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The Effect of Water Spray Cooling Treatment on Reproductive Phenology in a Douglas-Fir Seed Orchard

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Abstract

The effectiveness of reproductive bud cooling on the genetic efficiency in a Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] seed orchard was tested by comparing the reproductive bud phenology in three cooled and three uncooled years. The cooling system was found to influence two major elements affecting seed orchard genetic efficiency, namely pollen contamination levels and panmictic equilibrium, as well as a number of additional factors, including insect infestation, frost damage, seed yield, and management effectiveness. Based on these results, a solid-set overhead irrigation/cooling system is recommended for Douglas-fir seed orchards.

Key words: *Pseudotsuga menziesii*, seed orchards, overhead cooling systems, panmictic equilibrium, contamination.

Zusammenfassung

In einer Douglasien-Samenplantage wurde die Auswirkung der Kühlung reproduktiver (Blüten-)Knospen auf die genetische Effizienz geprüft, indem die Phänologie der Blütenknospen in drei Jahren mit Kühlbehandlung mit der in

drei Jahren ohne Kühlbehandlung verglichen wurde. Es wurde gefunden, daß die Kühlung zwei Hauptelemente beeinflusst, nämlich das Niveau der Pollenkontamination und das panmiktische Gleichgewicht, außerdem eine Anzahl zusätzlicher Faktoren, wie Insektenbefall, Frostschaden, Samenausbeute und Effizienz der Bewirtschaftung. Auf diesen Ergebnissen basierend, wird ein dauerhaft eingebautes Beregnungssystem für Douglasien-Samenplantagen empfohlen, das über Gipfelhöhe der Pflanzen sprüht.

Introduction

The advantages of seed orchards for production of consistent and abundant yields of genetically-improved seed for reforestation programs are recognized (cf. FAULKNER 1975). The resulting seed crop is expected to reflect both the genetic superiority and broad genetic base present among the orchard trees. The degree to which a seed orchard achieves this expectation is called the "genetic efficiency" (ADAMS and JOLY 1980). Several conditions are required to achieve maximum genetic efficiency in wind-pollinated seed orchards. These include: a) parental reproductive balance, b) isolation from background pollen, c) minimal rates of selfing, d) random mating with equal compatibility, and e) reproductive synchronization (WOESSNER and FRANKLIN 1973). In short, if a seed orchard crop is to reflect its expected theoretical genetic gain, the orchard itself must represent a nearly perfect, closed, panmictic population.

Several management practices have been implemented in seed orchards to increase the genetic efficiency. These in-

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clude location and design choice (GIERTYCH 1975; WERNER 1975) and crop-management options such as supplemental mass pollination (VAN DER SIJDE 1971). Water-spray colling of seed orchard trees has been proposed to reduce pollen contamination by delaying reproductive bud phenology (SILEN and KEANE 1969; FASHLER and DEVITT 1980). This procedure provides temporal isolation for the seed orchard trees and has been proven effective in the reduction of pollen contamination (EL-KASSABY and RITLAND 1986a) and in decreasing cone and seed insect damage (MILLER 1983).

It has been demonstrated for several coniferous species that heat sums have a significant role on flowering time (KRAMER and KOZLOWSKI 1979). As differences in origin among plus trees increase, differences in reproductive bud burst timing among their propagules are expected in a common environment (i.e., seed orchard). Indeed, significant differences in reproductive bud burst timing among clones and open-pollinated families in a Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] seed orchard have been reported and elevational differences accounted for the reported variation (EL-KASSABY *et al.* 1984).

The purpose of this paper is to determine the extent of reproductive bud delay by water cooling on the genetic efficiency in a Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] seed orchard by comparing the reproductive bud phenology during three years of cooling treatment with that from three uncooled years.

Materials and Methods

The 3.4 ha CIP Inc. (formerly Pacific Forest Products Ltd.) high-elevation Douglas-fir seed orchard at Saanichton, B.C., Canada, provided the material for this study. The orchard consists of a combined clonal/seedling breeding population with 63 clones and 37 open-pollinated families selected from elevations between 450 and 1,000 m on southern Vancouver Island and the south coastal mainland of British Columbia. The orchard is planted in a randomized incomplete block design replicated 16 times (16 blocks). For the purpose of pollen and seed management, the seed orchard population is differentiated according to elevation zones (450–599 m, 600–749 m, and greater than 750 m), and nature of material (open-pollinated vs. grafted trees).

