Effect of pollination period and strobili number on random mating in a clonal seed orchard of Picea mariana

By C. O'Reilly, W. H. Parker and J. E. Barker*)

School of Forestry, Lakehead University,
Thunder Bay, Ontario P7B 5E1, Canada

(Received 15th January 1982)

Summary

Clonal differences in timing of pollen release and in number of strobili were determined in a seed orchard of *Picea mariana* to estimate their effects on the genetic composition of the progeny. Four ramets each of 12 clones from northwestern Ontario, Canada were selected. Stages of pollen release and female receptivity were scored by a qualitative index; total numbers of male and female strobili were determined; and number of normally developed ovuliferous scales per mature seed cone was counted. Although the period of pollen release and female receptivity lasted only 16 days, minor differences in timing were present between clones. However, peak pollen release and maximum female receptivity coincided for all but two clones. Numbers of both male and female strobili were significantly different between clones, with just a few clones producing the bulk of the strobili. The genetic composition of a hypothetical seed crop derived from the 12 black spruce clones was estimated based on timing of pollination, numbers of strobili and ovuliferous scales. A small fraction of the 12 clones made the largest contribution to the genetic composition of the progeny. This result depended most heavily on the numbers of male strobili produced by each clone; the effects of the other contributing variables were largely overshadowed.

Key words: Seed orchard, *Picea mariana*, pollination, sexual phenology, reproductive dynamics.

Zusammenfassung

In einer *Picea mariana* (Mill.) B. S. P. — Samenplantage wurden die Pfropfklone auf Unterschiede im Blühverhalten untersucht, d. h. es wurden während der Pollenentlassung von je vier Pfropflingen von 12 Klonen aus Nordwest-Ontario alle weiblichen und männlichen Blüten gezählt, um daraus Auswirkungen auf die genetische Beschaffenheit der Nachkommenschaft zu schätzen. Gleichzeitig wurden die Stadien der Pollenentlassung und der Aufnahmefähigkeit der weiblichen Blüte durch einen qualitativen Index festgestellt. Obwohl beide Stadien nur 16 Tage andauerten, waren Klonunterschiede zu berechnen. Außer bei zwei Klonen stimmten die Maxima dieser Stadien überein. Die Anzahl sowohl der männlichen als auch der weiblichen Blüten war zwischen den Klonen signifikant unterschiedlich. Die genetische Beschaffenheit einer hypothetischen Saatguternte, die von diesen 12 Schwarzfichten-Klonen gewonnen werden kann, wurde auf der Basis des Zeitpunktes der Pollenverteilung, sowie der Blütenzahlen und der Zahl der Samenanlagen geschätzt. Nur ein kleiner Teil dieser 12 Klone würde den größten Teil der Nachkommenschaft ausmachen. Dieses Ergebnis hing hauptsächlich von der Anzahl der männlichen Blüten ab, die von jedem Klon produziert wurden waren. Die Einflüsse der anderen beteiligten Variablen wurden weitgehend überlagert.

Introduction

Perhaps the most basic assumption underlying clonal seed orchard design is that the systematic placement of ramets will maximize random cross-pollination. (Sweet, 1975). However, physical placement of clones is not the only factor affecting their reproductive dynamics. The timing of pollen release and female receptivity, as well as the relative numbers of male and female strobili produced by the clones also affect the genetic composition of the seed harvested from the orchard.

Differences between clones in the numbers of strobili produced and in the timing of pollen release and receptivity may limit the number of possible crossing combinations. If the clonal differences are small, as is often assumed in practice, the differences in timing and in strobilus numbers probably have little detrimental effect. However, large differences between clones will result in certain clones contributing disproportionate numbers of gametes to the seed that is produced.

Studies on clonal differences in timing of pollination and numbers of strobili have demonstrated the importance of these differences in determining the genetic composition of the progeny for a few species of conifers. Eriksson *et al.* (1973) and Johnsson *et al.* (1976) estimated that such differences had great effects for seed orchards of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.), respectively. As well, Nienstaedt and Jeffers (1970) have demonstrated significant differences in female cone production between clones of white spruce (*Picea glauca* (Moench) Voss).

Little information is available on the timing of pollination or numbers of strobili produced by black spruce (*P. mariana* (Mill.) B. S. P.) The objective of this study was to determine how these factors affect the genetic composition of the seed produced in a clonal seed orchard of black spruce.

