EFFECT OF A CLONAL ROW ORCHARD DESIGN ON THE SEED YIELDS OF LOBLOLLY PINE

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Abstract.--When ramets of the same clone are planted in a clonal row, the frequency of self-pollination is expected to increase. With an increase in self-pollination, the filled seed yield would be expected to decrease as a result of increasing the frequency of homozygous embryonic lethal alleles. Pine species are buffered against the deleterious effects of self-fertilization by the large number of embryonic alleles in the population with each individual tree having a different set of alleles. When an individual ovule contains both self and outcross pollen, a viable seed can be produced if the self-fertilized embryo aborts but the outcross-fertilized embryo survives. Thus, in a clonal row orchard, self-pollination increases but the impact on seed yields is expected to be relatively low. Experimental data indicated no significant reduction in the percentage of filled seeds from clonal rows when compared to a random design.

Additional keywords: *Pinus taeda,* pollen, self-pollination, embryonic lethal alleles.

INTRODUCTION

The amount of pollen reaching a ramet in a seed orchard is a mixture of (1) self pollen from the same ramet, (2) self pollen from other ramets of the same clone, (3) outcross pollen from neighboring ramets, (4) outcross pollen from non-neighboring ramets, and (5) background pollen from outside the orchard. It is important to determine the relative quantities of pollen from each of these sources to evaluate the impact of inbreeding in a seed orchard.

Unfortunately, quantifying each pollen component is difficult. Major problems are: (1) determining the phenology of each clone in the orchard and (2) determining the pollen dispersal patterns which vary as a function of relative humidity, temperature, wind direction, and wind velocity. Because

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female strobili (flowers) may be receptive to pollen for a week or more, some of these factors may have compensating effects. For a given ramet, the timing of female flower receptivity relative to the phenology of nearest neighbors, with other orchard clones, and with background pollen is the single most important factor.

Another factor in the success of embryo and seed development from the various sources of pollen is the action of recessive embryonic lethal alleles. The presence of embryonic lethal alleles in each individual mitigates against self progenies by effectively eliminating large numbers of self-fertilized embryos. With 10-12 embryonic lethal alleles, the probability is high (about 90%) that self-fertilized embryos will have at least one homozygous lethal and that the embryo will abort. With multiple pollen grains per ovule and multiple archegonia available for fertilization, self-fertilized embryos can abort and yet a filled seed develop from an outcross fertilization within the same ovule. Thus, mixtures of self and outcross pollen produce more successful outcross-pollinated embryos than self-pollinated embryos. The number of pollen grains per ovule, the ratio of self to outcross pollen, the numbers of archegonia per ovule, the number of embryonic lethals of the parents, all affect seed yields and genetic quality.

The objective of this study was to compare a random seed orchard design with clonal row designs. We compared self-pollination rates for a seed orchard with ramets of clones randomly assigned to positions to different clonal row designs. Self-pollination rates were estimated from a model using hypothetical values. Empirical data from one of the clonal row designs and the random design were used to test the model.

SEED ORCHARD MODEL DEVELOPMENT

We compared the relative amounts of pollen from the six different sources for four different seed orchard designs (table 1). The seed orchard designs include: random design with ramets planted on a 30 x 15 foot spacing; clonal row (CR30X15) with clones planted 30 feet apart and ramets within rows 15 feet apart; clonal row (CR15X30) with clones planted 15 feet apart and ramets within rows 30 feet apart; and clonal row (CR30X30) with both clones and ramets within rows planted 30 feet apart. These hypothetical values were developed as follows:

Self-pollination by the same ramet was assumed to be 15% for all of the designs studied except CR30X30. An arbitrary value of 17.5% was used for self-pollination by the same ramet at the least dense spacing since the proportionate contribution of pollen from other sources would logically be diminished. The proportion of pollination by unrelated, non-orchard pollen was assumed to be 40%. The proportions of pollinations from all other sources within the seed orchard were assumed to be proportionate to the frequencies of ramets of each type of male parent.

Frequencies were estimated for pollinators equal to or less than 90 feet from a target female and greater than 90 feet from a target female. This permitted weighting pollinations nearer the target tree more heavily than those lather than 90 feet from the target female.

The nearest neighbors are more important contributors to the pollen supply (Koski 1971). This author reported that 60% of pollen parents were within 32 m of a target female tree. This figure included self-pollinations by the target female. We used this percentage to estimate weights for frequencies of pollen parents within 90 feet and farther than 90 feet from the target female.