The overhead, solid-set irrigation system provided the cooling treatment during reproductive bud development in 1976, 1978 and 1983. A complete description of the system is reported elsewhere by FASHLER and DEVITT (1980).

Reproductive bud phenology information for the entire seed orchard population (every sexually-active tree) was collected in all six study years. Each tree was monitored every second day throughout the pollination period. The phenological classification followed those of Ho (1980) and OWENS *et al.* (1981). To achieve uniformity over the six years, data collected from earlier years which followed the classification of FASHLER and DEVITT (1980) were slightly modified to follow the previously mentioned monitoring system. In all years, the critical stage of female ("flower") receptivity was reached when the seed cone had just emerged fully from the bud scales. The dates of pollen shedding were the critical stage for the male reproductive stage. Reproductive phenology classes reflecting early, intermediate and late reproductive bud development were subjectively created (EL-KASSABY *et al.* 1984).

With the exception of 1977, background pollen levels were monitored through the use of pollen traps (glass slides coated with 27 parts epoxy resin and one part catalyst).

Pollen slides were placed inside and around the perimeter of the orchard and mounted on posts 175 cm above ground level. A total of five and six stations were used inside and outside the orchard, respectively. Four slides, one facing each cardinal direction, were placed at a 45 angle. After a seven hour exposure (approximately between 8:00 am and 3:00 pm) the pollen slides were collected and pollen grains were counted. EBELL and SCHMIDT (1964) have indicated that the greatest Douglas-fir daily pollen release occurred between 10:00 am and 4:00 pm. Pollen grains were counted using a light microscope (x100). A total of 30 fields (1.46 mm diameter) were counted for each slide and the average number of pollen grains per day per position was estimated. In addition to the pollen traps, the reproductive phenology of the surrounding stands was also monitored.

The time to female receptivity and pollen shedding for clonal and seedling trees was calculated as the number of days from January 1st of each year. The data were analyzed using one-way ANOVA to test differences among trees belonging to three elevational zones (450–599 m, 600–749 m, and greater than 750 m) under cooling and natural conditions.

Results

Differences in both the length of pollination period and the number of genotypes reproductively active at a given time, occur between cooled and uncooled years (Fig. 1). In the uncooled years, the extent of female receptivity and pollen release averaged 24.3 and 24.7 days, respectively. Not only is pollination occurring over a long period, but also the maximum number of receptive females and pollen shedding trees occurs over a relatively longer period as well. In general, the seed orchard peak pollination period averages 15 days in the uncooled years.

The situation in cooled years indicates a much-reduced pollination period (17.3 days for females and 18.3 for males), averaging seven days shorter. In addition, the maximal number of available flowering females and males occurs later than the local pollen flight and over a relatively short time averaging 11 days. The unusually cold spring temperatures in 1982 (an uncooled year) caused an imitation of the cooling treatment, producing somewhat sharper peaks in female receptivity and pollen density than would be expected with no cooling (Fig. 1). The overall length of the pollination period, however, remained longer than the average in cooled years.

The local pollen (background) flight (Fig. 1) suggests no delay between the period of maximum female receptivity and local pollen flight in uncooled years. The comparison in cooled years indicated a delay from eight days (1976) to 14 days (1983) for an average 11-day delay from the local pollen flight to the height of seed orchard flower receptivity.

Differences in the numbers of available receptive females and available pollen-shedding males were apparent at various stages (i.e., early, intermediate and late) in the pollination period in both cooled and uncooled years. Cooling appears to have greatly reduced the magnitude of these differences in 1976, although little effect is noted by cooling in 1978 and 1983. The disproportion in females and males suggest potential differences in the viable seed produced in each phenological class due to lack of pollen.

