

Female Reproductive Energy and Reproductive Success in a Douglas-fir Seed Orchard and its Impact on Genetic Diversity

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Abstract

The relationship between reproductive energy and reproductive success and its impact on clonal female gamete contribution were studied in a clonal Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] seed orchard. The effect of among- vs. within-clonal variation on seed-cone crop (energy) and filled-seed yield (success) was determined by partitioning their respective variance components. Clonal gametic representations were expressed using GRIFFIN'S (1982) parental-balance curves and CROW and KIMURA'S (1970) effective population number. Seed-cone and filled-seed yields produced similar parental-balance curves and female effective population numbers. Although similar parental-balance curves and female effective population numbers were produced, the actual clonal gametic representation differed when the contribution of any set of specific clones were considered. It was concluded that parental-balance curves and female effective population numbers provide a static description of the genetic representation and do not illustrate the dynamics of clonal reproductive outputs.

Key words: *Pseudotsuga menziesii*, seed orchards, reproductive energy, reproductive success, clonal gametic representation.

FDC: 161.6; 165.5; 181.5; 232.311.3; 174.7 *Pseudotsuga menziesii*.

Introduction

The production of seed crops that reflect the genetic superiority and diversity present in seed orchards' populations is a common goal of all seed orchard operations. The attainment of maximum reproductive output equality and phenological synchrony among seed orchard's clones as well as minimum inbreeding and contamination levels in seed crops all are fundamental pre-requisites to realizing that goal. Studies on seed orchards of several coniferous tree species have revealed that most of these fundamental pre-requisites are not fully met (see EL-KASSABY, 1989, for review). The realization that among-individual variation within tree populations, natural or artificial, exists in reproductive output is important for many reasons among which seedlot genetic composition is of a prime concern.

The diversity of forest tree species reproductive systems has attracted the attention of forest geneticists (ERIKSSON *et al.*, 1973; JONSSON *et al.*, 1976; GRIFFIN, 1982; O'REILLY *et al.*, 1983; SCHMIDTLING, 1983; BYRAM *et al.*, 1986; SCHOEN *et al.*, 1986; EL-KASSABY *et al.*, 1989; EL-KASSABY and REYNOLDS, 1990; EL-KASSABY, 1992). Most of these studies assumed, either implicitly or explicitly, that the female reproductive energy is equal to reproductive success (i. e., the number of filled-seeds per cone is equal across the different parental groups) when the contribution proportion of a specific clone to the resultant crop was determined. It should be stated that if the relationship between reproductive energy and reproductive success is not linear, then the estima-

tion of expected level of genetic variation that is based on the former will be substantially different from that of the latter. In a previous study, REYNOLDS and EL-KASSABY (1990) demonstrated the non linearity of the relationship between reproductive energy and reproductive success and the lack of similarity in the rank-order of trees based on cone crop and seed yield. Although the study of REYNOLDS and EL-KASSABY (1990) provided insight into the relationship between reproductive energy and reproductive success, it did not demonstrate the within-clonal variation when an entire seed orchard crop is considered. If within-clone reproductive energy and reproductive success variation exists, then it is expected that the changes in the observed levels of genetic variability in REYNOLDS and EL-KASSABY'S study could disappear with averaging over clones.

In this study, the within- and among-clonal variation in reproductive energy (cone crop) and reproductive success (filled-seed yield) are evaluated and their impact on the expected genetic diversity of cone/seed crops is assessed in a Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] seed orchard.

Materials and Methods

The Pacific Forest Products Limited's 3.7 ha, low-elevation clonal, Douglas-fir seed orchard (lat. 48° 35' N, long. 123° 24' W) provided the material for this study. The orchard was established in 1969 using 3 m x 3 m spacing and was genetically rouged in 1987 producing irregular spacing among the orchard ramets. In general, the rouging did not produce large gaps due to the initial narrow spacing. The average number of seed-cone producing ramets per clone for that year was 5.7 and ranging between 1 and 15.