Materials and Methods

The 4W Matawin Seed Orchard (lat. 48° 32', long. 89° 80') is located about 80 km west of Thunder Bay, Ontario. This seed orchard was established by the Ontario Ministry of Natural Resources and is approximately 10 ha in area. The orchard is split into 2 subunits, one for white and one for black spruce, each consisting of 18 blocks. All blocks contain 12 randomly distributed clones represented by 12 ramets each. In total, the orchard contains 100 different clones, 61 of black spruce and 39 of white spruce, although some clones were included in more blocks than others. All ortets were identified as plus-trees from Thunder Bay District in northwestern Ontario; they were all cone bearing trees that exceeded 40 years of age at the time of scion collection. Two years after grafting to white spruce root stock, ramets were

*) Present Address: Western Forest Products Ltd., 1020 Beckwith Ave., Victoria, British Columbia V8X 3S4

outplanted at 3.6 × 3.6 m spacing. The first established blocks were planted in 1966, and planting of the orchard was completed in 1972.

In the spring of 1979, 12 clones of black spruce were selected from 2 adjacent blocks planted in 1966 and 1967. From each clone 4 vigorous ramets were selected arbitrarily for study throughout the pollination period. The overall level of black spruce seed cone production was about average in 1979 for the Matawin Orchard.

Ten male buds were selected for each ramet from the fifth whorl down from the leader, and 10 female buds were selected from the third whorl down. These buds were scored every 2—3 days using a qualitative index of strobilus development similar to those of Polk (1966), Wasser (1967), and Borodina (1968). Maximum stages of pollen release and female receptivity of the buds were scored as 100%, while preliminary and waning stages were each scored as 50%.

Daily percentages and the midpoint dates of pollen release and receptivity were interpolated from graphs of each variable versus date. Correspondence of pollen release and female receptivity was determined by correlation analysis.

Total number of male and female strobili were determined for each of the 48 ramets of black spruce. For ramets producing more than 1,200 male strobili, the number was estimated rather than counted by determining an average number per branch for each whorl (based on 2 counted branches) and multiplying by the number of branches per whorl (Nienstaedt, 1980). For analysis, male strobili numbers were stratified into basic increments of 200. In addition, the heights of all ramets were measured, as the numbers of male strobili appeared to correspond to height. This apparent relationship was tested by correlation analysis.

Ten mature seed cones from each of the black spruce clones were dissected to determine the variation in the numbers of developed ovuliferous scales produced per cone. Only scales that bore potentially viable looking seeds were included in the counts.

Numbers of female strobili per ramet, numbers of ovuliferous scales per cone per ramet, and ramet height were analyzed by one-way analysis of variance (ANOVA) to detect signifficant between-clone differences. Numbers of male strobili and ramet height were tested by analysis of covariance to remove the suspected effect of height on the results.

The phenological data of pollen release and female receptivity make possible the construction of a model expressing the reproductive dynamics of a hypothetical seed orchard block, isolated from all others, and consisting of just the 12 studied clones of black spruce. An estimate of the genetic composition of the seed orchard progeny of these 12 black spruce clones was made based on the following 3 primary variables: 1) the timing and duration of pollen release and female receptivity, 2) the number of male and female strobili produced per clone, and 3) the number of normally developed ovuliferous scales per mature seed cone.

The method used to estimate the genetic composition of the progeny (O'Reilly 1981) was similar to those developed by Eriksson *et al.* (1973) and Jonsson *et al.* (1976). The daily percentage stage of pollen release per clone was weighted by total number of male strobili per clone to calculate the daily percentage clone composition of the pollen cloud. For each day of the pollination period the percentage clone composition of each of the 144 possible crossing combinations was calculated as the daily percentage clone composition of the pollen cloud multiplied by the daily percentage of female receptivity; these values were then adjusted for clone differences in number of female strobili and numbers of maturing ovuliferous scales produced. Daily contributions were summed for the total period of pollen release and female receptivity. Thus, the relative contribution of each clone was determined, both as a male and female parent. Finally, the contribution of each clone to the genetic composition of the progeny was calculated as the average of its male and female contributions. As well, the probability that self-pollen would reach the female strobilus was determined for each clone using this technique; each of the 12 possible matrix combinations indicating self-pollination were divided by the total contributions of the respective clones.

For purposes of comparisons, a simpler method of determining clonal contribution was also calculated; this method expressed each clone's contribution to the progeny based only on relative number of male and female strobili produced.