Table 1 presents the variation in reproductive bud-burst timing among and within elevational zones for clones and open-pollinated families for the six-year period. The total

COOLING TREATMENT

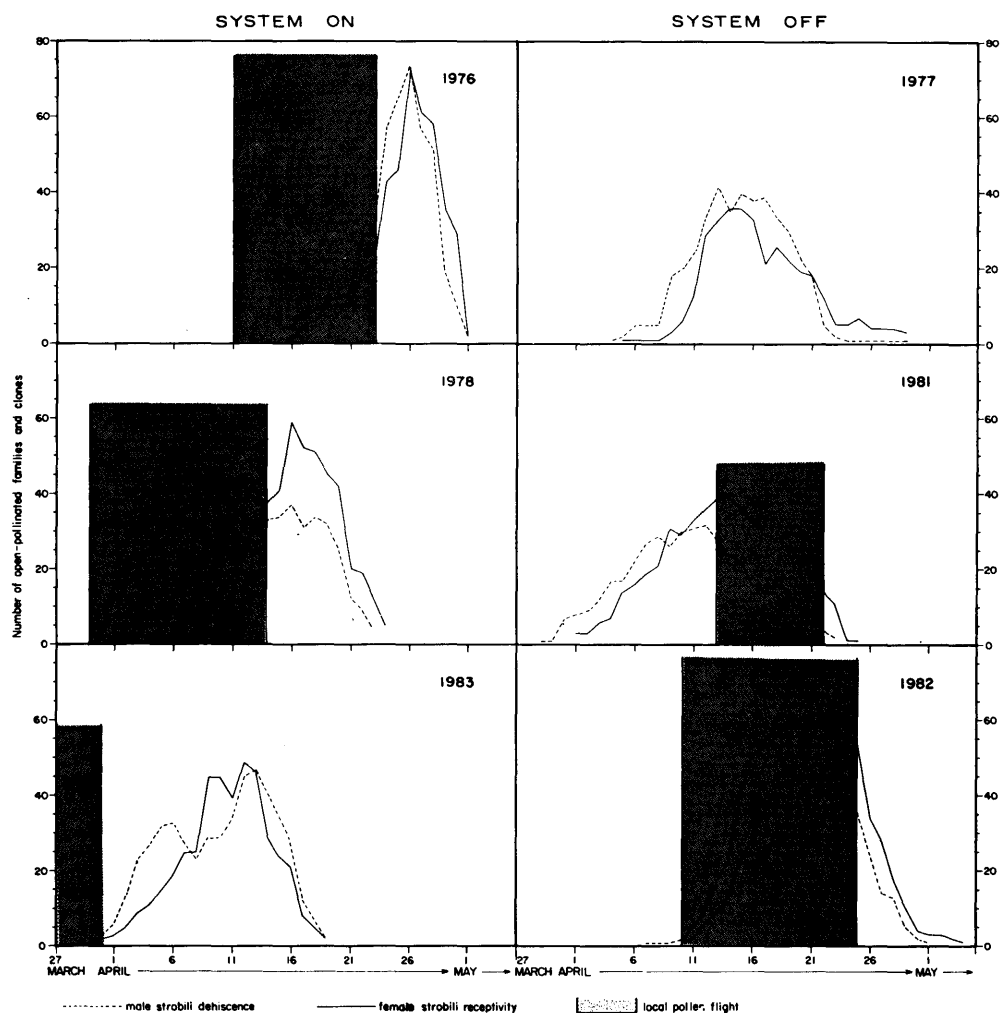


Fig. 1. — Comparison of pollination periods and local pollen flight between cooled (1976, 1978 and 1983) and uncooled (1977, 1981 and 1982) years.

number of significant difference cases among the three elevational zones for the uncooled and cooled years are six and three, respectively (Table 1). Significant differences for males or females in the uncooled years are twice as many as those observed in the cooled years. Thus, cooling treatment has an effect in reducing the observed differences in phenology among the three elevational zones; an important feature of the general reduction in flowering time from the cooling treatment.