The 1988 (good cone year) pollen management was limited to the use of an air blower. The air blower was used during the pollination season to enhance air movement within the orchard, hence improving pollen dynamics. During harvest (Sept. 1988), seed-cone crops were collected from all seed-cone bearing trees on an individual ramet basis. The actual number of seed-cones was recorded per ramet and where possible a sample of 20 cones was taken at random from each ramet within all clones for seed extraction. Cone samples were air dried at room temperature, seeds were extracted, de-winged and cleaned by hand. The average number of filled-seeds per cone per ramet was determined by dividing the total number of filled-seeds produced by the number of cones sampled. Then the total number of filled-seeds per ramet was estimated by multiplying the average number of filled-seed per cone per ramet by the number of cones harvested from each ramet. Filled and empty seeds were determined by cutting test (i.e., cutting every seed longitudinally).

Table 1. — Variance components (%) for seed-cone and filled-seed for the studied 35 Douglas-fir clones combined and for the 3 non-overlapping production classes (high, inconsistent, and low).

Trait	S.O.V. ¹	Var. Comp. ²	d.f.	Combined	d.f.	High	d.f.	Inconsistent	d.f.	Low
seed-cone	Among clones	σ^2_b	34	38.3**	3	31.3**	21	10.8**	8	69.8 ^{ns}
	Within clones	σ^2_w	166	61.7	21	68.7	98	89.2	47	30.2
		h^2_b		0.38		0.31		0.11		0.70
filled-seed	Among clones	σ^2_b	34	39.6**	3	34.6**	21	21.9**	8	75.8 ^{ns}
	Within clones	σ^2_w	166	60.4	21	65.4	98	78.1	47	24.2
		h^2_b		0.40		0.35		0.22		0.76

**), significant at the 0.01 probability level; ^{ns}), not significant.

¹) source of variation: among clones; $\sigma^2_b + k\sigma^2_w$, within clones; σ^2_w , where: σ^2_b , variance due to differences among clones; σ^2_w , variance due to differences among ramets within clone; k ; coefficient of variance component [$k=(1/c-1)(N-(\sum N_i^2/N))$ where c = number of clones and N_i = number of ramets within the i^{th} clone ($k = 5.74, 8.93, 6.10, \text{ and } 1.40$ for combined, high, inconsistent, and low cone/seed producing groups, respectively).

²) variance components.

The relationship between seed-cone crop and filled-seed yield among clones was assessed using PARSONS product-moment correlation. Within- and among-clonal variation in both seed-cone crop and filled-seed yield were evaluated using standard one-way ANOVA (Table 1). Heritability estimates for seed-cone crop and filled-seed yield were calculated using the clonal test method of VAN BUIJTENEN and YEISER (1989). Parental (clonal) proportional contribution to the actual seed-cone crop and filled-seed yield were determined following the method of GRIFFIN (1982). The female effective population number (N_{ef}) based on seed-cone and filled-seeds contributions were estimated following the method of CROW and KIMURA (1970).

Results and Discussion

Unlike the study of REYNOLDS and EL-KASSABY (1990) which was conducted on 30 individual trees representing 30 different genotypes, this study represents the situation all seed orchardists encounter (i. e., clonal size variation). Variation in clone size (i.e., variable number of seed-cone bearing ramets per clone) is expected to affect both seed-cone crop size and filled-seed yield. Significant ($p \leq 0.05$) correlations were observed between clone size and both seed-cone crop size ($r=0.55, n=35$) and filled-seed yield ($r=0.52, n=35$). The r^2 (coefficient of determination) values for clone size and seed-cone crop ($r^2=0.30$) and clone size and filled-seed yield ($r^2=0.27$) were low, indicating the presence of large amount of variation in the data that were not expressed by these two relationships (i.e., clone size alone is not the major factor affecting cone or seed yield).