Results

The 12 selected black spruce clones from the Matawin Seed Orchard began pollen release on June 4 and ceased on June 17 (*Table 1*). The megasporangiate strobili of these clones also became receptive on June 4, but the period of female receptivity lasted slightly longer than pollen release, continuing until June 19. Thus, the overall period of pollination lasted for 16 days. Midpoint dates of pollen release ranged from June 8 to June 13 inclusive, a range of only 6 days, while the range of midpoint dates of female receptivity was from June 9 to June 13, only 5 days. In spite of the considerable overlap between clones in both pollen release and female receptivity, pollination dates in *Table 1* demonstrate that not all of the 12 clones were involved in pollination over parts of the 16 day period.

Table 1. — Daily percentage pollen[1] release (♂) and female receptivity (♀) for 12 black spruce cones.

Clone Number[2]		Date (June, 1979) 4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
284	♂	18	28	59	100	86	72	63	28								
	♀	35	50	75	100	92	85	78	70	63	42	22					
492	♂	12	19	42	66	62	58	55	42	26	18	10					
	♀			20	43	52	62	73	85	99	67	32					
387	♂	8	19	33	45	61	78	95	66	35	24	13					
	♀		15	30	45	63	81	100	75	50	43	37	33	22	12		
386	♂	10	24	47	67	75	85	95	66	30	24	17	12	8	4		
	♀		21	41	67	75	87	100	72	40	32	23	13	8	5		
290	♂	7	10	23	35	53	72	90	66	40	27	15					
	♀	6	10	22	35	52	70	90	89	78	52	25					
491	♂	11	17	24	28	43	57	70	57	43	28	13					
	♀			12	28	50	75	98	86	75	51	25					
490	♂		5	15	25	39	55	72	63	56	37	18					
	♀	4	6	16	29	51	75	99	99	99	72	47	19	13	7		
304	♂				8	23	41	58	59	80	66	51	35	23	12		
	♀	4	11	16	23	44	67	91	95	100	73	42	9	8	5		
384	♂					23	46	69	82	95	73	51	29	20	9		
	♀					22	45	69	84	100	75	62	29	18	11		
291	♂						18	55	72	88	73	58	43	28	14		
	♀				3	30	59	90	94	100	80	62	43	28	14		
303	♂				2	13	24	35	50	65	62	60	58	32	17		
	♀	3	3	3	3	15	28	40	55	68	65	63	60	43	27	10	5
288	♂					12	24	36	49	61	55	50	45	30	17		
	♀	8	24	40	59	72	85	100	82	64	42	22	3	2	1		

[1] Mid-point dates of pollen release and female receptivity are underlined.

[2] Clones are ranked in order of pollen release.

Table 2. — Means and standard deviations (parenthetically) of ramet heights, numbers of male and female strobili per ramet, and numbers of ovuliferous scales per mature seed cone for 12 black spruce clones.

Clone Number[2]	Ramet Height (m)	No. of male strobili per ramet (x 200)	No. of female strobili per ramet	No. of ovuliferous scales per seed cone
284	2.95 (0.15)	1.00 (0.0)	19 (9.9)	34.8 (4.0)
492	3.21 (0.21)	3.74 (3.1)	178 (80.1)	43.1 (9.9)
387	3.77 (0.45)	1.50 (1.7)	27 (32.3)	33.9 (2.3)
386	4.34 (0.47)	4.75 (2.1)	119 (92.0)	43.0 (5.5)
290	4.14 (0.17)	13.00 (1.6)	91 (23.1)	43.1 (9.1)
491	3.32 (0.13)	1.00 (0.8)	25 (13.5)	--[1]
490	3.99 (0.27)	2.25 (1.0)	94 (38.4)	35.8 (6.4)
304	3.87 (0.21)	0.75 (0.5)	90 (44.5)	41.8 (5.6)
384	3.99 (0.58)	2.75 (1.0)	45 (16.4)	38.7 (2.8)
291	3.41 (0.49)	7.25 (3.9)	90 (24.6)	45.4 (3.6)
303	3.13 (0.17)	4.00 (3.6)	87(143.2)	36.2 (4.2)
288	4.73 (0.26)	22.75 (8.4)	122 (50.0)	27.9 (3.4)
Mean	3.74	5.40	82.3	38.5

[1] Mature seed cones were not collected from clone 491.
[2] Clones ranked in order of pollen release.