Discussion

The primary effect of the cooling treatment is the delay of reproductive development due to evaporative cooling. The comparison in this study of three years of orchard cooling with three intervening years without cooling verify a delay averaging seven days. Reproductive bud delay significantly improves genetic efficiency by reducing contamination from surrounding local trees (SILEN and KEANE 1969; FASHLER and DEVITT 1980). Results of contamination estimates for 1983 (cooled year, EL-KASSABY and RITLAND 1986a) and 1984 (uncooled year, EL-KASSABY and RITLAND 1986b) showed that the average contamination levels were close to $0.2\% \pm 5.7\%$ and $12.2\% \pm 9.2\%$, respectively. The extent of potential contamination for the "early" class for a cooled and uncooled year (1983 and 1984) was even more

dramatic. For trees flowering early in 1983 (cooled) the rate of contamination was 9% (EL-KASSABY 1985) while 24% was estimated for the same class in 1984 (EL-KASSABY and RITLAND 1986b). Thus, the cooling treatment improved the genetic quality of the seed orchard crop by reducing or eliminating contamination from outside pollen sources as well as by promoting crosses only among seed orchard trees.

Further improvement to the genetic quality could be attributed to better panmictic equilibrium within the seed-orchard population. The duration of receptivity of a seed strobilus ranges from four to six days (OWENS *et al.* 1981) and the optimal duration of pollen shedding varies between three to five days (BARNER and CHRISTIANSEN 1962). The longer pollination periods observed in the uncooled years could produce a continuum of various breeding population components throughout the pollination period, since females opening early would be unavailable for fertilization by pollen from later-flowering trees and *vice versa*. In cooled years, however, the orchard's overall pollination period is shorter (Fig. 1) thus improving panmixis.

The shorter pollination period produced by the cooling treatment may be explained by heat shock (BOYER 1973). In studies of heat effects upon plant development, heat is usually expressed in degree-hours or degree-days above a

Table 1. — Variation in reproductive bud burst timing among elevational zones.

Cooling	Year	S.O.V.	Clonal Trees				Open-pollinated Trees			
			Females		Males		Females		Males	
			df	MS	df	MS	df	MS	df	MS
ON	1976	Among Elev.	2	25.12 ^{ns}	2	5.78 ^{ns}	2	0.89 ^{ns}	2	0.45 ^{ns}
		Residual	50	15.31	50	8.37	35	2.58	35	2.23
	1978	Among Elev.	2	36.31*	2	42.03 ^{ns}	2	10.08 ^{ns}	2	45.51**
		Residual	57	10.46	58	21.68	35	8.21	35	8.30
	1983	Among Elev.	2	29.69 ^{ns}	2	73.86*	2	10.45 ^{ns}	2	16.36 ^{ns}
		Residual	49	18.23	60	18.34	33	7.57	34	15.80
1977	Among Elev.	2	20.22 ^{ns}	2	5.69 ^{ns}	2	19.71*	2	20.64**	
	Residual	29	32.85	44	17.85	35	7.01	35	4.96	
OFF	1981	Among Elev.	2	41.59 ^{ns}	2	261.95*	2	324.35*	2	1065.90*
		Residual	24	40.40	44	82.35	34	175.78	34	255.92
	1982	Among Elev.	2	19.43 ^{ns}	2	51.96 ^{ns}	2	106.49 ^{ns}	2	267.56*
		Residual	29	513.12	56	48.15	34	51.01	34	69.42

* Significant at $P < 0.05$; **, Significant at $P < 0.01$; ns, Not Significant

biologically-established threshold temperature. Heat sums associated with a phenological event for a given species often vary among locations and over years in the same location. Any change in source altitude or latitude of a species is always associated with changes in the average required heat units to attain a specific phenological stage. EBELL and SCHMIDT (1964) have demonstrated that Douglas-fir at a high elevation (2,500—3,500 ft.) required half of the degree-hours for pollen dispersal needed by populations at low elevation (1,000 ft) and the same latitude. BOYER (1973) has indicated that longleaf pine (*Pinus palustris* MILL.) required an average of 9,862 degree-hours above 50° F between January 1 and peak pollen shedding in North Carolina in 1967 and 1968, while values for the same two years in southwestern Alabama averaged 11,341 degree-hours. MAGOON and CULPEPPER's (1932) study on sweet corn supports this hypothesis with the added information that a smaller heat sum was needed for a single genetic strain of corn to reach maturity in Maine (cooler) than in Virginia (warmer).

