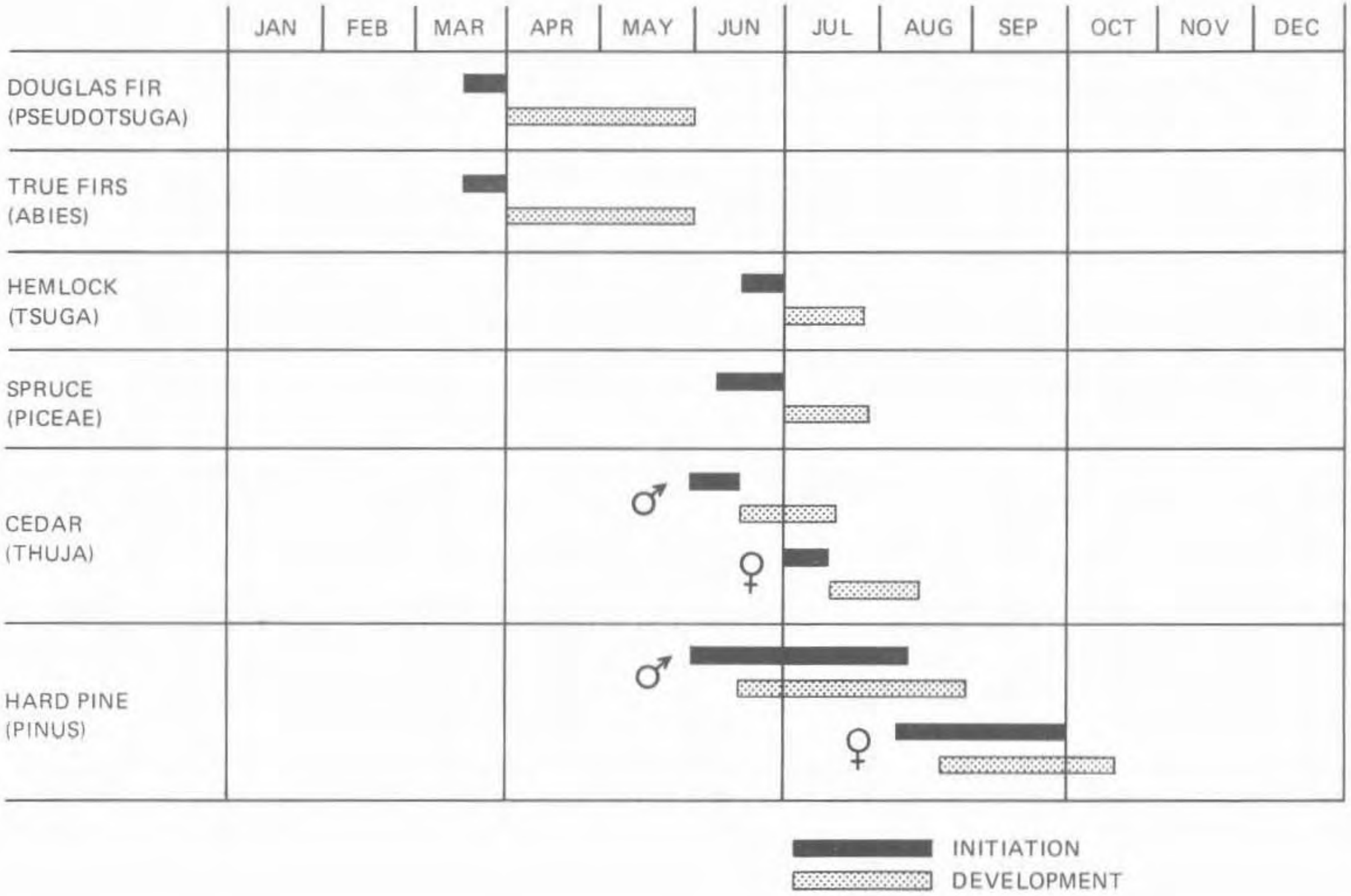


Figure 5 Probable time period for reproductive bud initiation and development in common Pacific west coast conifers. The bars on the figure represent time spans for initiation or development and not specific dates.

Table 1

Duration of Juvenile Period in West Coast Conifers

Conifer	Juvenile Period (Years)	References
Pseudotsuga	10-20	Allen, 1942
Picea	10-20	Holts, 1959
Tsuga	20-25	Piesch (personal communication)
Abies	20-40	Eis, 1970
Thuja	10-20	Eis, (personal communication)
Pinus (Lodgepole)	4-10	Righter, 1939

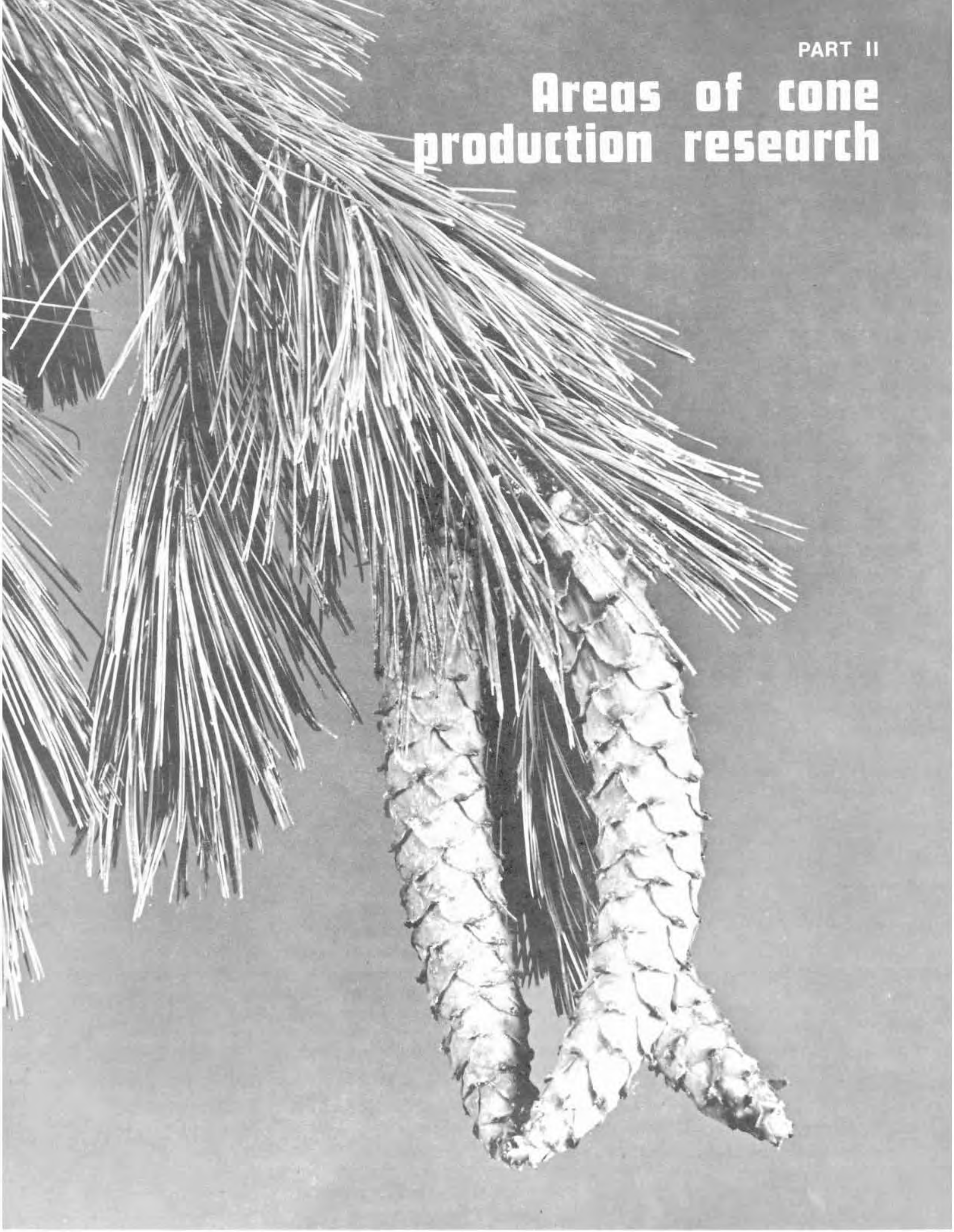
Table 2. Rating of Douglas-fir cone crops, western Washington and Oregon 1909-1956 (Taken from Lowry, 1966. Forest Sci. 12: 186).

Year	Rating	Year	Rating
1909	Medium	1934	Abundant
1910	Failure	1935	Light
1911	Abundant	1936	Abundant
1912	Light	1937	Light
1913	Failure	1938	Medium
1914	Abundant	1939	Medium
1915	Light	1940	Failure
1916	Failure	1941	Abundant
1917	Light	1942	Failure
1918	Abundant	1943	Light
1919	Failure	1944	Light
1920	Light	1945	Medium
1921	Light	1946	Abundant
1922	Failure	1947	Light
1923	Abundant	1948	Light
1924	Failure	1949	Medium
1925	Light	1950	Light
1926	Light	1951	Light
1927	Light	1952	Failure
1928	Light	1953	Failure
1929	Light	1954	Light
1930	Medium	1955	Failure
1931	Light	1956	Medium
1932	Medium		
1933	Medium		

Source: U. S. Forest Service and Weyerhaeuser Timber Company.

PART II

Areas of cone production research



PART II

AREAS OF CONE-PRODUCTION RESEARCH

A. JUVENILITY

Since trees normally will not produce cones while in the juvenile condition, the results of breeding can not be tested or used for a number of years. The progeny of two selected parents can not be expected to produce seed until they reach the adult phase, an interval of 10 to 40 years, depending upon the species. Hence tree breeders must wait at least a decade before they can use their improved seed for reforestation and even longer if they desire further genetic experimentation. In addition, by the time the trees are producing seed in usable amounts, they usually have attained a size that makes controlled pollination and cone collection difficult.

In view of its importance, the phenomenon of juvenility and maturity has been of primary concern of tree breeders and horticulturalists and has been dealt with in a number of extensive reviews (Robbins, 1957; Schaffaltizky de Muckadell, 1959; Wareing, 1959). Maturity is distinct from aging or loss of vigor (Wareing, 1959). As a tree increases in size and complexity, its growth slows and changes occur in the form of the shoot, e.g. loss of apical dominance (Matthews, 1963). If cuttings are taken from an aged tree and grafted onto a young rootstock, the cutting is reinvigorated and regains the growth characteristics of a young plant, but grafting will not convert a mature cutting to the juvenile condition (Schaffalitzky de Muckadell, 1959). In other words, aging, which reflects the nutrient conditions of the plant, can be reversed but maturity, which reflects a permanent change in the cellular metabolism, can not (Wareing, 1959).

Although woody plants require a certain time period before reaching maturity, the period is not determined by a number of seasonal growth cycles. Longman and Wareing (1959) grew seedlings of birch under conditions of continuous long days and under cycles of growth and dormancy. The continuously grown plants successfully reduced the juvenile requirement, whereas the plants grown under artificial growth cycles did not. They concluded that the attainment of an absolute size was the primary factor determining the transition to maturity, regardless of how the size was obtained. Wareing and Robinson (1963) confirmed these results and showed that size also caused the transition to maturity in Japanese larch. Later, Robinson and Wareing (1969) established that the transition of juvenile to mature was not due to size per se. By means of continuously decapitating and regrowing black currant seedlings, they were able to obtain flowering at a size below the normal minimal level. From this, it was suggested that phase changes of the shoot apex resulted from some mechanism within the apex which was set into motion after the apical meristem had passed through a number of cell divisions.

In ivy, there is some indication that the factor responsible for reproductive phase change does not occur within the apex. Doorenbos (1954) grafted mature scions of ivy onto rooted cuttings of juvenile plants and found that the new growth was juvenile. If the grafts were reversed, young grafts on mature rootstock, there was no effect. Dorrenbos concluded that some substance from the juvenile rootstock was transferred to the shoot apex of the adult graft and caused it to revert to the juvenile condition. This hypothesis was further substantiated by Frank and Renner (1956), who found that if rooted juvenile cuttings were combined with adult shoots in a nutrient-filled vessel, the adult shoots produced juvenile growth. They also showed that adult shoots would revert to the juvenile condition if they were subjected to low temperatures or x-rays.