Generally, periods of pollen release and female receptivity coincided closely for each clone (*Table 1*). Although two of the 12 clones, 492 and 288, had midpoint dates that were 3 days apart, clonal midpoint dates of pollen release correlated significantly with those of female receptivity ($r = 0.64$; $r_{0.05}$, 10 df $= 0.58$).

Numbers of male and female strobili, ramet heights, and number of ovuliferous scales per seed cone are presented in *Table 2*. ANOVA demonstrated that interclonal differences were significant ($P < 0.01$) for each of these variables.

The mean number of male and female strobili per ramet per clone was 1,079 and 82, respectively (*Table 2*). Average numbers of male strobili per ramet per clone ranged from 150 to 4,550, while the average numbers of female strobili ranged from 19 to 178 per ramet per clone. Although the average heights of ramets were significantly different between clones and the correlation of height against number of male strobili was significant ($r = 0.60$), analysis of covariance showed that after removal of clonal height differences, there was still a significant clonal difference in male strobili numbers between clones.

The most notable feature in *Table 2* is the disproportionate production of male and female strobili among the 12 clones. Only 2 clones, 288 and 290, produced more than half (ca. 55%) of the total number of male strobili. A similar trend is also evident, although less pronounced, in the production of female strobili; four clones, 492, 288, 386, and 290, produced more than half (ca. 52%) of the total number of female strobili.

The average number of normally developed ovuliferous scales per mature seed cone varied from a low value of 27.9 to a high value of 45.4. The average number for all clones was 38.5 (*Table 2*). Unfortunately, scale data for clone 491 were not available since this clone had dropped all of its seed cones by the time our collections were made in the spring; however, this clone was one of the lowest proceducers of both male and female strobili

The percentage contributions of male and female gametes for each of the 12 black spruce clones comprising a hypothetical isolated seed orchard block are listed in *Table 3*. Also listed are the hypothetical overall clonal contributions to the seed orchard progeny determined by averaging each clone's male and female contributions. As well, *Table 3* lists calculated probabilities that self-pollen reached the female strobili of each clone.

Table 3. — Hypothetical percentages of male and female gamete contributions to seed orchard progeny and probabilities that self-pollen will reach their own female strobili for an isolated block of 12 black spruce clones (see text for an explanation of the calculations).

Clone Number[3]	Gamete Contributions to the Progeny: Female	Male	Average[1]	Probability of Self-Pollen reaching female strobili
288	8.76	27.85	18.31 (23.75)	21.17
290	10.11	22.80	16.46 (14.65)	25.20
492	19.85	6.34	13.10 (11.94)	6.57
386	13.23	10.63	11.93 (9.71)	13.87
291	10.55	10.89	10.72 (10.17)	13.87
303	8.11	5.28	6.70 (7.49)	7.99
490	8.70	3.47	6.09 (6.51)	3.45
304	9.70	1.31	5.51 (5.14)	1.35
384	4.52	4.81	4.67 (4.42)	5.77
387	2.36	2.93	2.65 (2.53)	3.25
491	2.46[2]	1.63	2.05 (2.03)	1.71
284	1.67	2.05	1.86 (1.71)	3.93

[1] Values in parenthesis are based only on the number of male and female strobili.
[2] The contribution of clone 491 was calculated assuming that this clone produced the average number of ovuliferous scales per seed cone.
[3] Clones are ranked according to their average gamete contribution.

The most important feature of *Table 3* is the disproportionate gamete contributions made by the different clones to the seed orchard progeny. Two clones, 288 and 290, contribute over half of all the male gametes produced by the 12 clones. Similarly, an additional 3 clones, 492, 386 and 291, together contribute nearly half of the female gametes to the progeny. Collectively, these 5 clones contribute about 72 percent of the total gametes to the progeny. This value is considerably in excess of the 41.7 percent that would be expected if all clones made equal contributions, i. e. if panmixia existed.

For purposes of comparison, the average gamete contributions of each of the 12 black spruce clones were calculated based only on numbers of male and female strobili, and these values are listed in parentheses in *Table 3*. These contributions based on a simpler calculation deviate somewhat from the more comprehensive values that also incorporate pollination timing data as well as numbers of ovules; however, the general ranking of clones is similar by either calculation. Thus, the relative numbers of male and female strobili give a reasonable approximation of a black spruce clone's gamete contribution without considering periods of pollen release and female receptivity or numbers of ovuliferous scales produced per seed cone.