Thus, in the random design there were no ramets of the target female closer than 90 feet; but the frequency of ramets of that clone farther away was (100-1)/(4000-1) = .025. These ramet frequencies were multiplied by the weights estimated from Koski's relationship to arrive at the values in table 1.

Table 1. Hypothetical pollen distribution models for 10-year-old loblolly seed orchards with random vs 3 clonal row designs with 3 spacing configurations.[1/]

SOURCE OF POLLEN	ESTIMATED PERCENTAGE OF POLLEN FOR TARGET RAMET			
	RANDOM DESIGN[2/]	CLONAL ROW DESIGNS[3/4/]		
		CR30X15	CR15X30	CR30X30
	(Percent)			
Self Same Ramet	15.0	15.0	15.0	17.5
Self Other Ramets				
Within 90 Ft	0.0	5.3	2.6	4.7
Outside 90 Ft	0.5	0.4	0.5	0.5
Outcrosses				
Within 90 Ft	23.8	18.5	21.2	17.2
Outside 90 Ft	20.6	20.8	20.7	20.1
Background	40.0	40.0	40.0	40.0
Total	100.0	100.0	100.0	100.0
Total Self	15.5	20.7	18.2	22.7

1/ Orchard contains 40 clones with 100 ramets of each clone.

2/ Ramets of the same clone are not closer than 90 feet.

3/ Clonal rows are 20 trees long with 5 rows for each clone. A block consists of 1 row per clone for each of 40 clones.

4/ First number = distance between clonal rows; second number = distance between ramets of the same clone within rows.

With clonal row designs, the number of ramets of the same clone within 90 feet of a target female ramet increased (table 2). Thus, higher frequencies are expected for self-pollination with clonal row designs. Estimates ranged from 15.5% self pollination with random designs to 22.7% with a clonal row of twenty ramets spaced 30 feet x 30 feet (CR30X30) table 1.

Table 2.--Number of self and outcross ramets within a circle with a 90-foot radius comparing random design to three clonal row designs of different spacing configurations.

PLANTING DESIGN	MAXIMUM NUMBERS OF RAMETS WITHIN A 90 FOOT RADIUS		
	TOTAL	SELF	OUTCROSS
Random 15x30	55	1	54
Clonal Row CR30X15	55	13[1/]	42
Clonal Row CR15X30	55	7	48
Clonal Row CR30X30	29	7	22

1/ The number of self for clonal row designs are maximum values because ramets on the ends of clonal rows have fewer ramets within 90 feet.

Based on these estimates of the pollen source components, the percentage of self pollen increased with clonal row designs but not by as much as one might think. We tested this model using empirical data from a random design seed orchard compared to one of the clonal row designs.

TESTING THE MODEL

Seed yields and the percentages of filled seeds per cone were observed in the Weyerhaeuser Company's NC Loblolly Seed Orchard at Lyons, Georgia. A portion of the orchard consisted of 18 clonal rows, each with 20 ramets per clone. The clonal rows were 15 feet apart and ramets within rows were 30 feet apart (CR15X30). The trees were grafted in 1977 and planted in 1978. The study trees were approximately 26 feet tall and 8 inches d.b.h. in 1985.

With 30 feet between the ramets in a clonal row, trees in row positions 1-4 and 17-20 had fewer ramets of the same clone within 90 feet than ramets in row positions 5-16. Five ramets from five clones were selected as observation trees from row positions 1, 2, 3, 4 and 10 to evaluate the effect of row positions. These ramets had respectively 3, 4, 5, 6, and 6 ramets of the same clone within a 90-foot radius. Fiberglass screen cages were installed around three clusters of developing cones on each study ramet in May 1985 to prevent damage from insects (Bramlett et al. 1976). Mature cones were collected in October 1985 and air-dryed until open. Seeds were extracted by hand. The axes of cones that opened poorly were drilled and their scales separated. More than 95% of the seeds were extracted using this method. All extracted seeds were radiographed and scored as filled or empty. A total of 157 cones from the caged branches were analyzed from the 25 sample trees. In addition, 134 uncaged cones from the same clonal row ramets were collected, and their seeds extracted and analyzed in the same manner. Seeds were analyzed from 78 cones from 13 ramets in a RD orchard.