Whether the stimulus responsible for terminating the juvenility of the plant results from the condition of the apex following cell division or from a translocated substance which alters the metabolism of the apex is still a matter of speculation. Robbins (1957) and Wareing (1959) feel that in the life of the plant there are two physiological stable states of the meristem, both of which are transmitted through cell division. As a result of a certain number of cell divisions, a transition occurs from one state (juvenile) to the other (mature). Since the mature tissue ultimately produces embryos that are again in the juvenile condition, Wareing (1959) has postulated that the transition does not involve a nuclear genetic change but involves different states of the cytoplasm. These cytoplasmic factors are self-duplicating and are passed from one cell generation to the other. Similar hypotheses were put forward by Frost (1938), who found that embryos produced by the nucellar (adult) tissue in Citrus retained the same juvenility as embryos produced by fertilization. There has been no suggestion, however, of the nature of these cytoplasmic factors or how they are changed by age.

There is some question as to how phase change could occur without affecting the genetic activity (Ali and Westwood, 1966; Bonner and Zevaart, 1962). The different metabolic pathways of reproductive tissue must require specific enzymes and therefore different DNA (deoxyribonucleic acid) transcribed RNA (ribonucleic acid). Ali and Westwood (1966) analyzed nucleic acids as related to juvenility in several Pyrus species. They found that phase change had no effect on the DNA content but juvenile leaves had substantially less RNA than adult leaves. From this, it was hypothesized that juvenile plants do not flower because the messenger RNA responsible for synthesizing "floral protein" is not transcribed by the nuclear DNA.

Precocity or early flowering has been found to be genetically transmissible (Teich and Holst, 1969; Heimburger and Fowler, 1969). Schrock (1949) found that a high proportion of the progeny of precocious Scots pine was also precocious. Smith and Konar (1969) reported that only seedlings from one of 60 clonal seed sources of longleaf pine exhibited early flowering. Heimburger and Fowler (1969) selected and crossed early flowering Scots pine and found that transmission of precocity was under strong genetic control. The inheritance of early formation of ovulate strobili seemed to be determined by recessive genes. Teich and Holst (1969), in a similar study on Scots pine, reported that inheritance of precocity appeared to be controlled by a single major gene whose expression was dominant or recessive, depending upon the clone with which it was crossed. These workers also found evidence of a maternal or cytoplasmic influence on the inheritance of precocity. Thus possibly both cytoplasmic and genetic factors play a role in the juvenile-mature transition.

Regardless of whether the change at phase transition resides in the cytoplasm or chromosomes, or whether the stimulus develops within the apex or is translocated there, the main question is the identity of the factor causing phase change. The work with ivy seems to indicate a translocatable biochemical substance, possibly a hormone (Doorenbos, 1954; Frank and Renner, 1956). Stoutemeyer et al. (1961) and Goodin and Stoutemeyer (1961) found that gibberellic acid could revert the mature form of ivy to the juvenile form if used at high temperature. Gibberellic acid has been used successfully to induce maturity in members of the Taxodiaceae and Cupressaceae (Kato et al., 1959; Sato, 1963; Hashizume, 1959; Pharis et al., 1965, 1969; Pharis and Morf, 1967, 1968, 1969). Pharis and his colleagues induced coastal and giant redwood and western red cedar to produce cones less than one year after germination by using gibberellin sprays. It would appear, therefore, that the hormone gibberellic acid directly affects the phase change phenomena. Pharis (1970) has put forward the theory that juvenility is a period during which there is a limiting concentration of one or more hormones necessary for reproductive growth. When these hormones are supplemented by an exogenous application, flowering occurs.

In spite of these findings, many questions on phase change are still unanswered. What is the role of gibberellin in flowering and does it act alone or in combination with other plant growth hormones to trigger the synthesis of enzymes leading to flowering? Does the flowering substance induce the nuclear DNA to form new RNA or does it repress some inhibitor which prevents RNA transcription? Where does this stimulus come from? the shoot apex itself or other parts of the plant? If it comes from the former, what causes it to be synthesized after a certain number of cell divisions (Wareing 1959)? If it comes from other parts of the plant, what organ is its site of synthesis and why does it take so long to be effective in the apex? These questions and many like them are still awaiting concrete answers and it is apparent that only through further experimentation will the cause or causes of phase change be unravelled.

B. PERIODICITY

(1) Initiation versus Differentiation.

In most investigations, the yearly differences in the amounts of cones were presumed to result from differential formation of reproductive primordia (Duff and Nolan, 1958; Stephens, 1961). The destiny of the primordia was believed to be fixed at the time of formation and the number of cones produced depended upon how many reproductive buds were initiated. As a result, treatments used to induce cone production were timed to coincide with the time of primordia initiation (Matthews, 1963). Recently, it has become evident, for Douglas-fir, that in sexually mature trees, the number of cones produced is not entirely dependent upon the number of primordia initiated but is determined by the proportion of primordia that develop as reproductive buds (Silen, 1967; Eis, 1970; Owens, 1969; Ebell, 1971).

Silen (1967) observed that the number of reproductive buds in Douglas-fir decreased linearly as elevation increased. This decreased was not accompanied by a decrease in the total number of buds, but was found to be due to lack of development and abortion of potential reproductive buds at higher elevations. Owens (1969), in a detailed anatomical study on Douglas-fir, stated that buds are initiated as undifferentiated primordia in early spring and then generally develop along five different pathways, depending upon environmental and physiological factors, although these pathways may be reversible (Fig. 1). He indicated that prior to poor cone years a similar number of buds are initiated as prior to good years but many potential pollen-cone buds become latent or abort, while potential seed-cone buds develop into vegetative buds or become latent and abort. These results were confirmed by Ebell (1971), who reported that although cone production was greatly enhanced on the girdled half of a double-stemmed tree, the total buds per shoot were not significantly different between the control and girdled stems. He stated that the effect of girdling was the result of an increasing percentage of reproductive buds completing normal development.

The results make it apparent that the most crucial period in cone production in some species is the one just after initiation, during which the bud primordia are growing and differentiating. During this time, the buds are probably sensitive to external and internal stimuli. Thus if treatments are going to be effective, they must be applied in or before this differentiation period. As pointed out, the period of differentiation varies, depending upon the species (Fig. 5), and this factor must be taken into account when applying cone-induction treatments.

Besides being dependent upon the differential development of buds, the number of cones is also regulated by the total number of buds produced. Damaged or diseased trees will generally produce less new growth than healthy trees (Baker, 1950). Also, conditions of water stress resulting from dry summers can restrict growth the following spring (Kozlowski, 1968). Brix (personal communication) has found that climatic conditions during the spring-summer growing season regulate the number of leaf primordia of the following year. The 1970 Annual Report of the Pacific Northwest Forest and Range Experiment Station (1971) reports that the number of reproductive buds in Douglas-fir can be affected by the environmental conditions of the previous summer. Eis (1972) obtained similar results from Douglas-fir and grand fir. Thus bud initiation should not be completely discounted as a factor in cone-crop periodicity; therefore, weather conditions of the the summer preceding bud formation apparently play a more important role than was previously thought.

(2) Effect of External Factors on Cone Production

In the numerous studies on cone production, the basic object has been to establish which factors regulate the number of cones produced, thereby permitting control of seed crops. Cone production, like growth, is not a simple process and is affected by a host of environmental (external) parameters as well as by complex physiological (internal) processes within the tree. Consequently, research on cone production has produced an enormous range of experimental approaches and voluminous literature. It may appear futile to deal with all these reports, but it is only through an understanding of how every parameter affects cone production that cone-crop periodicity will be explained and subsequently controlled.

(a) Temperature

Temperature plays a significant role in cone production (Matthews, 1963). Maguire (1956) utilized a 23-year record of cone production and temperature of a Pinus ponderosa stand to establish that above average temperatures in April and May of the year of cone initiation led to good cone crops 27 months later. In a similar study on Pinus ponderosa, Daubenmire (1960) found no effect of the April-May temperature, but recorded that higher than average temperature from June to September was closely correlated with good cone crops two years later. Unlike other conifers, most pine species in moderate climates require three seasons between cone initiation and maturation (Ferguson, 1904). Detailed observations of beech masts in Europe (Matthews, 1955; Holmsgaard and Olsen, 1960; Matyas, 1969) have established that high temperatures during June and July lead to good seed crops the following year. Excessively hot, dry summers also enhance cone production of white and black spruce the following year (Fraser, 1958).

There have been three extensive investigations into the relationship between climate and cone production in Douglas-fir (Lowry, 1966; Van Vredenburch and La Bastide, 1969; Eis 1972). Lowry (1966) statistically analyzed the meteorological and cone-production records of Douglas-fir in the northwest coast over a 48-year period. He found that cone crops were significantly correlated with cool temperatures during bud initiation in March and with warm January and June temperatures during the year of cone maturation. Lowry also established that cool mid-summers were beneficial to cone production two years later. In other words, summer temperatures occurring 8-10 months before bud initiation (Owens, 1969) were important in cone production. In a similar detailed study on Douglas-fir in the Netherlands, Van Vredenburch and La Bastide (1969) substantiated Lowry's findings. Their data are summarized in Table 3. These workers also were unable to explain the beneficial effect of cool summers 24 to 26 months before cone production. However, similar to the situation in beech (Matthews, 1955) and spruce (Fraser, 1958), they established that high temperatures during June and July were positively correlated with the cone crop 14-15 months later. Eis (1972) has recently analyzed the relationship between Douglas-fir and grand fir cone crops and climatic conditions on Vancouver Island, B.C. and has established the same correlations as Lowry (1966) and Van Vredenburch and La Bastide (1969). He feels that climatic conditions of the summer prior to bud initiation significantly affect the cone crop and should be more fully investigated.

Temperature could alter cone production in various ways. Reproductive bud differentiation takes place during the summer preceding cone production for Douglas-fir and spruce (Owens, 1971). Thus higher than normal temperatures during this time may affect various metabolic processes leading to reproductive bud development. The effect of cool summers on cone production two years later may be explainable in terms of the number of buds initiated. As discussed earlier, Brix (personal communication) found that low temperatures during the summer increased the number of leaf primordia formed. Since buds are produced in the axils of these leaves the following spring, the number of leaves could directly affect either the number of buds produced or their function. Low temperatures during summer could enhance the number of leaves formed and thereby possibly enhance bud formation and development into reproductive structures the following year. In any case, a major cause of periodicity is apparently the opposing requirements for cool summers for bud initiation and warm summers for cone differentiation and development.

(b) Moisture

Moisture supply is correlated with cone production, but the type of response is variable and depends both upon the species of tree and the time of year. In pines, high rainfall during May to July has been correlated with high cone production the following year (Wenger, 1957; Shoulder, 1967). However, high precipitation in April and May followed by low rainfall in June and July has a detrimental effect on cone production (Shoulders, 1967). Controlled irrigation experiments have shown that watering pines during the growing season, from March to November, increases the number of pollen cones produced in the next season but has either no effect on the seed cones or slightly reduces their number (Barnes and Bingham, 1963; Barnes and Bengston, 1968; Bengston 1969; Dewers and Moehring, 1970). Combinations of irrigation and drought have been found to enhance seed-cone production. Dewers and Moehring (1970) found that loblolly pine ramets subjected to April - June irrigation followed by July - September drought bore a significantly larger conelet crop than controls the following year.