Discussion

Differential timing of male and female pollination events was inconsequential for individual clones of black spruce at the Matawin Seed Orchard. Although statistically significant differences existed between clones in timing of pollen release and female receptivity, these two events coincided closely within most clones *(Table 1)*. Thus, the maximum number of possible crossing combination among the 12 clones was not limited by the timing aspects of pollination.

The relatively short period of pollination reported here for black spruce is probably not indicative of the whole of black spruce's range since all of our study clones were selected from ortets growing in one site region in northwestern Ontario. The short, 6 day range in midpoint dates of pollen release and female receptivity suggest that little would be gained by ranking clones for controlled, supplemental pollinations. None of the potential 144 clones crosses were eliminated due to lack of clonal synchrony. This result is in contrast to those reported by FASHLER and SZIKLAI (1980) for a coastal population of *Pseudotsuga menziesii* (MIRB.) FRANCO, a species with a longer pollination period growing in an area with a longer spring warm-up than the Thunder Bay area.

Numbers of male and female strobili were found to vary significantly between clones. Part of this variation might have resulted from the relatively young age of the ramets; *i. e.*, as the ramets age and become more mature, strobilus production might become more balanced. However, differences in strobilus production between seed orchard clones are largely dependent on genetic factors; poor cone producers in one year are consistently poor in other years (WRIGHT 1953, ELIASON and CARLSON 1969, NIENSTAEDT and JEFFERS 1970, ERIKSON *et al.* 1973, JOHNSSON *et al.* 1976). To determine whether there are chronically poor strobilus producers at the Matawin Seed Orchard will require several years of additional data.

Overall, differences in male strobili production between clones were far more extreme than differences in female strobilus production. The effects on seed orchard progeny that result from this differential production of male gametes are important. Generally, the black spruce clones producing the largest number of male strobili will contribute the bulk of the gametes to the orchard's seed production.

Table 3 indicates that clones producing large numbers of male strobili have high probabilities that self-pollen will reach their female strobili. These data are probably not very significant in terms of deleterious effects on the seed orchard progeny. If black spruce follows the pattern observed for other spruces (references reviewed by FRANKLIN 1970), it is likely that self-pollination in this species results in self-fertilization; however, the bulk of selfed embryos in spruce ultimately abort resulting in unfilled seed. Nonetheless, an actual assessment of the seed quality of disproportionately heavy pollen producers at the Matawin Orchard would be desirable to test the predictions generated by the hypothetical model; *i. e.*, do heavy male strobilus producers have higher percentages of unfilled seed than other clones?

Significant variation existed between clones in the number of normally developed ovuliferous scales produced by mature seed cones. However, this variation is overshadowed by the effect of strobilus number and probably could be ignored in future studies of black spruce seed orchard progeny.

This study considered only 12 of the actual 61 black spruce clones planted at the Matawin Seed Orchard. The pollination data gathered for these clones was used to determine the reproductive dynamics of a hypothetical seed orchard block consisting of only these 12 clones. Thus, the calculated estimates of gamete contributions by the 12 clones are hypothetical in that no such block actually exists and in that the calculations neglect cross pollinations from foreign sources or with the remaining 49 black spruce clones; presumably, in reality a certain percentage of external pollinations would occur. However, setting up a hypothetical model based on only 12 clones probably is fairly representative of actual pollination figures at the Matawin Seed Orchard for three reasons. 1) The 12 study clones were selected at random from the first planted blocks and thus, are an unbiased sample of the 61 black spruce clones; presumably another sample of 12 of the 61 clones would show a similar range of variation in pollination events and numbers of gametes produced. 2) The probability of pollination from sources outside the seed orchard is very low since the orchard is located within an extensive, near-pure stand of *Pinus banksiana* LAMB. 3) The orchard is laid out in blocks that each consist of only 12 clones. Thus, due to the special arrangement of this particular seed orchard, the pollen cloud present in any one block will mainly be derived from only 12 of the total 61 clones. However, all of the calculations of gamete contributions and probabilities of self-pollination presented in *Table 4* undoubtedly are too high to the extent that pollen from adjoining blocks would be present in the local pollen cloud, particularly on windy days.

A major caveat concerning the results of this study is that our sampling only considers one year's data. Observations in orchards of other conifer species indicate large variation in strobilus production and seed set from year to year. Although each clone has its own rhythm, clonal differences are much less pronounced in good flowering years with fewer resulting deviations from random crossing.