The average number of seed-cones per clone varied between 22 (clones # 4 and 11) and 634 (clone # 31) (Fig. 1). Although significant correlation was observed between clone size and seed-cone crop, this relationship should be viewed with caution. For example, clones # 31 and 25 were the highest in clone size with 15 and 14 cone-bearing ramets they ranked number 1 and 31 as cone producers (Fig. 1). Clones # 17 and 12 each with 5 and 12 cone-bearing ramets, respectively, ranked number 3 and 7 as

cone producers (Fig. 1). Finally, clone # 16 with only one ramet (ranked number 4) outproduced clone # 6 (ranked number 30) with 6 ramets (Fig. 1).

The average number of filled-seed per clone varied between 421 (clone # 11) and 17,245 (clone # 21), (Fig. 1). Similarly, clone size and filled-seed yield relationship, although significant, could be misleading. For example, the two largest clones (#'s 31 and 25) ranked number 3 and 31 as seed producers (Fig. 1). Clones 17 and 12 ranked number 4 and 15 as seed producers in spite of their large clone size difference (5 vs. 12 ramets, respectively).

The studied clones were clustered in 3 non-overlapping groups. These are: 1) small number of consistently high cone/seed producing clones (4 clones), 2) few consistently low cone/seed producing clones (9 clones), and 3) large number of inconsistent cone/seed producing clones (22 clones) (Fig. 1).

The correlation between seed-cone crop size and filled-seed yield was significant ($r=0.93, n=35, p < 0.01$), however, the rank of these clones based on cone crop size differed from that based on filled-seed yield (Fig. 1). Once again, indicating that this relationship should be viewed with caution.

The cone-crop and seed-yield parental-balance curves and the rate of distortion appeared to be identical (Fig. 2). However, it should be noticed that, in general, the clonal representation on these 2 seemingly identical curves is different (Fig. 1 and 2). In this case, only 5 out of 35 clonal combinations produced similar genetic representation (15%, 74%, 94%, 97%, and 100%). The female effective population number estimated also produced similar values for seed-cone ($N_{ef} = 9$) and filled-seeds ($N_{ef} = 9.5$). The proportions of female effective population and actual numbers (N_{ef}/N) were 0.257 and 0.271 for seed-cone crop and filled-seed yield, respectively, indicating uneven unequal contributions.

The among-clones variation accounted for a significant ($p < 0.01$) 40% of the total variance components for both cone and seed analyses (Table 1). When the clones were grouped into the 3 non-overlapping cone/seed production groups, the among-clonal variation accounted for 31% to

35 % and 11 % to 22 % significant ($p < 0.01$) variance components for the high and inconsistent group, respectively, while non-significant 70% to 76% of the total variation was observed for the low production group, indicating the presence of large within-clonal variation in the inconsistent production group (Table 1). The broad sense heritability estimates for seed-cone and filled-seed production were generally high reflecting the observed among- and within-clonal variation indicating that the reproductive output attributes are under genetic control (Table 1).

The results presented for parental-balance curves (seed-cone crop and filled-seed yield) as well as female effective population numbers indicate that the degree of deviation from equal contribution is virtually identical, however, the rank of the 35 clones based on cone production differed from that on seed yield, indicating that these estimates provide a static description of the genetic representation and do not illustrate the dynamics of clonal reproductive outputs.