In beech, Fagus silvatica L., desiccation during the growing season, rather than irrigation, is an important factor in inducing flowers (Holmsgaard and Olsen, 1960, 1961, 1966). Holmsgaard and Olsen (1966) subjected potted beech grafts to drought at different periods from May 27 to June 15 for different lengths of time. They established that drought significantly enhanced flowering and that plants subjected to drought latest in summer and for the longest duration showed the best response. Similar to beech, Douglas-fir also responds to summer drought (Ebell, 1967), although high precipitation during the period of bud initiation in March and April has been found beneficial for cone production (Lowry, 1966; Van Vredenburch, and La Bastide, 1969). Alvim (1960) established that coffee plants would not flower unless they underwent a certain period of water stress, and suggested that stress removed an inhibitor which allowed the plant to flower.

Table 3. Summary of results of optimum weather requirements for a good to abundant cone crop in the U.S.A. and the Netherlands (Taken from Van Vredenburch and La Bastide, 1969. Silvae Genet. 18: 184.)

Month No.	Month	Apparent weather requirements in western Oregon and Washington*)	Apparent weather requirements in district "Veluwe" the Netherlands	Remarks
26	Jun		Cool, cloudy	
25	Jul	Cool		
24	Aug		Cool	
23	Sep			
22	Oct			
21	Nov			
20	Dec			
19	Jan			
18	Feb			
17	Mar	Moist, cloudy	Moist	
16	Apr			Bud primordia initiated**)
15	May			
14	Jun		Sunny, warm & dry	
13	Jul		Sunny, warm & dry)	
12	Aug		)	Foliar organ initiation***)
11	Sep			
10	Oct			
9	Nov			
8	Dec			
7	Jan	Warm		
6	Feb			
5	Mar		)	
4	Apr		)	Pollination
3	May		)	
2	Jun	Not cold		
1	Jul			
0	Aug			
00	Sep			Seeds fall

*) Adapted from original tables. Lowry, W.P.: Apparent meteorological requirements for abundant cone crop in Douglas-fir. Forest Sci. 12:185-192 (1966).

**) Owens, J.N. and F.H. Smith (1965).

***) From different sources

Despite these interesting correlations between moisture and cone and flower production, there has been no attempt to analyze the actual water potential of the plant and to follow its seasonal changes. Water potential is a measure of the free energy of water in the plant cell and is affected by conditions in the atmosphere, plant and soil. Investigation of this parameter and cone production would help to clarify the actual relationship between moisture and the reproductive process.

(c) Light Intensity and Photoperiod

There is some indication that light intensity affects the cone- and flower-production process. Nanda (1962) reported that in closed stands of teak, only dominant and co-dominant trees flower and then only on the upper part of the tree. On trees on the stand margin, flowering only occurs on the non-shaded side of the tree. Brøndbo (1970) indicated that it is quite common to have abundant flowering on trees growing on south slopes, or on free standing trees. Winjum and Johnson (1964) stated that Douglas-fir formed most cones on the south side of the crown and more on the west than on the east side. Smith and Stanley (1969) also found that the side of slash pine which received the greatest amounts of solar energy produced the most cones. Sarvas (1962) has suggested that light intensity may have differential effects on reproductive development in Scots pine. He stated that seed cones form mainly in areas of the tree receiving full light, while pollen cones usually form in shaded areas. It is not clear whether these cone responses are related strictly to light or to the related increase in temperatures.

Besides light intensity, many plants require certain periods of light and dark to flower. This requirement, called photoperiodism, is the primary factor controlling flowering in many herbaceous plants and shrubs and has been the subject of considerable investigation (Meyer et al., 1960). Unfortunately, the effect of photoperiod on flowering in conifers is not so clear-cut (Matthews, 1963). Mirov (1956) obtained pine plants from many different provenances and grew them at Placerville or Berkeley, California. Although these plants were displaced from their usual latitudinal habitat, they all flowered normally and Mirov concluded that they were day-neutral. Lanner (1963) similarly found no effect of photoperiod on cone production of knobcone pine. Wareing (1958) felt that photoperiod was not effective in reproductive development or Scots pine since there was a change in day-length of only 1½ hours between June 21 and August 30, the times of cone differentiation.

In spite of these negative findings, there is some evidence that photoperiod may affect flowering. Larson (1961) caused Jack pine to flush at different times in the spring and thus under different photoperiods, by holding the plants in a cold room. He established that pollen-cone production was greatest on plants removed from the cold room on April 20 while seed-cone production was greatest on plants removed on April 6. Longman (1961) reported that young potted Pinus contorta formed more seed cones than controls if grown under short-day periods out of doors. It has also been established that photoperiodism is involved in the induction and development of cones in juvenile conifers, as will be explained in the section dealing with hormones (Pharis and Morf, 1968; Pharis et al., 1969, 1970). Thus photoperiodism may yet be found to be effective in controlling cone periodicity in sexually mature trees.

(d) Spacing (Thinning)

Thinning forest stands have been consistently shown to stimulate cone production on released trees (Wenger, 1954; Bilan, 1960; Phares and Rogers, 1962; Reukema, 1961). Bilan (1960) reported that released loblolly pine produced six times as many cones as non-released trees three years after treatment. Wenger (1954), and Allen and Trousdell (1961) found that release would stimulate good cone production in loblolly pine in both poor and good seed years. Reukema (1961) stated that thinning enhanced cone production in Douglas-fir in good seed years but not in poor ones. The cause of the beneficial effect of thinning the forest stands is believed to be due to the improved light, temperature, moisture and nutrient conditions resulting from the release of trees from competition.

(e) Gravity

Geotropic stimulation has been used for some time to stimulate flowering in fruit trees but has seldom been applied in conifers (Longman and Wareing, 1958). Longman et al. (1965) trained branches of young Japanese larch into either horizontal or downward positions during March and April. They found that the bending treatments markedly enhanced cone production, and that the amount of cones was directly proportional to the degree of bending. Of the cones produced by the treated branches, 95 per cent were pollen cones. Melchoir (1961) obtained similar results on grafted Japanese larch by bending the top of the crown. Bending, however, has had no effect on birch (Longman et al., 1965) and there are no reports of its effect on conifers other than larch.

(f) Fertilizer Treatment.

One of the most commonly used techniques for improving the development of cones on conifers has been the application of nitrogenous fertilizers (Matthews, 1955). Fertilization has been carried out on a wide variety of coniferous species with varying degrees of success. Many different factors will affect response to fertilizers and consequently many of the results are conflicting. Appendix 1 lists a number of different fertilizer experiments and their effect in inducing a cone crop. In Douglas-fir, fertilization has enhanced the number of trees that bear cones as well as the number of cones produced per tree. This enhancement has usually occurred in naturally good seed years, and fertilization has been relatively ineffective in years of cone crop failures (Steinbrenner et al., 1960; Ebell, 1972). Ebell and McMullan (1970) have shown that the nitrate form of nitrogen is more effective in producing cones in Douglas-fir than the ammonium form. This difference is apparently due to the different type of nitrogen metabolism resulting from nitrate-nitrogen as opposed to ammonium nitrogen rather than the total nitrogen concentration. Stoate et al. (1961) have established that cone production will be enhanced in Douglas-fir if fertilization takes place at the time of bud break. Fertilization two weeks before or after bud break was ineffective in producing cones. Proper application of nutrients around the time of bud differentiation will apparently stimulate the development of reproductive buds and prevent latency and abortion (Ebell, 1972).

The variable results of the fertilization trials shown in Appendix 1 probably arise for a number of different reasons. First, in the majority of cases, the forest soil was not analyzed for nutrient content before fertilizer application. Thus there is no indication if the fertilizer was added in excessive or deficient amounts of if elements other than nitrogen were limiting. Secondly, the fertilizers were added at different times of the year. It has already been stressed how each coniferous species has its own peculiar period of reproductive bud differentiation. Unless fertilization is planned to coincide with this differentiation period, there is a strong possibility that the treatment will be ineffective. Hence fertilization of hemlock should probably take place during June and July rather than April and May, as in Douglas-fir. Third, as shown by Ebell and McMullan (1970), some forms of fertilizers, e.g. ammonium, although supplying nitrogen to the soil, will not induce cone production. Fourth, rainfall after fertilizer application may negate the beneficial effects on cone production (Ebell, 1972). Finally, environmental conditions at the forest site and numerous other aspects may provide limiting factors in spite of the amount of nutrients in the soil.

Despite these variable factors, fertilization is the most accepted means of inducing cone crops. This is probably mainly due to its added advantage of enhancing the growth and vigor of seed trees (Steinbrenner et al., 1960). It is evident that greater attention must be paid to time, method and application before fertilization will become a consistently useful technique.

(g) Girdling. Strangling and Pruning

The use of girdling, strangling and pruning to induce flowering arose out of the carbon: nutrient theory proposed by Klebs. Klebs (1910) reported that conditions that favored carbon assimilation and/or limited the uptake of soil nutrients led to enhanced flowering. It was reasoned that the carbohydrate concentration would increase in the crown if the translocation of nutrients to the roots was impeded by damaging the phloem. The increased carbohydrate content in the crown would, in turn, enhance the formation of cones. Although findings have indicated that an altered carbohydrate content may be a result rather than a cause of cone production (Ebell, 1971), wounding treatments have been successfully used to induce cone crops (Matthews, 1963).

Appendix 2 lists some wounding experiments on various conifers and their effect. In almost every case, girdling of the stem by two semi-circular overlapping cuts enhanced cone crops in subsequent years. For pines, this usually occurred in the third year after girdling (Bower and Smith, 1961), whereas in Douglas-fir, enhancement of cones occurred in the second year following girdling (Ebell, 1971). Although girdles were applied at various times of the year, some evidence shows that there is an optimum time for girdling. Melchior (1960) girdled

European larch at intervals of four weeks during the growing season and found that girdling up to the end of May enhanced the number of flowers formed the following year, while girdling after the end of June enhanced cone production two years later. Melchoir felt that this effect occurred because cones were initiated during the month of June. Ebell (1971) carried out a detailed investigation on the effect of time of girdling on cone production of Douglas-fir by girdling at weekly intervals from April 17 to July 4. He established that the optimum time for girdling was about one month before vegetative bud break. This time coincided with that of bud initiation, as shown by Owens (1969). Girdling later than one week after vegetative bud break gave an adverse effect. Thus girdling, like fertilization, must be correctly timed to coincide with the period of bud initiation and differentiation.

Strangulation or severe restriction of the translocation pathway has been shown to be much less effective than girdling in enhancing cone crops (Appendix 2). Holst (1959) and Heitmuller and Melchior (1960) found that strangulation of trees enhanced cone production. However, Mann and Russell (1957), Melchior (1961) and Stephens (1961) reported that it produced no result, and Holmes and Matthews (1951) and Bilan (1960) stated that it had an adverse effect. The poor response to strangulation of the phloem has been suggested to be due to the much slower and therefore poorly timed alteration of physiological processes (Ebell, 1971). In addition to its variable response, strangulation treatments may also cause irreparable damage to the tree (Stephens, 1961). In fact, Bilan (1960) stated that "their beneficial effect on seed production is negligible and the risk of losing trees to storm breakage or root starvation is high".

Pruning likewise has been quite variable as a cone-induction technique. Heitmuller and Melchior (1960) obtained very little success with root pruning Japanese larch, while Stephens (1961) obtained enhanced cone production in eastern white pine. Holst (1959) found that root pruning caused increased cone production in white spruce and red pine, especially when carried out in combination with fertilizer. Branch pruning and removing buds from Scots pine not only enhanced cone production but caused increased amounts of pollen-cone primordia (Melchior and Heitmuller, 1961; Wareing, 1953). Pruning, however, requires further experimentation before it becomes an acceptable technique.

(h) Stress Conditions

After an injury, trees frequently respond by producing a substantial cone crop, usually called a stress crop (Brøndbo, 1970). These stress crops result from a variety of factors such as frost damage (Ebell, 1971), incompatible graft unions (Brøndbo, 1970), disease or insect attack (Kessler, 1969; Muelder and Hansen, 1961), logging injury, etc. Muelder and Hansen (1961) have suggested that the stress effect is due to an alteration of the carbohydrate to nutrient ratio as a result of restricted nutrient transport. In fact, this reaction of stressed plants is partly responsible for the numerous girdling and wounding experiments already described. However, there is very little information to substantiate this C/N theory and the factors causing flowering in stressed plants are unknown.