The most significant implication of the calculated gamete contributions of the 12 black spruce clones is that these contributions are so variable. Differences in timing of pollination and differences in numbers of ovuliferous scales per seed cone between clones do not much affect these estimates. By comparison, the differences in numbers of strobili produced among the 12 clones are much more significant. Thus, additional variables need not be considered to get a reasonable estimate of each clone's contribution to the seed orchard's progeny. Similar results were obtained by ERIKSSON *et al.* (1973) for Norway spruce and JONSSON *et al.* (1976) for Scots pine in Sweden.

Acknowledgements

This research was supported by a portion of a Canadian Forestry Service Subvention Fund Grant made to the School of Forestry, Lakehead University. We thank Mr. GEORGE KOKOCINSKI, Ontario Ministry of Natural Resources, for his assistance and cooperation in all phases of this work. We also thank DR. GORDON MURRAY and DR. HANS NIENSTAEDT for their contributions to this study, and DR. ROB FARMER, DR. PEGGY KNOWLES, and 3 anonymous reviewers for their suggestions to improve the manuscript. The summary was translated by DR. SIEGFRIED ZINGEL.

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Intersectional Hybridization of Populus Sections, Leuce-Aigeiros and Leuce-Tacamahaca[1])

By W. G. RONALD

Agriculture Canada, Research Station
Morden, Manitoba ROG 1JO, Canada

(Received 22th January 1982)

Summary

Production of intersectional *Leuce-Aigeiros*, *Leuce-Tacamahaca* hybrids is described using species of the *Leuce* section as the female parent. Two female clones which are complex hybrids derived from crossing three aspen and white poplar species proved outstanding in crosses, producing more seed than two of their parental species. Several tri-sectional *Populus* crosses *(Leuce-Aigeiros-Tacamahaca)* involving up to five species are reported as well as a range of new interspecific crosses involving two sections. These hybrids have intermediate morphology between parental species. Their growth rate is satisfactory and preliminary propagation studies indicate that such hybrids could be used to transfer rooting factors to *Leuce* poplars providing the F_1 hybrids prove fertile.

Key words: Populus, hybridization, intersectional, breeding significance, forestry, horticulture.

Zusammenfassung

Die Herstellung von intersektionalen *Leuce-Aigeiros*, *Leuce-Tacamahaca* Hybriden wird beschrieben, bei denen Arten der *Leuce*-Sektion als weiblicher Elter benutzt wurde. Zwei weibliche Klone, die komplexe Hybriden aus Kreuzungen von 3 Aspen und Weißpappeln darstellen, bewiesen hervorragende Kreuzbarkeit, indem sie mehr Saatgut als zwei ihrer Elternarten produzierten. Verschiedene Pappel-Kreuzungen dreier Sektionen *(Leuce-Aigeiros-Tacamahaca)*, die bis zu fünf Arten einschließen, werden als ebenso gut wie eine Serie neuer interspezifischer Kreuzungen zwischen zwei Sektionen angesehen. Diese Hybriden haben intermediäre morphologische Eigenschaften zwischen den Elternarten. Ihr Wachstum ist ausreichend und vorläufige Untersuchungen über die Vermehrung ergaben, daß solche Hybriden zum Transfer von Bewurzelungsfaktoren in Leuce-Pappeln geeignet sind, vorausgesetzt die F_1-Hybriden erweisen sich als fertil.

Introduction

The search for hybrid vigor or heterosis has encouraged forestry breeders to investigate a wide range of interspecific crosses. Perhaps no greater efforts have been made than in the genus *Populus*, a genus in which many hybrids can be propagated readily as clones, permitting the full utilization of heterosis due to additive and dominance gene effects. Interspecific hybridization is intriguing in *Populus* for this complex genus has more than 30 species in 5 taxonomic sections. *Turanga* and *Leucoides*, sections consist of few species with limited distributions and minor economic value. The three remaining sections contain many species with widespread native range and important economic value in forestry and horticulture. These three sections, *Leuce* (consisting of both Eurasian and North American aspen species and Eurasian and North African white poplars), *Tacamahaca* (represented by the balsam poplars of Asia and North America), and *Aigeiros* (represented by the European black poplar and North American cottonwood) are of major interest to tree breeders in every continent.

Although interspecific hybridization is considered generally to be a widespread natural and induced phenomenon in *Populus*, it is in fact limited mostly to intrasectional crosses and to intersectional *Tacamahaca-Aigeiros* crosses; intersectional *Leuce-Aigeiros* and *Leuce-Tacamahaca* cros-

[1]) Contribution No. J-175.