Influence of Host Genotype on Douglas-Fir Seed Losses to *Contarinia oregonensis* (Diptera: Cecidomyiidae) and *Megastigmus spermotrophus* (Hymenoptera: Torymidae) in Western Oregon

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ABSTRACT Seed losses to the Douglas-fir cone gall midge, *Contarinia oregonensis* Foote, and Douglas-fir seed chalcid, *Megastigmus spermotrophus* (Wachtl), were measured in a Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, clonal seed orchard and in a Douglas-fir progeny plantation in western Oregon. Seed losses to both insects differed significantly ($P < 0.05$) among clones and among the progeny of selected parental crosses. Seed loss differed more than three times between least-infested and most-infested clones or progeny. Seed losses in the progeny plantation indicated that resistance to these two insects is a heritable trait, with greater resistance showing a tendency to dominate over lesser resistance. Insect responses to host genotype may be modified by factors associated with the position of the tree within the stand. Implications of these results for tree improvement programs and seed orchard management are discussed.

KEY WORDS Insecta, Douglas-fir cone gall midges, Douglas-fir seed chalcids, cone and seed insects

DESPITE THE INCREASING IMPORTANCE of tree improvement programs for reforestation purposes, relatively few studies have addressed the effect of insects on the production of genetically selected seed. Insects feeding on cones and seeds have been shown to concentrate on particular clones of pines (Merkel et al. 1965, DeBarr et al. 1972, Goyer & Nachod 1976, Williams & Goyer 1980, Jenkins 1982, Askew et al. 1985). In Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, Hedlin & Ruth (1978) reported that differences in losses to insects among Douglas-fir clones in seed orchards in British Columbia were small and of no practical importance. On the other hand, Roques (1981) reported significant clonal variation in Douglas-fir susceptibility to seed chalcids, *Megastigmus spermotrophus* (Wachtl), in France but later (Roques 1986) found no clonal variation when the cone crop was small relative to chalcid abundance. No studies have examined the heritability of resistance of Douglas-fir cones and seeds to insect damage or the impact of insects on production of selected genotypes in progeny seed orchards.

Tree improvement programs have two primary goals: to provide genetically superior (rapidly growing) trees and to maintain genetic diversity in managed forests (Askew et al. 1985, Krugman 1986). If host genotype influences insect damage to cones and seeds, then insects could influence overall production of superior seed by reducing the seed output of an orchard and could influence genetic diversity by selectively reducing seed production by particular clones or progeny. Our purpose in this study was to examine the degree of susceptibility of Douglas-fir clones and progeny of selected crosses to destruction of seeds by insects in western Oregon.

Materials and Methods

The clonal study was conducted in 1985 at the Beaver Creek Seed Orchard, operated by the U.S. Forest Service, 27 km southwest of Corvallis, Benton County, Oreg. Two contiguous blocks containing the same 24 randomly distributed clones of Douglas-fir (originally collected from the Oregon Coast Range) were selected on the basis of number of replicates (7–35 ramets per clone) throughout the two blocks and representation of distance (range, 10–500 m) from cone and seed insect sources in an adjacent unmanaged stand. The trees were 20 yr old and 8–12 m in height at the time of the study. The abundant cone crop produced during 1985 was preceded by small cone crops in 1983 and 1984.

The progeny study was conducted in 1984 at a Douglas-fir progeny plantation operated by the U.S. Forest Service, 6.5 km southwest of Monmouth, Polk County, Oreg. The plantation represented 51 distinct parental crosses (11 male parents × 6 female parents from the same parental pool). Parents 1 and 3 were from the west side of the Willamette Valley in western Oregon, and the remainder were from the east side. None of the trees in this plan-

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Table 1. Percentage seed lost to *Contarinia oregonensis* and *Megastigmus spermotrophus* in a Douglas-fir progeny plantation in western Oregon

Parent	No. crosses	% seed lost to[a]	
		C. oregonensis	*M. spermotrophus*
1	9	53 (3.4)	6.6 (1.2)
2	10	66 (3.4)	5.9 (1.2)
3	8	62 (3.5)	7.3 (1.2)
4	11	58 (3.3)	9.4 (1.1)
5	9	62 (3.4)	7.0 (1.2)
6	10	62 (3.4)	9.5 (1.2)
7	6	59 (3.8)	6.3 (1.3)
8	5	66 (4.1)	6.5 (1.4)
9	5	66 (4.1)	7.0 (1.4)
10	6	59 (3.8)	6.7 (1.3)
11	6	51 (3.8)	10.2 (1.3)
12	5	63 (4.1)	8.1 (1.4)
Overall	45	60 (3.0)	7.5 (1.0)

[a] $\bar{x}$ (95% confidence limit based on pooled SD).

tation was related to trees in the seed orchard. We sampled 45 crosses, each represented by four seedlings planted in a row in each of five blocks. These blocks occupied the northwest and southwest slopes of a low hill (5 m maximum elevation difference) and were surrounded to the north, west, and south by a 50-m buffer of commercial grass and to the east by a plantation of ponderosa pine, *Pinus ponderosa* Douglas ex Loudon. No other Douglas-fir occurred within 500 m of the plantation. These trees were 12 yr old and 5–6 m in height at the time of study. This plantation produced its first cone crop in 1983. The cone crop produced in 1984 was much smaller than that produced in 1983.

In both studies, five cones were collected at random from each tree at the time of cone maturity in August. All cones were collected from trees producing fewer than five cones. Individual cones were labelled by block, clone or family, and tree, then air dried. Dried cones were dissected scale by scale. Total seeds (number of scales × 2), seeds fused to Douglas-fir cone gall midge (*Contarinia oregonensis* Foote) galls, and seeds damaged by other insects were recorded. Galled and ungalled developed seeds were sliced to record incidence of the Douglas-fir seed chalcid. The response variables analyzed were the number of galled seeds (including some chalcid-infested seeds) as a percentage of total potential seed, and number of chalcids in galled and ungalled seeds as a percentage of total potential seed.