(3) Effect of Internal Factors on Cone Production

(a) Nutrition

It has long been recognized that reproduction affects the nutrient status of the tree (Matthews, 1961). Holmsgaard (1956) reported that beech trees showed a considerable reduction in radial increment for up to two years after a good flower crop. Eis et al. (1965) found that large cone crops in Douglas-fir, grand fir and western white pine reduced the width of the annual ring, the amount of reduction being directly correlated with the size of the crop. Smith and Stanley (1969) established that within a tree the greatest radial increment and largest number of branches were produced on the portions of the tree bearing the least number of cones. It is apparent, therefore, that the development of reproductive structures places a substantial demand on the metabolic substrate of the tree. In fact, Fielding (1960) has estimated that a Monterey pine plantation loses up to 30 cubic feet of wood per acre over a rotation of 40 years as a result of reproduction.

Work with radioactive isotopes has shown that developing cones mobilize and act as sinks for carbohydrate and nitrogen reserves at the expense of vegetative structures (Dickmann and Kozlowski, 1968, 1970; Rook and Sweet, 1971). Dickmann and Kozlowski (1968, 1970) supplied cone-bearing branches of red pine with $^{14}CO_2$

at various times from May to August. They determined that strobili mobilized almost three times as much carbohydrate from old needles (especially 1-year-old) as was mobilized by the shoot. Rook and Sweet (1971) found that developing cones of Douglas-fir obtained nutrients at the expense of other developing plant structures, especially the roots. They reported that developing cones had a photosynthetic rate slightly less than leaves and that they retained almost all their photosynthate.

It has been postulated that the utilization and draining of the carbohydrate and nitrogen reserves by the reproductive structures during good cone years is the primary cause of periodic cone production (Owens, 1969; Ebell, 1971). The amount of cone production seems to be dependent upon the differentiation of the bud primordia rather than their initiation (Silen, 1967). In a good cone year, the drain of developing cones on nutrients during the spring restricts the number of new branches produced and reduces their nutrient supply. Since the reproductive buds develop on these new branches, the numbers of bud loci are possibly reduced and there is less metabolic substrate and energy available for continued bud development (Ebell, 1971). If this is the case, many potentially reproductive buds become latent or abort, with a resulting cone crop failure the following year. Removal of the growing cones during the spring period leads to enhanced development of reproductive buds (Owens, 1969; Ebell, 1971). Years of heavy crops will thus be followed by years of light production or crop failures, thereby giving rise to a periodic cycle of at least one year.

Although the nutritional status of the tree may be an important factor in affecting cone crop failure, it may not be similarly important in cone crop success. Many of the early workers on reproductive development subscribed to the C/N theory (Brøndbo, 1970). Recent findings have tended to indicate that concentration of nutrients per se is not the primary factor controlling flowering. Bilan (1960) stimulated cone production by girdling or strangling loblolly pine trees but found that neither treatment affected the total amount of carbohydrate reserves. Barnes and Bengston (1968) reported that ammonium nitrate fertilization enhanced cone production in slash pine but did not affect carbohydrate concentrations. Ebell (1971) obtained enhanced cone numbers by girdling one stem of double stemmed Douglas-firs but found no correlation between carbohydrate concentration and cone production. These results indicate that concentration of nutrients is the consequence rather than the cause of flowering, similar to the situation in fruit trees (Davis, 1957).

There is strong evidence that the composition of nutrients rather than their concentration may be actively involved in the promotion of cones. Ebell and McMullan (1970) obtained good cone production by fertilizing Douglas-fir with nitrate nitrogen, but not with ammonium nitrogen, although both forms of fertilizer gave similar foliar nitrogen levels, total sugar concentration and shoot growth responses. With the nitrate form, there was an increased concentration of the total amino acids, arginine, lysine, ornithine and various guanidine substances. Ammonium fertilization, on the other hand, gave higher concentrations of protein and α- aminobutyric acid. Similar changes were found by Ebell and McMullan (personal communication) in well-watered and water-stressed Douglas-fir. They established that the cone producing droughted trees contained higher total amino acids, arginine and monosubstituted guanidino compounds, but lower amounts of α - aminobutyric acid than the barren well-watered trees. In both these experiments, the amino acid arginine showed the greatest increase in concentration in the cone-producing trees. Large increases in arginine were also reported by Barnes and Bengtson (1968) for fertilized slash pine. On the basis of their findings, Ebell and McMullan (1970) have put forward the theory that the level of arginine regulates the development of reproductive tissues in conifers. They feel that high levels of arginine stimulate the development of buds into reproductive structures, while fluctuations in the amino-acid levels lead to natural cone-crop periodicities. This theory bears some merit since abnormally high increases of arginine have been found under cone-inducing treatments. Further research will evidently be required to determine if arginine is actually involved in the reproduction process or is just a by-product of cone-production metabolism.

(b) Hormones

(i) Auxins

In herbaceous plants, auxins have been shown to inhibit flowering in both short-day and long-day plants (Leopold, 1964). With short-day plants (SDP), application of exogenous auxin during the long dark period inhibits flowering and is reversed by application of anti auxins ex. 2,3,5-triiodobenzoic acid (Bonner and Livermann, 1953; Salisbury and Bonner, 1956; Sawhney, et al., 1971). Treatments that reduce the number of auxin-producing leaves or confine the auxins to the stem tips by bending will also permit flowering (Fisher, 1957). Bonner and Livermann (1953) have suggested that in SDP, the factor controlling flowering is the decrease in auxin level during the long uninterrupted dark period. Similar to SDP, long-day plants (LDP) grown under long days can be restricted in flowering by the addition of high concentrations of auxins but can be stimulated by lowering the auxin concentration. Leopold and Thimann (1949) reduced endogenous auxin levels in barley by x-ray treatments or by the use of coumarin and obtained enhanced flowering in direct proportion to the amount of treatment. If LDP are grown under short days, auxin application promotes rather than inhibits flowering (Bonner Livermann, 1953).

Thus auxins play a major role in the flowering of herbaceous plants. There is some evidence that auxins may likewise be involved in the flowering of conifers; however, this evidence is still of an indirect nature. One indication of auxin participation in the flowering process is that of the characteristics of juvenility. Plants in the non-flowering juvenile state show failure of leaf abscission and good rooting ability (Schaffalitzky de Muckadell, 1959), both of which are features of a high auxin concentration. In sexually mature red pine, flowering occurs at a time in the season when extension growth ceases and thus during a period of lower auxin supply (Duff and Nolan, 1958). Training of branches of Japanese larch in a downward or horizontal position similarly markedly reduces extension growth and enhances flowering, suggesting lower auxin levels (Longmann and Wareing, 1958; Longman, 1961). Actual analyses of the endogenous growth hormones have shown that the concentration of growth promoters is low during the period of flower bud initiation (Giertych and Forward, 1966; Hashizume, 1960a).

The concentration of auxin appears to exert some influence on the sex differentiation of conifers. Wareing (1958, 1959) noted that when Scots pine reached maturity, the first reproductive structures to be produced were seed-cone buds. These buds were formed on the strong leading shoots near the apex of the tree. Later, after a certain period of aging, pollen-cone buds were produced on lower branches of the basal region of the tree. As the tree aged further, the pollen-cone buds were formed progressively higher on the branches close to the seed-cone buds. This pattern of reproductive bud distribution has been correlated with the nutrient status of the tree (Wareing, 1958). However, it also closely parallels the known pattern of auxin concentration (Giertych and Forward, 1966), i.e., higher concentrations at the terminal portions of the tree and lower at the basal portions. Wareing (1953) showed that removing the terminal bud in Scots pine would hasten the production of pollen cones. Giertych and Forward (1966) established that fertilizer application caused an increase in the concentration of growth promoter in the lower crowns of red pine and resulted in twice as many seed cones and half as many pollen-cone clusters per potential site as on the control trees. Hashizume (1960a) obtained an indication that the level of growth-promoting substance during sex differentiation seemed a little higher in the portion bearing seed cones than in the portion bearing pollen cones.

(ii) Gibberellins

Gibberellin is a common name given to compounds having the basic gibberellic acid structure and having growth regulatory properties. Unlike the auxins, gibberellins have been shown to exert a positive effect on the flowering of herbaceous plants and have been the subject of numerous investigations (Leopold, 1964). It is well established that gibberellin induces flowering in long day requiring plants growth under short days (Lang, 1957) and in plants requiring low temperatures (Chaikalhian, 1961). Recent work (Hodson and Hamner, 1970) indicates that gibberellin may also be an essential component in initiating flowers in short-day plants. Chailakhian (1961, 1968) has proposed the theory that gibberellin is a major component of florigen, the suggested flowering hormone complex. He feels that florigen consists of gibberellin, which controls growth and development, and anthesins, which control flower initiation. Both of these components are required for flowering. In long-day plants, gibberellin is in limiting supply and requires long days for synthesis, while anthesins are freely available. In short-day plants, gibberellin is not limiting but anthesins are and require long nights to be synthesized. Lang (1956) similarly feels that gibberellin initiates flowering by stimulating stem growth or mobilizing actions associated with growth.

Gibberellins have proven to be very effective in inducing cones in certain conifers (Kato et al., 1959), especially in the Cupressaceae and Taxodiaceae. Intensive research in Japan has established that cones can be induced by applying gibberellin sprays to the foliage the summer prior to cone production

(Hashizume, 1960b, 1961; Kato et al., 1959; Sato, 1963). Response to the gibberellin varies, depending upon the species of conifer used, and although certain species like Japanese cedar show marked stimulation, others like Douglas-fir show no effect. In the Cupressaceae, however, the flowering response to GA is generally positive and repeatable. In addition to initiating flowering, GA treatments also affect the sex differentiation process. Treatment of Japanese cedar during June and August causes mainly pollen cones while treatment during August and September causes mainly seed cones (Hashizume, 1959). Pollen cones are also promoted with gibberellin concentrations of 10-200 ppm, while seed cones are promoted with concentrations of 200-300 ppm. Both pollen and seed produced by gibberellin-treated trees have been shown to be normal and viable and the germination rates of this seed and later seedling growth was almost equal to that of non-induced seed (Sato, 1963).

In North America, gibberellins can terminate juvenility and stimulate cone production in several west coast conifers (Pharis et al., 1965, 1969, 1970; Pharis and Morf, 1967, 1969). Arizona cypress, western red cedar, coastal redwood and giant redwood all produce cones within one year after germination when treated with gibberellin sprays. In addition to gibberellin, normal development of the cones also requires a certain photo-periodic sequence. Thus western red cedar produces cones in response to gibberellin under long days and requires a sequence of long day → short day → long day for full development (Pharis and Morf, 1967; Pharis et al., 1969). Also, Arizona cypress produced ten times as many pollen cones in response to gibberellin under long day conditions as under short day.

PART III

Evaluation of cone production research

PART III

EVALUATION OF CONE - PRODUCTION RESEARCH

A. EVALUATION OF AREAS FOR FUTURE RESEARCH

It is evident from Part II that cone production research to date has taken many different approaches and utilized several different techniques. Despite numerous contributions, there are still many gaps in our knowledge of the flowering process and, consequently, a lack of a suitable control procedure. Such control can likely be developed as a result of further research. However, in a field as large as tree reproduction, the scope for additional research is enormous, whereas research funds are limited. It is essential to be selective and determine the areas of research with the highest probability of providing a reliable technique for controlling cone production. This section delineates these areas and their potential benefits.