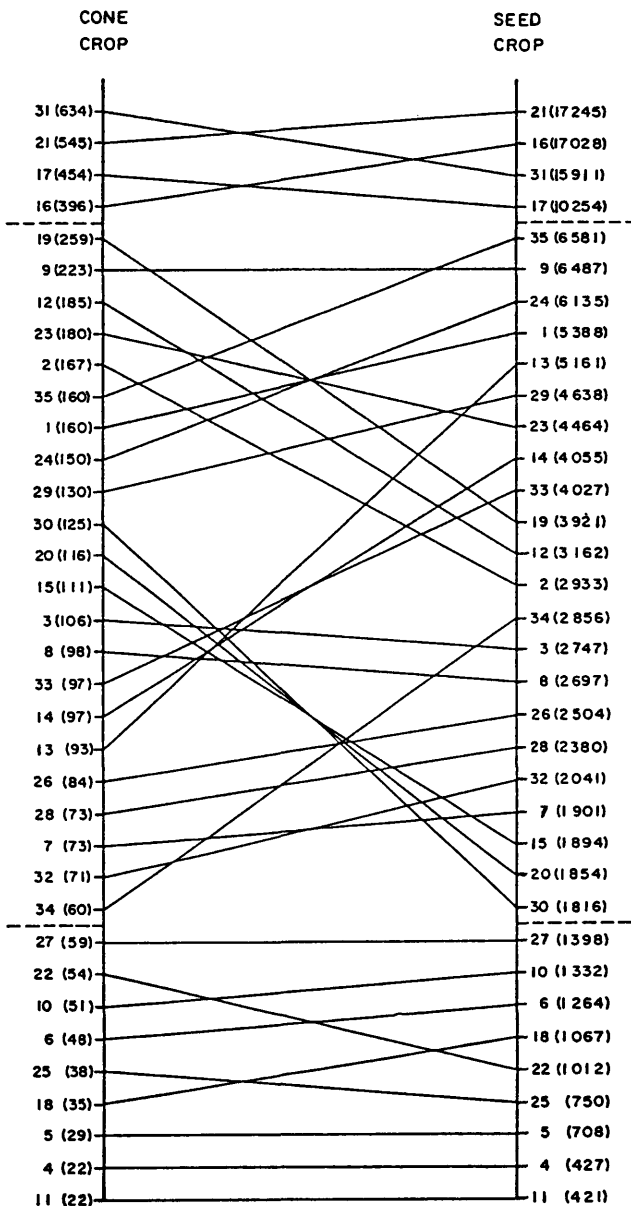


Fig. 1. — Rank order for 35 Douglas-fir clones, based on seed-cone and filled-seed yields (values represent the clonal cone and seed yield averages).

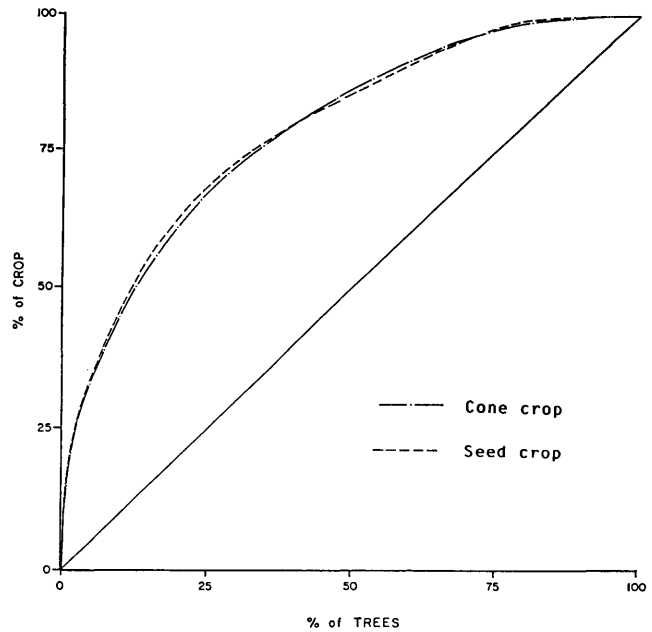


Fig. 2. — Cumulative seed-cone and filled-seed yields (parental-balance). Straight line represents equal contribution.

The above results corroborated the observation of REYNOLDS and EL-KASSABY (1990) and extended the reproductive energy and reproductive success non-linearity from individual tree basis to clonal level. The high heritability estimates obtained for both cone and seed production further substantiated this observation. In Douglas-fir, it was reported that in the absence of pollination, seed-cones continue their development reaching harvest size (OWENS *et al.*, 1991), thus any crop estimation procedure that is based on visual inspection of the seed orchard cone crop will produce inaccurate estimates even if appropriate sampling methods are used (BARTRAM and MILLER, 1988).