Data were pooled by tree in both studies. In the progeny study, the data were further pooled by block-×-family combination. Pooled data were averaged, and mean proportions of seed damaged by each insect were transformed to the arcsine of the square root for analysis of variance (ANOVA). Transformed data were analyzed by two-way ANOVA, with genotype and position as main factors. Results were considered significant at the $\alpha = 0.05$ level.

Table 2. Percent seed lost to *Contarinia oregonensis* and *Megastigmus spermotrophus*, by block, in a Douglas-fir progeny plantation in western Oregon

Block	No. trees per block	% seed lost to[a]	
		C. oregonensis	*M. spermotrophus*
1	32	67 (5)	10 (3)
2	33	69 (5)	11 (3)
3	30	70 (6)	7 (3)
6	32	48 (5)	13 (3)
7	37	46 (5)	12 (3)
Overall	164	60 (2)	11 (1)

[a] $\bar{x}$ (±95% confidence limit based on pooled SD).

Results

Significant differences among clones were found for transformed proportions lost to the cone gall midge ($F = 5.4$; df = 23, 470) and seed chalcid ($F = 6.3$; df = 23, 470). Based on 95% confidence limits, 3 clones showed losses >3% to the midge and 5 clones showed losses <2%, compared with an overall mean of 2%; 1 clone showed losses >2% to the chalcid and 11 clones showed losses <0.5%, compared with an overall mean of 0.3%. Losses to the Douglas-fir cone moth, *Barbara colfaxiana* (Kearfott), and the fir coneworm, *Dioryctria abietivorella* (Groté), were too low and variable to show significant clonal effects ($Fs < 1.5$, df = 23, 470).

Distance from the potential influence of the adjacent, upslope unmanaged forest was examined as a second factor in the ANOVA (Schowalter et al. 1985). The effect of distance was not significant either independently or interacting with clone.

Data for the progeny study are summarized in Table 1. Significant differences among crosses were found for transformed proportions lost to the cone gall midge (two-way ANOVA; $F = 2.5$; df = 44, 115) and seed chalcid ($F = 1.6$; df = 44, 115). Examination of means and 95% confidence limits for the 45 crosses suggests heritable patterns of resistance to the cone gall midge and seed chalcid (Table 1). The highest seed losses to cone gall midges occurred in progeny of Parents 2, 8, and 9; the lowest seed losses occurred in progeny of Parents 1 and 11, even when crossed with Parents 2, 8, and 9. The highest seed losses to seed chalcids occurred in progeny of Parents 4, 6, and 11; the lowest seed losses occurred in progeny of Parents 1 and 2, even when crossed with Parents 6 and 11 (but not 4).

Seed losses also differed significantly by position (block) within the plantation ($F = 26$ and 4.4 for midge and chalcid, respectively; df = 4, 115). Blocks 1, 2, and 3 on the southwest slope had higher seed losses to midges but lower seed losses to chalcids than did Blocks 6 and 7 on the northwest slope (Table 2). The poor cone yield and resulting incomplete replication of crosses among blocks prevented evaluation of the cross-×-block interaction.

The seed chalcid oviposits in cones later than the midge and might be influenced by midge abundance. In the clonal study, chalcids were found in galled seeds in only two clones, 4 and 9. In the progeny study, 35% of the chalcids were found in galled seeds. We examined the effect of midge damage as a covariate in the ANOVA for chalcid damage. The midge effect was not significant in either study.

Discussion

Others also have found significant differences in cone and seed insect activity among clones of Douglas-fir (Hedlin & Ruth 1978; Roques 1981, 1986). We found that at low population levels, cone gall midge and seed chalcid infestation varied more than 3-fold among clones in western Oregon. Roques (1981) reported similar results at low chalcid densities in France. At the much higher population levels observed in the progeny plantation, seed losses to these insects varied nearly 2-fold for the midge and 4-fold for the chalcid among progeny of parental crosses (Table 1), in contrast to results reported by Hedlin & Ruth (1978) for British Columbia and Roques (1986) for France.

Heritability of resistance is suggested by our results (Table 1). Resistance appeared to be a dominant trait as indicated by relatively low seed losses for offspring of a resistant and a susceptible parent. To our knowledge, this study is the first to suggest that resistance to insects may be a dominant trait. These results could have important implications for tree breeding programs.

Our data also suggest that host resistance to insects can be modified by position (i.e., exposure to insect populations) as shown in other studies (Schowalter et al. 1985, Thompson 1985, Schowalter & Stein 1987). Trees on the southwest slope of the progeny plantation had higher seed losses to cone gall midges but somewhat lower seed losses to seed chalcids than did siblings on the northwest slope. Because the progeny plantation had produced its first cone crop in 1983, resident populations in 1984 probably were small and aggregated according to dispersal patterns the previous year. Increase in resident populations over several years in the clonal orchard would have overshadowed any position effect.

The results of this study indicate important factors to consider in projecting seed production or implementing tree improvement programs. At $1,100/kg ($500/lb) for Douglas-fir seed, a >2-fold difference in seed losses to insects between resistant and susceptible trees has considerable economic importance. Such a difference also has important consequences for the contribution of selected genotypes in the final seed harvest. Production of different genotypes is affected by many factors, including variation in cone and pollen production, number of seeds per cone, and number of trees per clone or cross. This variation could be complemented or exacerbated by selective insect activity. Local site factors also may affect seed production and insect activity (Schowalter et al. 1985).

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