(1) Morphology of Reproductive Cycles in Conifers

Research on the sequential anatomical changes involved in the reproductive cycles is necessary for a proper understanding of the reproductive process and is a helpful supplement to other areas of cone production research. For instance, anatomical investigation of Douglas-fir has established that reproductive bud transition occurs during April and May, around the period of vegetative bud break (Owens, 1969). This period coincides with the optimum time for fertilizing (Stoate et al., 1961; Ebell, 1972) and girdling (Ebell, 1971) for cone production. Thus identification of the time of bud differentiation in Douglas-fir has indicated at what time induction treatments should be made for best results. Despite the obvious usefulness of this morphological research, the reproductive cycles of other commercially important conifers, e.g. spruce and hemlock, have received very little study. As pointed out in Part I, the phenomena of flowering and seed production are peculiar to each tree species and each has its own time sequence of reproductive development, its own climatic requirement, its own response to stimulatory treatment and its own metabolic pathways. It would appear to be of prime importance to extend research to elucidate the reproductive developmental process of these other valuable coniferous species, as well as to provide further information on Douglas-fir.

(2) Gibberellin Stimulation of Flowering

The only consistently successful treatment for cone induction in conifers has been application of the plant growth hormone, gibberellic acid (Sato, 1963; Pharis and Owens, 1966). Unfortunately this treatment has only been found to work on members of the Taxodiaceae and Cupressaceae, and there has (Pharis and Morf, 1967, 1968, 1969). This lack of response may be due to gibberellin not being the sole regulator of flowering, as in herbaceous plants (Lang, 1956), or to the type of gibberellin used. There are currently 33 chemically characterized gibberellins and probably more exist (Pharis, personal communication). These gibberellins may not all give the same response when applied to a plant; some may be effective, others moderately so and still others very successful in promoting a particular response. It is important to realize that failure to induce flowers may not mean that gibberellins are nonactive in the flowering process. It is only through identification of the endogenous gibberellins and screening all the gibberellins for their flowering response, as is being carried out by Pharis on Douglas-fir (Pharis, personal communication), that the actual effect of gibberellins on flowering in the Pineaceae will be established. In view of the importance of gibberellin research on both the juvenility and periodicity problem, and in the light of its probable basic reaction in cellular metabolism, this type of investigation should be expanded and continued.

(3) Physiology of the cone-production process and effects of auxins

The least studied and possibly the most important of all areas dealing with the cone-production process is the metabolic reactions leading to cone production. Although cone development is outwardly manifested by the appearance of the buds, the origin of the cone-production process is the activation of certain genes within the bud cells. In poor cone years, most if not all of the bud primordia in Douglas-fir either develop into vegetative buds, abort or become latent (Owens, 1969). During a good cone year, many of these bud primordia develop into reproductive structures. Somehow metabolism is altered, causing the undifferentiated buds to become reproductive.

Since the metabolic processes of the cell are directed by enzymes, which, in turn, are controlled by ribonucleic (RNA) and deoxyribonucleic acids (DNA) of the nucleus (Wagner and Mitchell, 1964), the control of this metabolic change must reside in the DNA sequences or genes of the chromosomes. The initiation of reproductive bud development, therefore, must be due to the activation of the genes for reproductive growth. It is the factor or factors which trigger this process that are the actual controllers of flowering.

Obviously it is of prime importance to establish the nature of this factor or factors. Investigations of inductive treatments show that many different treatments can initiate the flowering process, e.g. girdling, fertilizing, drought, etc. These treatments, however, must all elicit the same metabolic response. By determining what similar metabolites or biochemical pathways occur as a result of each successful inductive treatment, insight will be gained as to the nature of the controlling factor. Research on the amino acid (Ebell and McMullan, 1970), carbohydrate (Ebell 1971) and gibberellin (Pharis, 1970) levels of cone-producing and non-cone-producing trees have shown some encouraging results in this area but more needs to be done. One line of research that may prove rewarding is the effect of auxins on reproduction.

Auxins have been shown to act on a basic level in plant metabolism and to elicit a wide range of responses, including rooting, apical dominance, cambial activation and cell elongation (Meyer et al., 1960). As mentioned in Part II, there is indirect evidence that auxins may be involved in the flowering response of conifers (Giertych and Forward, 1966; Hashizume, 1960a; Wareing, 1953). High concentrations of auxins seem to be correlated with absence of reproductive development, lower levels with seed-cone formation and even lower levels with pollen-cone formation (Hashizume, 1960a). In spite of these findings, there have been few investigations of the direct relation between auxin metabolism and cone production in conifers. This would be an important line of investigation since it would help elucidate the causes of juvenility and periodicity, and, in view of the complex interaction between auxin and other growth hormones (Shien and Jackson, 1971; Sawhney et al., 1971), would permit a clearer understanding of the mode of action of hormones such as gibberellin on cone production.

Research on the effects of auxin on cone formation may also be of value in other areas. Once cones are formed and seemingly healthy, they frequently fail to reach maturity and drop off the tree during the spring (Sweet and Thulin, 1969). Research with herbaceous plants has shown that abscission is correlated with low auxin levels in the shoot (Moe, 1971). If premature abscission of coniferous cones is similarly due to low levels of endogenous auxins, application of napthalene and phenoxy compounds in the form of sprays, similar to horticultural practises, may be useful in preventing early abscission and loss of cone crops.

B. ECONOMIC EVALUATION OF CONE-PRODUCTION RESEARCH

The three areas of research: (i) morphology and phenology of the reproductive cycle, (ii) gibberellin stimulation, and (iii) auxin physiology, have been identified as the most promising sources of control over cone production. The next aspect is to ascertain what level of involvement the CFS should undertake with respect to these areas. In (i) and (ii), external research is already underway and CFS support would ensure its continuation. Research on auxin physiology, however, is not being pursued and is an area in which the CFS could stimulate activity either through an internal research program or by supporting work of others.

If such support is forthcoming, what research programs should be followed? To answer this question, the benefits and costs of the undernoted courses of action have been evaluated by means of a simple model (see Appendix 3):

(1) No support for any research program.
(2) Support for external research.
(3) Initiation of an internal research program.
(4) Initiation of an internal research program in combination with support to external research.

The evaluation in Appendix 3 deals exclusively with high elevation coastal Douglas-fir since it is the species in that zone for which improvement in seed supply is most urgently required.

A basic component of an economic appraisal is the estimation of time necessary for success of the research approach. Success, in this evaluation, is defined as gaining the ability to develop practical, low cost means of controlling and increasing cone production. The time required to achieve "success" in any research program influences the potential contribution that will be made. Obviously, research information gained five years from now will be more valuable than the same information delayed a further five years. The longer it takes for a CFS supported program to achieve its goal, the less it will represent an improvement over research progress without such support. Delays in research effectiveness may also force forest managers to look elsewhere for solutions to their seed supply programs. Similarly, unforeseen research and technological developments may change the definition of the research problem before a solution is reached.

Forecasting research success times is at present a matter of subjective judgement because of the difficulty in estimating both the complexity of the cone-production problem and the effectiveness of the research approach utilized. Table 4 shows the estimates of time to research success for alternative cone-production research programs. The five-year minimum period forecast for the success of CFS supported research is based on the minimum amount of time required to move from current knowledge to practical application of techniques for stimulating cone production. The 10-year minimum period forecast for success in the absence of CFS support is based on the continuation of current university research programs in western Canada, the high level of research interest in conifer cone production elsewhere, and the premise that without CFS support the development of research results into practical techniques applicable in B.C. would be delayed.

The long maximum research success times forecast for the internal and external research alternatives are based on two factors: the slow rate of progress made in past cone-production research efforts in British Columbia, and the possibility that research areas that look promising now may, in fact, provide only part of the answer to cone-production stimulation, and new approaches will be necessary. The much shorter time period for a combined internal-external program reflects the judgement that if difficulties do slow research progress, a cooperative program with a higher level of resources and a wider range of expertise will overcome them much more rapidly than independent approaches.

Table 4. Research success times for alternative research programs.

Research Alternative	Scientist Man Years	Research Minimum	Success Time Maximum
1. No CFS Research	0	10 Years	20 Years
2. Internal CFS Research	1	5 Years	20 Years
3. CFS Supported External Research	2[1]	5 Years	20 Years
4. Internal and External Research	3[1]	5 Years	10 Years

[1] A scientist man-year at an external research institution (e.g. University) is generally not equivalent to a CFS scientist man-year.

How will the variation in research success time affect the potential contributions of cone-production research, and what are these contributions likely to be?

Four major potential contributions of cone-production research on Douglas-fir have been identified in Appendix 3:

1. maintaining low seed costs
2. avoiding seed shortages
3. facilitating direct seeding
4. accelerating tree improvement benefits

All contributions relate to improving the supply of Douglas-fir seed in British Columbia. Although only high elevation Douglas-fir is dealt with in the Appendix, the benefits estimated could apply to this species in other zones and to other western conifers. Until recently the supply of seed has not been a major problem in the province's reforestation program. Now, with a rapidly growing program relying on unpredictable natural cone crops, seed shortages are developing. Reforestation costs continue to increase, making a highly mechanized method, such as direct seeding, increasingly desirable provided sufficient seed is available. Pressures to increase the productivity of forests are also developing, and progress toward this end can be aided by ensuring the production of large quantities of genetically improved seed. The economic benefits expected from applying successful research to high-elevation coastal Douglas-fir cone production for each alternative research program and length of success time are outlined in Appendix 3 and summarized in Table 5. Estimation of the economic benefits is limited to the 20-year-period, 1972-91. In this case, 20 years is considered a realistic horizon for research forecasting and planning. Projection over a longer period would lose meaning because of the many uncertainties associated with cone-production research and its potential contributions. A shorter period would eliminate the long-term potential contribution and place undue emphasis on the need for rapid success.

The benefit and cost values in Tables 5 and 6 represent the discounted 1972 value of annual streams of benefits or costs dating from the year of demonstrated research success or the beginning of the research program. Table 7 combines the value shown in the previous two tables to display the net economic values attributable to CFS supported research, if it is successful in stimulating the cone production of coastal Douglas-fir.

The values in Table 7 refer only to high elevation coastal Douglas-fir and to the economic benefits expected from applying cone-production research to that species before 1991. Research results could probably be applied to other species and thus circumvent other seed supply problems that exist or may develop, e.g. white spruce. This would generate additional benefits of a similar magnitude to those shown in Table 5. The analysis of research benefits also neglects the long-term benefits that will result from the acceleration of tree breeding work, and the benefits that will come from increasing knowledge about the biological processes associated with cone production in conifers.

Cone-production research can be recommended as a worthwhile investment from the standpoint of economic efficiency, especially when these values, and those displayed in Table 7, are considered. But research should only be undertaken if there is confidence that success will be achieved in 15 years, and preferably 10 years. Beyond the 15-year limit, both quantified and non-quantified research benefits decrease in magnitude. Only the combined internal-external program provides the probability of attaining results within an economically beneficial period of time. In decision theory terms, it is the alternative that maximizes the minimum expected returns. But this conclusion is highly dependent on the estimated, research success times. If the maximum success time of the combined program were changed from 10 to 15 years, there would be little to choose among the three research alternatives open to the C.F.S. All would show negative minimum returns in comparison with the alternative of no research support. Under these conditions, a new more-conservative alternative, external research, could be followed for two or three years until research success time for a more costly combined program could be predicted with greater assurance. The prospect of a rapid breakthrough would not be unduly delayed by following this alternative.

C. RECOMMENDATIONS

From the scientific and economic evidence presented, it is apparent that there are real benefits to be gained by speeding up research on cone production. Successful control of cone-production can probably be obtained within 10 years if a combined internal-external research program were pursued.

Table 5. Potential economic-contributions of successful cone production research applied to high-elevation coastal Douglas-fir: 1972-1991.

Research Alternative	Economic contributions	
	Minimum success time $ present value	Maximum success time $ present value
1. No CFS Research	327,000	19,000
2. Internal CFS Research	1,009,000 1/	19,000 2/
3. CFS Support for External Research	1,009,000 1/	19,000 2/
4. Internal and External Research	1,013,000 1/	327,000

1/ The contributions in a favourable situation will be nearly 50% lower if a good natural cone crop occurs in the period 1972-76. This would alleviate seed shortages that rapid research results might also resolve.

2/ No additional economic contributions are expected from alternatives 2 and 3 because the time needed for success occupies the whole of the forecasting period.