In conclusion, this study demonstrated: 1) female reproductive energy is not equal to reproductive success, 2) both seed-cone and filled-seed production are under genetic control, 3) female gamete contribution is asymmetrical as in most seed orchards, 4) parental-balance curves and female effective population number estimates provide a static description of the maternal genetic representation and do not illustrate the dynamics of clonal reproductive outputs, and 5) estimates of maternal genetic contribution that are based on cone count are different from that based on seed even when seemingly identical parental-balance curves are produced.

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Black Walnut Provenance Performance in Seven 22-Year-Old Plantations

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Summary

In 1967, black walnut (*Juglans nigra* L.) seedlings of different geographic origins were planted in seven common garden plantations within the species' natural range in the midwestern United States. After 22 years, height, d.b.h., and survival measurements revealed that local trees (from within 100 miles north and south of the plantation) had the greatest survival at all locations, and those from areas 200 miles south of the planting site grew significantly taller than trees from more southerly locations. Survival in the Minnesota and Iowa plantations was highly cor-

related with latitude and longitude of seed source; northern and western seed sources had higher survival. Height and d.b.h. correlations were highly significant in all plantations. High heritabilities implied that much of the geographic variation in height and d.b.h. is under genetic control and that seed source selection should be included in black walnut improvement programs.

Key words: *Juglans nigra* L., seed source, tree improvement.

FDC: 232.12; 176.1 *Juglans nigra*.

Introduction

Black walnut (*Juglans nigra* L.) is the most valued and desired tree species in the central hardwood forest. The natural range of the species extends from the eastern United States west to South Dakota and east Texas (*Figure 1*), and variation throughout this extensive range provides

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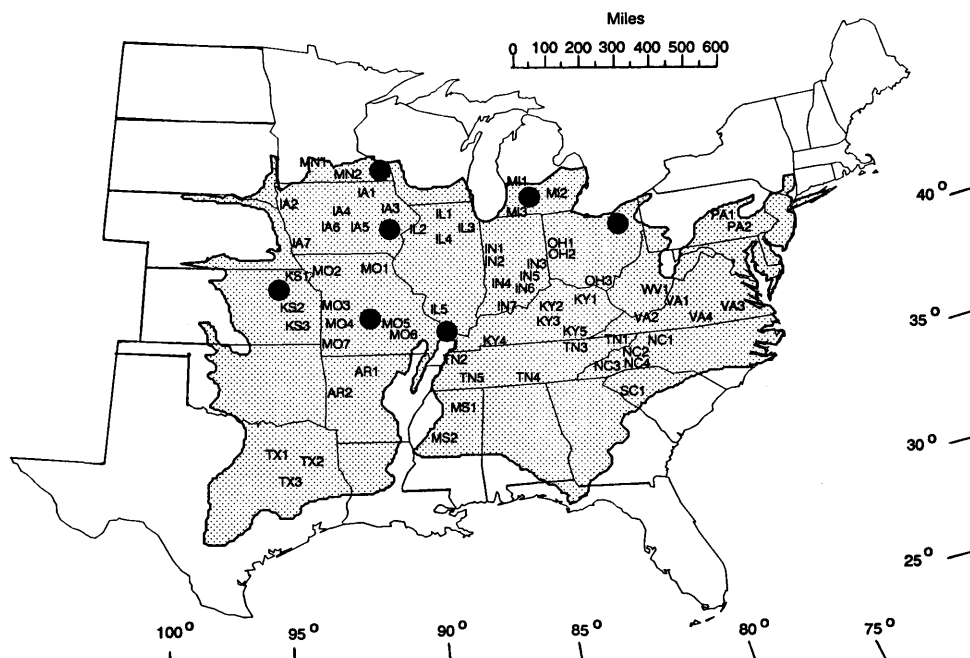


Figure 1. — Approximate natural range of black walnut is indicated by shaded area. Circles indicate plantation sites and state abbreviations represent provenances.