In our study, variation in bud burst timing was reduced in the years when the trees were exposed to the cooling treatment. The ANOVA results on both the clonal and open-pollinated trees support MAGOON and CULPEPPER's work and indicate that flowering actually progressed at a faster pace after the cessation of the cooling treatment. The heat units delivered to the trees in the latter part of the season (i.e., after cooling) is higher per day than received in the earlier part (i.e., no cooling). In other words, a larger heat-sum may be needed for the same effect in early than in late flowering years (i.e., cool vs. warm springs). Differences between the cumulative degree days above 5° C between 1981 and 1982 for a four-month period (January to April) have shown to drastically affect the timing and magnitude of the reproductive bud phenology in that orchard (EL-KASSABY *et al.* 1984, Table 3 and Fig. 1). In our study, the reduced variation among sources from low, medium and high elevations may also have reflected this phenomenon.

An extended pollination period may also increase the chance of selfing, particularly in periods characterized by a decreased number of flowering trees. However, the cooling treatment caused a compaction of the pollination period, improving the likelihood of panmixis and increasing the

frequency of outcrossing. Assessment of the exact effect on outcrossing rate is a difficult parameter to identify in the current study due to the confounding effect of possible pollen contamination, hence the considerable data gathered on filled and empty seed yields is not presented. This relationship and the effect of contamination on the net outcrossing within this orchard seed crop are discussed in detail elsewhere (EL-KASSABY *et al.* 1986a, EL-KASSABY and RITLAND 1986a and b, RITLAND and EL-KASSABY 1985).

Other effects of cooling have been shown advantageous in earlier reports. A substantial reduction in frost damage to both receptive females and developing conelets has been observed in cooled years. The shift and delay in the reproductive phenology have reduced the chance of damage caused by the late spring frosts common to the Saanichton area (CHILTON 1980). The cooling system is being used also as a frost-protection system similar to systems routinely used in agricultural and horticultural crops (LOMBARD *et al.* 1966, GILBERT *et al.* 1970, GAY *et al.* 1971, ANDERSON *et al.* 1975). It must also be emphasized that the cooling of the orchard trees and the subsequent delay of the reproductive phenology could set up the majority of the crop to very late severe frosts (N. WHEELER, personal communication). Fortunately, such events were not experienced in the Saanichton area during this study.

The cooling treatment has been effective also in reducing the amount of insect damage (MILLER 1983). By retarding the phenological development of seed orchard strobili, trees are forced out of synchronization with the insect population which, having responded to the local weather conditions, subsequently lay their eggs outside the seed orchard. This physical prevention of insect infestation may be the only safe alternative for seed orchards located in populated suburban areas sensitive to the application of pesticide sprays. Annual surveys for the Douglas-fir cone gall midge (*Contarinia oregonensis* Foote) have indicated that a pesticide spray is needed in uncooled years. Dimethoate is the insecticide used operationally in Douglas-fir orchards for control of cone and seed insects and the application is effective only when applied before the conelets are in their pendant position (JOHNSON and HEDLIN 1967). Within a non-cooled orchard, variation in the time when conelets reach

this stage is at its maximum, therefore, an effective control method requires several application times.

In addition to affecting the dynamics of orchard flower phenology and seed predation, the effect of cooling is apparent also on seed-orchard management procedures. A shorter, more-compact pollination period has improved management effectiveness by reducing costs. Less labour has been needed in the cooled years, with fewer visits per tree for supplemental mass pollination and less need to pollinate intermediate flowering trees, after cooling and open pollination, their seeds exhibit high embryo heterozygosity (EL-KASSABY *et al.* 1986b) and high seed yield (EL-KASSABY *et al.* 1984). This treatment may then be focussed on the early and late phenological classes where it can effectively increase the pollen cloud gene pool and produce a greater proportion of seeds of high genetic quality. Other seed orchard management practices will also be undertaken over a shorter period due to the shorter pollination period, thereby reducing the labour cost of additional seasonal employees, however, larger crews are needed for that period.

In conclusion, reproductive bud cooling has been shown to be effective in a variety of biological and managerial seed orchard factors. The data indicate that a solid-set irrigation/cooling system is highly recommended for Douglas-fir seed orchards. The restriction on tree height and the availability of a reliable water source are two limiting factors for this technique. Top pruning is an effective method for keeping the orchard trees to a manageable size. The cost and scarcity of water source are usually the major limiting factors for the overhead irrigation/cooling system.

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