Table 6. Costs to Canadian Forestry Service of alternative research approaches: 1972-1991.

Research Alternative	Research costs	
	Minimum success time $ present value	Maximum success time $ present value
1. No CFS Research	0	0
2. Internal CFS Research	114,000	228,000
3. CFS Support for External Research	57,000	114,000
4. Internal and External Research	171,000	275,000

Table 7. The net value of successful cone-production research applied to high-elevation coastal Douglas-fir: 1972-1991.

Research alternative	Net values of Research			
	Minimum success time		Maximum success time	
	Present net value $	Benefit cost ratio	Present net value[1/] $	Benefit cost ratio
2. Internal CFS Research	568,000	6.0	-228,000	1.0
3. CFS Supported External Research	625,000	12.0	-114,000	1.0
4. Internal and External Research	511,000	4.0	33,000	1.1

[1/] These net values have been derived from Tables 5 and 6 in the following way: for Internal CFS Research: $1,009,000 - 327,000 = $682,000 which is the economic contribution attributable to CFS expenditures; the net contribution is $682,000 - 114,000 = $568,000; the B/C ratio is 682,000/114,000 = 6.0.

On this basis, it is recommended that the CFS:

(1) Provide financial support to research centers dealing with anatomical investigations on the phases of reproductive development and with effects of gibberellic acid on juvenility and periodicity. These areas of research have been shown to be among the most promising for controlling cone production and are being actively pursued by well-established research groups. Financial support would allow the acceleration of these research programs by additions to staff and equipment and would generate substantial economic benefits.

(2) Establish a new research program to clarify the physiology and biochemical basis for flowering. This program should be oriented toward the primary factors involved in the metabolism of flowering, especially the role of the plant growth hormone, auxin. The program should be integrated so that it supplements and strengthens current research on the effect of gibberellins on flowering, while providing a basic understanding of the flowering process and the control of juvenility and periodicity. In composition, the program should consist of both basic and applied research so that maximum profit can be gained from any significant finding at the earliest possible time.

Since the actual effects of auxin on the flowering process of conifers is as yet untested, it is further recommended that this program undergo critical review within two years of its initiation.

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APPENDIX 1

Fertilizing Experiments - Summary of Those Reviewed

Species	Age (years)	Location	Treatment	Rate of Application	Date of Treatment	Results	References
Douglas-fir	13	Campbell River, B.C.	$(NH_4)_2SO_4$ and $Ca(NO_3)_2$	100, 400 800, 1600 lb/acre	May 19/	Observed 1966. $Ca(NO_3)_2$ significantly increased cone production while $(NH_4)_2SO_4$ did not. Best stimulation with mid-levels of nitrate fertilizer.	Ebell and McMullan, 1970
Douglas-fir	Mature	Vancouver Island, B.C.	a) NH_4NO_3 b) $(NH_4)_2SO_4$ c) $(NH_4)_3PO_4$ d) N-P-K e) Superphosphate	Not given	Oct. 1954 Spring 1955	In the fall application treatments b), c) and d) caused more and bigger cones in 1955. In the spring application treatments a) and d) caused large cone crops in 1956.	Stoate, Mahood Crossin 1961.
Douglas-fir	Young	Vancouver Island	NH_4NO_3	400 lbs. per acre	Feb. Mar. Apr./58 May June	Stimulation of cones occurred when application was done at bud break. Variation of little more than two weeks either side of bud break failed to enhance cone production.	Stoate, Mahood, and Crossin 1961.
Douglas-fir	20	Yacolt, Wash.	NH_4NO_3 and P_2O_5	N+P lb/acre 100 + 100 100 + 200 200 + 100 200 + 200		Retreated half of the plots on May/56 and all plots on May/57. Fertilization increased production of both ♀ and ♂ cones, with best response from highest treatment.	Steinbrenner, Duffield, and Campbell, 1960.
Douglas-fir	Mature	Haney, B.C.	NH_4NO_3	200 lb/acre	May/63	Significantly increased both ♂ and ♀ cones in 1964.	Smith, Walters and Kozak, 1968.

Appendix 1 (continued)

Species	Age (Years)	Location	Treatment	Rate of Application	Date of Treatment	Results	References
Douglas-fir	13	Mt. Prevost Robertson Valley, B.C.	NH_4NO_3; $(NH_4)_2SO_4$ $Ca(NO_3)_2$ Urea Treble PO_4 $CaCN_2$ KCl,NP,NPK,NK $CaCO_3$	200 and 400 lbs. per acre	Initially July and Sept./57 various re-treatments	Cone production increased by spring treatment and retreatment of NH_4NO_3 $(NH_4)_2SO_4$, $CaNO_3$, urea, NP and NPK.	Ebell, 1962
White spruce	10	Chalk River, Ontario	NH_4NO_3	200 g/plant	May	Cone production effectively increased	Holst, 1959
Slash pine	21	Baker Co. Florida	NPK 7-7-7 or 3-18-6	20 and 40 lbs/ acre	20 lb/ acre Apr/54 & 20 lb. 6 wk. later	Observed April/55. Increase in number of male and female flowers but 7-7-7 stimulated better than 3-18-6.	Mergen and Voigt, 1960
Slash pine	6	Lake City, Florida	NPK 3-12-6	5, 10 and 15 lbs./ tree	April Mid-June and Aug/54	Observed February 1955. Significant increase in numbers of female flowers and number of trees flowering.	Hoerkstra and Mergen, 1957
Slash pine	grafts	Olustee, Florida	Uramite 20% super-phosphate	Uramite .2 lb/tree and .3 lb/tree 20% P_2O_5 at 50 lb/acre	April/60 1961 1962	No significant effect	Bengston, 1969
Slash pine	grafts	Olustee,	NH_4NO_3	50 and 100		Irrigation was applied in combination with fertilizer. Treatments increased amount of female flowers but not male flowers.	Barnes and Bengston 1968

Appendix 1 (continued)

Species	Age (Years)	Location	Treatment	Rate of Application	Treatment	Results	References
Scots pine	grafts	Brussels Belgium	NPK 12-18-20	0.5 kg per plant	May/63	Observed in Spring of 1964. Significant increase in number of female flowers.	Nanson, 1965
Longleaf pine	45	Alexandria, Louisiana	N PK 15-25-10	250, 500 and 1000 lb/acre	March and May/58	Generally more fertilizer induced more cones but results were related to amount of rainfall. Maximum flowering required high rainfall in all months.	Shoulders, 1967
Longleaf pine	60	Little River, NPK Alabama		1,900 lb per acre	Application each Spring from 1967	Recorded results for seven years. Applied irrigation throughout study. No significant effect.	Croker, 1962
Longleaf pine	Mature	South Alabama & Mississippi	NPK	19 and 44 lbs/acre	Feb/49 and Feb/51	Observed 1951. Treated trees produced more cones as a result of fertilization	Allen, 1953
Short leaf	37	Douglas Co. Missouri	NPK various doses	averaged 200 lb.	½ Apr /58 and ½ Apr 1959	Significant increase in cone production in 1960.	Brinkman, 1962
Red pine	18	Lynn Tract Simcoe Co. Ont.	NH_4NO_3 and K_2SO_4	N-at 0, 64, 128 lb/acre and K at 43 and 86 lb/acre	May 17	No effect on cone production the same year	Armson and Chopwick 1964
Red pine	8 and 14	Chalk R. Ontario	NH_4NO_3	200 g. per plant	May 30 (young plants June (older plants)	No effect on young plants but increase in amount of female flowers in older seedlings	Holst, 1959

Appendix 1 (continued)

Species	Age (Years)	Location	Treatment	Rate of Application	Date of Treatment	Results	References
Red pine	45- 75	Southeast Manitoba	NH_4NO_3	300 lb per acre	May/22 1962	About a 41% increase in female flowers in 1964.	Cayford and Jarvis, 1967
Red pine	53-55	Lower Michigan	A) Urea ureaform at P at K at B) urea at ureaform at and P at	at 169 lb/ac 131 lb/acre 60 lb/acre 196 lb/acre 338 lb/acre 262, K a) 120 390 lb/acre	May, 1961	Fertilization interacted with thinning to enhance cone formation. Best stimulation with higher fertilizer application.	Cooley, 1970
Sugar pine	Mature	Stanislaus Forest California	NPK 16-20-0; $(NH_4)_3PO_4$	100 lb./tree	Spring 1951 1952 1953	From 1953-56 the fertilized trees bore three times as many cones.	Shubert, 1956
Eastern white pine	20-30 and 40-50	Univ. of New Hampshire	NPK 10-10-10	Average 21 lb. per tree	May, 1957	Observed in 1959. Fertilization improved cone production; effect relatively the same in both age of trees.	Hocker, 1962
Eastern white pine	a) 22 b) 14 c) 7	Simsbury, Conn.	$(NH_4)_2SO_4$	18,53 and 158 lb/acre	a) Jul/59 b) & c) Aug./59 All on Apr. & June/70	Observed 1959-1962. No flowers induced in youngest two stands b) and c). Number of female flowers increased in stand a) in 1960 but not number of trees flowering. No effect in 1961 and 1962.	Stephens 1961
Western white pine	11 and 28	Northern Idaho	NPK	1, 5, 10 and 15 lb. per tree	May	No obvious effect of fertilizer treatment	Barnes and Bingham, 1963

APPENDIX 2

Girdling, Strangling and Pruning Experiment - Summary of Those Reviewed

Species	Age (Year)	Location	Treatment	Date of Treatment	Results	Reference
Douglas-fir	19	Victoria, B.C.	Partial	a) Aug 26/57 b) May 14/58	Greatly increased ♀ cone production in 1959 but not in 1960 (Poor cone year). Cone production increased in 1961 and 1962. ♂ cones also increased.	Ebell, 1971
Douglas-fir	20-25	Victoria, B.C.	Partial Girdle	Weekly from April 17/67 to July 4/67	Increased cone production with maximum response just before vegetative bud break and smaller response 1 week after. Later girdling was harmful.	Ebell, 1971
Slash Pine	6	Lake Butler, Florida	Strangling and Partial Girdle	2nd week in April/54	Observed in Feb. 1955 - No effect with and treatment unless in combination with fertilizer. Girdling more beneficial than strangling.	Hoekstra & Mergen, 1957.
Slash Pine	21	Lake Butler, Florida	Partial Girdle & Root Pruning	April/54	Observed in Feb., 1955 - Increased ♀ flower crop but no trend in ♂ flower production. Number of flowering trees increased.	Hoekstra & Mergen, 1957
Sand Pine	3	—	Pruning and Girdling	June	No Effect	Mergen, 1961
Loblolly Pine	21	Durham, N.C.	Partial Girdle and Strangling	1st two weeks April/52	Observed 1954. Cone production increased on both girdled and strangled trees.	Bilan, 1960
Loblolly Pine	25	North Louisiana	Partial Girdle	Feb/56	Observed 1958 - Ringed trees produced twice as many cones as non-ringed. Viability and germination not affected by ringing.	Hansbrough and Merrifield 1963
Loblolly Pine	25	Southeast Virginia	Knife cut and Partial Girdle	a) April/48 b) April/47	a) Observed 1950 and 1951-No effect, knife wound healed over. b) Observed, 1948 - Increase in ♀ cones.	Wenger, 1953

Appendix 2 (continued)