RESULTS

Clonal row vs random design

Neither caged nor uncaged cones from the clonal row ramets had significantly different numbers of extracted seeds, from uncaged cones collected from RD ramets (table 3). Mean values were 100, 107, and 99 respectively for caged clonal-row ramets, uncaged clonal row-ramets, and uncaged random design ramets. These data indicate that the reproductive capacity for the total number of seeds was not related to caging of developing cones or to orchard planting design. Clonal effects, as expected, strongly influenced the number of extracted seeds per cone. Clone A and B produced significantly more seeds per cone than clones C, D, and E (table 3).

Filled seeds per cone were increased by caging the cones from the time of fertilization to cone maturity (Table 3). The mean value of 79 filled seeds per cone for caged, clonal row trees was significantly higher than the filled seed yield per uncaged cone from the same ramets in the clonal row (49) or from different ramets of the same clones in the RD part of the same orchard (53). The difference is attributed to insect attack on the uncaged cones during the summer of cone development. Seedbug attack during this time period produces empty seeds while ovules damaged prior to fertilization appear as aborted ovules rather than empty seeds. (Bramlett et al. 1977)

Empty seeds from caged cones are caused by factors other than insects. The action of homozygous embryonic lethal alleles is considered the primary cause when insect damage is eliminated. Other possible causes of empty seeds are fungal damage, poor pollen vigor, and abnormal development.

The percentage of filled seeds per cone was used to estimate the impact of self pollination on seed yields. Caged clonal-row cones had significantly higher percentages of filled seeds (79) than noncaged clonal row cones (50) and random design cones (52). Assuming that both were reduced the same by insect damage, there was no significant reduction in percentages of filled seeds from clonal rows.

Table 3.--Extracted Seed, filled seed, and percentage of filled seed from clonal row ramets and random-design ramets of the same clones.

CLONE	CLONAL ROW CAGED	CLONAL ROW UNCAGED	RANDOM DESIGN UNCAGED	CLONAL MEAN
		EXTRACTED SEEDS PER CONE		
A	124	134	127	129 a
B	109	127	121	119 a
C	83	83	76	81 b
D	99	99	67	92 b
E	84	86	101	89 b
MEAN	100 a	107 a	99 a	102
		FILLED SEEDS PER CONE		
A	100	58	54	75
B	87	60	73	73 ab
C	59	30	34	42 c
D	85	64	42	70 ab
E	63	39	59	54 bc
MEAN	79 a	49 b	53 b	62
		PERCENTAGE FILLED SEEDS		
A	81	43	41	58 b
B	78	46	59	62 b
C	72	36	46	52 b
D	86	65	57	74 a
E	77	42	53	59 b
MEAN	79 a	50 b	52 b	61

The expected differences in percentages of self-pollinations between a random design and a clonal row design with 15 feet between rows and 30 feet between ramets was 18.2-15.5 = 2.7% (from table 1). The expected reduction in the percentage of filled seeds assuming an average of 10 embryonic lethal alleles is 1.5% (Koski, 1982). The non significant difference measured in the empirical study (51.6-49.9 = 1.7%), was surprisingly close to the expected value.

The effect of row position on seed yields

There was no significant difference in the percentage of filled seeds among the 5 sample ramets in different positions in rows (table 4). Mean values varied from 82.8 percentage filled seeds in row position 2 to 76.6 for row positions 4 and 10. Individual clones had significantly different mean values ranging from 71.4 percentage filled seeds for Clone C compared to 86.1 percent filled for Clone D.

Table 4.--Percentage of filled seeds from five row positions in a 20-tree loblolly pine clonal row orchard

CLONE	NO. OBS	ROW POSITION 1	2	3	4	10	AVG
		Percent					
A	21	81.5	68.7	77.3	92.1	81.3	80.2 ab
B	36	66.0	87.9	73.6	77.6	91.3	74.5 b
C	36	85.5	78.7	69.7	69.6	60.3	71.4 c
D	33	89.7	90.0	86.0	80.9	83.9	86.1 a
E	31	76.4	81.3	82.8	69.6	72.9	76.7 bc
	157	78.8 a	82.8 a	78.1 a	76.6 a	76.6 a	78.6

CONCLUSIONS

Results from this study indicated no significant differences in seed yields or percentages of filled seeds between ramets in clonal rows and ramets of the same clone in a random orchard design. Furthermore, within the clonal rows, position had no significant effect on the percentages of filled seeds per cone.

A theoretical pollen distribution model to predict the percentage of filled seeds from different seed orchard designs was developed and found to accurately predict the observed decrease in the percentage of filled seed between two different orchard designs

Thus, the concept of clonal row seed orchard designs should not be rejected based on presumed large increases in self-pollination and self-fertilization.

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