Species	Age (Year)	Location	Treatment	Date of Treatment	Results	Reference
Loblolly Pine	Mature	Texas	Crown Pruning	July/58	Observed April 1959 - Removing crown top stimulated cones in lower crown. Observation in 1963 showed negative results with more ♂ and ♀ cones on controls.	Anon. 1959 Anon. 1963
Longleaf Pine	6"-12" dbh	Alexandria, Louisiana	Partial Girdle Strangling	Summer, 1952	Observed 1955 - Ringing unsuccessful on trees less than 10" dbh. but stimulated cone production on larger trees. Strangling had no effect.	Mann and Russell, 1957
Longleaf Pine	29	North Central Florida	Partial Girdle	May/64	Observed Dec/64 - No effect on ♀ strobili but ♂ strobili increased 8 times.	Varnell, 1970
Eastern White	40-50 & 20-30	Durham, N.H.	Girdling & Strangling	May/57	Observed - 1958. 50 year old stand showed increased cone production in 1958 while the 30 year old stand showed an enhanced cone crop in 1959. Effects of girdling were not lasting.	Hocker, 1962
Eastern White	a) 22 b) 14 c) 7	Simsbury, Conn	Partial Girdle Strangling Pruning	a) July/59 b) Aug/59	Observed 1960 - No flowering in stands b) and c) from 1959 to 1962. In stand a), ♂ flowers were rare but girdling enhanced ♀ flowers and a combination of girdling and pruning gave the maximum effect. Strangling gave no effect.	Stephens, 1961
Shortleaf Pine	50-80	Ovachita, Arkansas	Partial Girdle	Winter/57	Observed 1960 - Girdled trees gave substantially more cones.	Bower & Smith 1961
Red Pine	10	Chalk River, Ont.	Root Pruning	April 30 June 7 June 27 Aug. 1	No effect	Holst, 1959

Appendix 2 (continued)

Species	Age (Year)	Location	Treatment	Date of Treatment	Results	Reference
Red Pine	14	Chalk River, Ont.	Girdling Strangling	Early June	Significant increase in ♀ cone production	Holst, 1959
Red Pine	80	Chalk River, Ont.	Girdling	--	Cone production increased	Holst, 1959
Red Pine	15 25 35	Wisconsin	Spiral and Partial Girdle Strangling	--	Cone production increased up to four years after treatment. Spiral girdle was the most efficient but did cause crown mortality.	Hitt, 1954
Corsican Pine	20	Alice Holt, Hampshire	Girdling Strangling	Sept. 21/48 Jan./49 May/49	Observed Jan. 1950 - January treatment was the least and May the most effective. Cone crop increased in all cases.	Holmes and Matthews, 1951
Japanese Larch	4 (Grafts)	Hessen, Germany	Girdling Pruning	May/58	Observed 1959 - Total number of ♂ and ♀ flowers increased with girdling even though 1959 was a poor flower year. Strangling produced no effect.	Melchior, 1961
Japanese Larch	4 (Grafts)	Hessen, Germany	Girdling Pruning	June/56	Observed in 1958 - Very little effect with pruning but strangling increased the number of ♀ flowers.	Heitmuller and Melchior, 1960
European Larch	Grafts	Hessen, Germany	Girdling	Monthly, 1957	Girdling up to the end of May increased number of flowers in 1958. Girdling from the end of June to July caused increased flowers in 1959.	Melchior, 1960

Appendix 2 (continued)

Species	Age (Year)	Location	Treatment	Date of Treatment	Results	Reference
Chestnut	7	Wallingford, Conn.	Girdling	May 27/57	Observed 1958. Abundance of flowers formed even when girdle was bypassed by grafting shoots from below the girdle to above it.	Graves, 1958
Black ash	30	New York	Spiral and Full Girdle Strangling	May/35	Observed Oct. 19, 1935. Full girdling increased seed production.	Pond, 1936
White spruce	10	Chalk River, Ont.	Root Pruning	April 30 June 7 June 27 Aug. 1	Little stimulation unless combined with fertilizer. Greatest stimulation with April treatment and reduced effect with later treatment. ♀ flowers enhanced the most.	Holst, 1959

APPENDIX 3

Evaluation of Benefits and Costs of Cone-Production Research

Introduction

In the main text, the benefits and costs of cone production research were used as a basis for recommending a CFS research policy in this area. This appendix presents assumptions and data that were used to quantify these economic estimates and their method of analysis.

Four research alternatives were selected to represent the choices facing CFS research managers:

1. no research support
2. internal research program only
3. external research program only
4. combined internal-external research program

The first option, no research support, was included as a control alternative as well as for a legitimate alternative course of action. To measure the benefits of any research program, events with and without that research must be compared. With cone-production research, the analytical question is not what contribution successful research will make, but what the increase in contributions will be if research success is accelerated.

The second and third alternatives are standard options open to any research agency. Only the cost differences between these alternatives are considered in the analysis. The managerial advantages and disadvantages are not discussed.

The fourth option was selected to represent the virtues of a team approach to cone-production problems, combining an intensive and new internal program with acceleration of existing external programs by providing additional support.

The economic returns from the alternative research options will depend to a large extent on the number of years taken to reach success. Predicting research success time is, however, a most difficult task and rather than make specific forecasts we chose to estimate the plausible range of success times for each alternative. These ranges are displayed in Table 4 and are used throughout the appendix to calculate research benefits and costs.

Only monetary benefits and costs are analysed. The evaluation is further limited to analysing the monetary benefits of improving the supply of high elevation, coastal Douglas-fir seed within the next 20 years (1972-1991). Douglas-fir is the predominant species in coastal reforestation programs and high-elevation seed (i.e., from elevations greater than 2000 feet) is eminently in short supply. Resolving this problem is expected to yield the greatest short-term economic gains from cone-production research. Moreover, an extension of the analysis to cover possible improvements in the supply of seed from low elevation coastal Douglas-fir and other conifers is not expected to change the relative standing of each research alternative. It would require much additional effort for small returns.

The following sections examine high-elevation coastal Douglas-fir seed requirements over the next 20 years, the seed supply situation that may result from different research success times and wild-cone crop conditions, the research benefits that may result from changes in the seed supply picture, and research costs.

High-elevation coastal Douglas-fir requirements

The requirements for high elevation Douglas-fir seed in the next 20 years were estimated from forest industry companies and B.C. Forest Service data. The companies provided information on their requirements for elevations over 2000 feet for 10 years, and the Forest Service specified their requirements for 15 years for elevations between 1500 and 2500 and over 2500 feet. These data were extended to 20 years by calculating requirements per year and projecting over five or 10 more years. The Forest Service requirement for elevations between 1500 and 2500 feet were distributed equally between high- and low-elevations.

The combined requirements for the 20-year period totalled 12,900 lb. This, of course, does not include seed currently in storage and which, in the absence of a good cone crop, should be sufficient to supply a major portion of the requirement in the next five years. The Forest Service has, for example, over 3000 lb of high elevation seed in storage. Only certain provenances are now in critically short supply, and it may be possible to relieve some specific shortages by means of small scale, high-cost cone collections.

The requirement which averages 860 lb of seed per year for 15 years beginning in 1976 may prove to be an overestimate. It is based on the assumption that the present practice of planting Douglas-fir on almost all sites in the lower coastal region will continue while there is some indication that other species may play an increasing role at higher elevation and thus reduce the need for Douglas-fir seed. However, cone production in the replacement species is also inconsistent, collection can be expensive, and cone-production research may possibly produce much the same total benefits despite the changing species balance.

Meeting seed requirements without CFS research support

How will the requirement for 860 lb per year of Douglas-fir seed be met in the absence of a CFS supported cone-production research program?

There are three potential sources of seed open to the forester:

1. wild stands
2. seed orchards
3. seed production areas

Wild cone crops are unpredictable but, when abundant crops occur, substantial amounts of cones and seed can be collected. At least 10-year's supply of 8600 lb and probably more could be collected should an abundant crop occur in the forecasting period. The critical factor in future seed supplies is the timing of this crop. Only if it is delayed after 1975 is there likely to be a serious and general shortage of high-elevation Douglas-fir seed. The analysis takes this into account by developing two seed supply forecasts: the first, displayed in Table 8, assumes there will be no wild cone crop until 1982; the second, displayed in Table 9, assumes there will be an abundant wild cone crop before 1977, the earliest year successful research started in 1972 could make any impact on seed supply. Table 9 also incorporates an assumption that research on cone production now proceeding without CFS support would be successful by 1982 and thus change seed supply after that date (see Table 4).

These two tables display extreme forecasts - the worst and the best seed supply situations that could be expected without CFS research support. They assume no change in seed-collection policy or technology over the next 20 years. Improvements in seed-collection activities would serve to reduce all research benefits except the acceleration of tree improvement.

Tables 8 and 9 were developed from the following data and assumptions.

1. Wild stands

Special collections can be made in years when cone crops are not good or abundant to meet seed shortages. Because this is not general practice, no estimates of the amount or cost of seed that could be collected are available. In Table 8 it is assumed that no more than 50% of the five-year demand (4300 lb) will be met by special collections. Problems with collecting specific provenances of seed and with the general quality of seed are assumed to limit the capacity of special high-cost collection efforts.

No special collection efforts are necessary under the conditions assumed for the seed supply forecast displayed in Table 9.

2. Seed orchards

A total of 82 acres of high-elevation Douglas-fir seed orchards have been established in 1971. On this total only 12 acres, located in an area favourable for cone production, are productive. Without research, this small proportion is expected to produce at the rate of 10 to 15 lb per acre every two or three years[1]. The remaining area is expected to remain barren. Additional seed orchards now planned and expected to produce after 1976 would raise the productive area from 12 to 52 acres, and the seed supply from this source from 310 lb in the period 1972-76 to 1240 lb for each five year period thereafter.

With successful non-supported research by 1982, the present barren acreage is assumed to become productive, raising the total average to 122 acres. Research is also expected to raise seed production to 25 lb per acre[2] every two to three years, and

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[1] B.C. Forest Service, Research Division, estimate.

[2] The effect of cone-stimulation techniques on the production of seed is not known for obvious reasons. Douglas-fir seed orchards have produced 25 lb of seed per acre under favourable conditions in Washington State, U.S.A. 10 to 15 years after establishment.

Table 8. High-elevation Douglas-fir seed supply - 1972-91. Research not supported by CFS; not successful by 1991; no natural cone crop by 1981.

Seed source	Seed supply in pounds			
	1972-76	1977-81	1982-86	1987-91
Wild-stand collection	0	0	6800	0
High-cost wild-stand collection	0	2150	0	0
Seed orchard	310	1250	1250	1250
S.P.A.	160	160	2560	160
Total	470	3560	10510	1410
Total required	4300	4300	4300	4300
Shortfall or Surplus	-3830[1]	-740	+6210[2]	-2890

[1] Shortfall assumed to be met by seed already in storage, and by small number of high-cost wild-stand collections.

[2] Part or all of surplus would be collected to meet future shortfalls in seed supply.

Table 9. High-elevation Douglas-fir seed supply 1972-91. Research not supported by CFS; successful by 1981; natural cone crop by 1977.

Seed source	Seed supply in pounds			
	1972-76	1977-81	1982-86	1987-91
Wild-stand collection	0	6800	0	0
High-cost wild-stand collection	0	0	0	0
Seed orchard	310	1250	4100	6100
S.P.A.	160	2560	4800	4800
Total	470	10610	8700	10900
Total required	4300	4300	4300	4300
Shortfall or surplus	-3830[1]	+6310[2]	+4400[2]	+6600[2]

[1] Shortfall assumed to be met by seed already in storage and/or by high-cost wild-stand collections.

[2] Surplus would only be collected to meet increased demands of a direct seeding program.

Table 10. High-elevation Douglas-fir seed supply 1972-91. CFS research successful in five years; no natural cone crop for 10 years.

Seed source	Seed supply in pounds			
	1972-76	1977-81	1982-86	1987-91
Wild-stand collection	0	0	6800	0
High-cost wild-stand collection	0	0	0	0
Seed orchard	310	4100	6100	6100
S.P.A.	160	4800	4800	4800
Total	470	8900	17700	10900
Total required	4300	4300	4300	4300
Shortfall or surplus	-3830[1]	+4600	+13400	+6600

[1] Shortfall assumed to be met by seed already in storage and/or by high-cost wild-stand collection.

Table 11. Periods of potential benefits under alternative research success times.

Potential Contribution	Research Success Time (years)		
	5	10	20
Seed cost	1977-81[1]	no measured benefits	
Seed shortage	1977-81[1]	"	
Direct seeding	1977-91	1981-91	no measured benefits
Tree improvement	1977-91	1981-91	"

[1] Maximum of five years' benefits expected because it is improbable that the lack of good crop years at high elevation will continue after 1981. If a good cone crop occurs before 1977, there will be no short-term benefits under the seed cost or seed shortage categories. No allowance is made for the possibility that without research another seed shortage may develop before the end of the forecasting period.

total production to 6100 lb by 1987.

3. Seed-production areas

Seed-production areas are subject to the same climatic limitations as wild cone crops. In a good seed year, such production areas have been known to produce up to 60 lb of seed per acre. With an average production of 30 lb per acre, the total production from 80 acres of high elevation Douglas-fir seed production areas now established on the B.C. coast would be 2400 lb. Some production can be expected during years without good wild cone crops because of management. One tenth of the total acreage (8 acres) is assumed to average 20 lb per acre in every five-year period without a good wild cone crop (160 lb every 5 years).

With successful research by 1982, production on all 80 acres is assumed to rise to 60 lb per acre every five years (4800 lb every 5 years).

Seed supply 1972-91 with CFS research support

CFS supported research has three possible success times - five, 10 and 20 years (Table 4). The latter two would result in the same seed-supply conditions as those shown in Tables 9 and 8, respectively. Success in five years would improve the seed supply over the period 1976-81 when a seed shortage is expected if no wild-cone crop occurs.

With rapid research success, seed orchards are expected to become highly productive, with 82 acres producing 50 lb per acre every five years (4100 lb over 5 years), expanding to 122 acres producing at the same level after 1981.

Seed-production areas are similarly assumed to increase their contribution to seed supply markedly, with all 80 acres producing 60 lb per acre every five years starting in 1976. The results of these assumptions are shown in Table 10.

Quantifying cone-production research benefits

Four sources of potential monetary benefits are expected to result from the changes in high-elevation coastal Douglas-fir seed supply that successful research may produce. They are as follows:

1. maintaining low cost seed supplies
2. avoiding seed shortages
3. facilitating direct seeding
4. accelerating tree improvement gains

The extent of each potential contribution is governed by the time taken to achieve success in the research program and the change in cone production, and thus seed supply picture, induced by that success.

Table 11 shows the relationship between expected benefits and the three success times defined in Table 4 in the main text.

The potential monetary benefits[3/] of cone production research are summarised in Table 12 and are discussed below.

1. Maintaining low seed costs.

Without successful research, and an abundant wild cone crop before 1982, the seed supply situation in 1976-81 will be critical enough to require special high-cost cone collections. 2150 lb will have to be collected in this way between 1976 and 1981.

Current wild stand collection costs for high-elevation Douglas-fir seed range from $15 - $20 per lb in locations where there are moderately good to good cone crops. Special collections, when the cone crops are poorer, will be more expensive. If special seed collections cost an average of $20 per lb more than the collection cost in a year with a good cone crop. The extra cost amounts to $8500 per year for the five-year period 1976-81.

Direct seed-collection costs from seed orchards and seed-production areas are not expected to exceed costs of collecting wild-cone crops in an abundant year. Both operations also require capital inputs, which can be substantial in the case of seed orchards, but this should be considered as a cost of obtaining improved seed, not a cone-collection cost. Thus the total costs of seed collection with successful research are not expected to be higher than the total costs without research. If research is successful in five years, therefore, a cost saving of $8500 per year for five years can be claimed as a benefit accruing to that research.

[3/] A discount rate of 10% was used to obtain the present (1972) values.

2. Avoiding seed shortages

Without successful research or an abundant wild cone crop before 1981, the predicted seed shortages will cause reforestation delays. The cost of these delays will depend partly on the timing of slash burning (which cannot be much delayed for fire precaution reasons), the length of the delay and its effect on rotation length, and the effect of increased brush cover on planting costs.

Table 8 shows a shortfall of 740 lb of seed between 1977-81, which suggests that delays in reforestation will be experienced on nearly 30,000 acres because of these shortages (25 lb of seed required for 1000 acres of planting). These delays could extend to five years or more. Average bare root planting costs are now $30 to $35 on well-burned sites, but can double under adverse conditions. Reforestation costs in the 1980's are unlikely to remain the same, and changes in technique and increases in labour costs make cost predictions difficult. For this analysis, reforestation delays on over 30,000 acres between 1977-81 are assumed to cause an additional planting cost of $35 per acre. A total additional cost over the five-year period of $1,050,000 results from this assumption.

This additional cost is large in comparison to the cost of special seed collections. It results from the assumption that these collections are limited to 2150 lb in a five-year period. If this limitation does not hold, the benefits of rapid research success (when a good wild cone crop is delayed until after 1981) will be greatly reduced.

The effect of the above reforestation delays upon allowable cut calculations, and thus on available wood supplies, is even less predictable. The delays would represent no more than a temporary setback in efforts to reduce rotation ages (and thus to increase allowable cut), and the effects would vary among management units, depending on actual rotation ages at the time of the delays and the volume of old growth remaining to be cut. Also, present forest policy specifies only that areas must be restocked within seven years of harvesting. On these grounds, no attempt was made to quantify the effect of delays in reforestation on wood supplies.

3. Facilitating direct seeding

Direct seeding is by far the cheapest method of artificially regenerating Douglas-fir available to coastal foresters. While the risk of failure is greater, its rapidity and simplicity have great appeal in a time of rising labout costs. In the U.S. and parts of eastern Canada, large areas have been and continue to be seeded with satisfactory results. In B.C., direct seeding has remained an experimental technique, ostensibly because of seed shortages. Other factors may be important, but it is possible that with improved seed supplies, most of the obstacles will be removed and seeding will be used on an operational scale. The following analysis assumes that following successful cone-production research, high-elevation Douglas-fir seed would be distributed over 5000 acres per year for five years and then 10,000 acres per year for the remaining years in the forecasting period. These acreages would be concentrated on those low and poor site lands above 2000 feet which are more difficult to plant and have only a poor to medium chance of successful natural regeneration.

Cost savings from seeding rather than planting these areas would amount to $15 to $20 per acre on the basis of current costs.[4] These savings would be offset to some extent by the need to produce much larger quantities of seed than would be required for planting. With successful research, a surplus of seed will be produced that will meet part of the increased requirements, but extra seed-production areas will also be required.

Douglas-fir seeding operations in the Pacific Northwest use from ¼ to ½ lb of seed per acre from 250 to 500 lb per 1000 acres compared to 25 lb per 1000 acres for planting. An area of 10,000 acres seeded per year would require, at most, 5000 lb per year plus an additional 30% to allow for re-seeding. The surplus expected from existing production facilities (tables 9 and 10) falls far short of this requirement. Extra seed-production areas of up to 400 acres, producing 60 lb of seed every five years, must be established at a cost of $300 per acre to meet assumed direct seeding needs.

Table 13 shows the method of calculating the net benefits of direct seeding if cone production research is successful in five and 10 years' time.

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[4] Neither seeding nor planting are wholly successful in achieving restocking. It is assumed here that both reforestation methods will require from 5-10% restocking by planting.

Table 13. Direct seeding benefits of cone production research

Research Situation	Direct seeding factors	Direct seeding needs, costs and benefits		
		1976-81	1982-86	1987-91
Successful in 5 years	Area seeded in acres	5000 ac.	10,000 ac.	10,000 ac.
	Seed required	16500 lb	33,000 lb	33,000 lb
	Seed available (Table 10)	4600 lb	13,400 lb	6,600 lb
	Additional seed required	11900 lb	19,600 lb	27,400 lb
	Extra Seed-Production Area production (400 a.)	12000+lb	24,000 lb	24,000 lb
	Cost of extra S.P.A.	$120,000	-	-
	Direct seeding cost saving at $20/acre	$100,000	$200,000	$200,000
Successful in 10 years	Area seeded in acres	----	5000 a	10,000 a
	Seed required	----	16500 lb	33,000 lb
	Seed available (Table 9)		4400 lb	6,600 lb
	Additional seed required	----	12100 lb	26,000 lb
	Extra SPA production (400 a)		12000+lb	24,000 lb
	Cost of extra SPA	----	$120000	-
	Direct seeding cost saving at $20/acre	----	$100,000	$200,000

4. Accelerating tree improvement benefits

The increased quantities of seed from seed-production areas and seed orchards, that would result from successful cone-production research, would lead to an acceleration of tree improvement gains. Table 14 shows the areas of reforestation that could be established from 'improved' seed without successful research, and with research that is successful in five and 10 years. The totals vary according to amount of direct seeding carried out, amount of wild seed available and amount of improved seed available, and are derived from the seed supply forecasts contained in Tables 8, 9 and 10, using the conversion factor of 25 lb of seed for each 1000 acres planted.

These average data are used to assess the total increase in allowable cut arising from the increasing use of improved seed shown in Table 13. The total increases in cut are valued at the average stumpage price paid in the Vancouver District from 1968 to 1970 - $7.00 per cunit. Secondary benefits, based on the value added in the processing of the additional wood, are not included.

Two additional sources of benefit associated with the acceleration of tree improvement gains are the possible gains from seed with both parents known (full-sib seed) and avoiding the replacement of existing seed orchards. Successful cone-production research will accelerate the rate at which tree breeding progresses and may make high-yielding Douglas-fir seeds available within the 20-year forecasting period. The expected yield is around 10% for full-sib seed. There are many uncertainties about this contribution however, and no analysis has been attempted.

Table 14. Reforestation with improved seed

Research Situation	Seed Source	Acreages of reforestation with improved seed 1977-81	1982-86	1987-91
Research success time 20 yr	Seed orchards	50,000	50,000	50,000
	Seed production areas	12,000	96,000	12,000
Research success time 10 yr	Seed orchards	50,000	149,000	125,000
	Seed-production areas	96,000	16,000	40,000
Research success time 5 hr	Seed orchards	149,000	130,000	130,000
	Seed-production areas	16,000	35,000	35,000

A recent B.C. Forest Service document[5] indicates that by using improved seed, forest industry companies (and the Forest Service) will be able to claim increases in allowable cut. The allowance for seed-production area seed is 3% of volume at rotation age and for seed-orchard seed with one parent known (half-sib seed), 5%. For the average site, in the Vancouver Forest District, with a mean annual increment of 73 cu ft per year,[6] the increase in annual allowable cut is 2.2 cu ft per acre and 3.7 cu ft per acre, respectively.

If successful research is not forthcoming within the next 10 years, forest industry companies with seed orchards now unproductive may replace them with new orchards sited in the Saanich and Sechelt peninsulas where Douglas-fir cone crops are known to be more frequent than in other locations. Successful cone production research could prevent this expenditure (up to $5000 per acre not including preparation of orchard stock). However, the urgency to increase wood yields may make forestry agencies on the coast unwilling to bet on the uncertain prospect of successful research. Research benefits related

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[5] B.C. Forest Service Functions and Programme of the Forest Productivity Committee. Victoria, B.C. Mimeo report. Jan. 1972.

[6] B.C. Forest Service Forest Inventory Statistics of British Columbia 1967. Victoria, B.C. 1969.

to factors of this type are excluded from the analysis.

Research costs

Internal research costs were assessed on the basis of employing one additional research scientist. The direct cost per year of an internal cone-production program was estimated at between $25,000 and $30,000, including salaries of scientist and technician, operational budget and equipment expenditures. The higher figure was used in the analysis. Overhead allowances for administration, accommodation and other costs were not included, on the grounds that the analysis should consider only the marginal or additional costs of a new research program, not the average costs of all internal research programs. The average cost would, in fact, be much higher, between $45,000 and $50,000 per year per research scientist.

The external research costs were based on the usual range of payments by the CFS in support of research by individuals at Universities in British Columbia. This range if from $5,000 to $10,000. An average of two such payments per year at $7,500 each was assumed for the analysis.

The combined program cost was derived simply by adding the foregoing costs together to obtain a total of $45,000 per year.

The present (1972) value of research costs are summarised in Table 6.