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## FACTORS LIMITING SEED PRODUCTION OF *TAXUS BREVIFOLIA* (TAXACEAE) IN WESTERN OREGON<sup>1</sup>

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Seed production of Pacific yew (*Taxus brevifolia*), an understory conifer, was studied at four sites in western Oregon over 2 yr. The effects of pollen supplementation, overstory canopy, and predator exclusion on ovule attrition were examined. Supplemental hand-pollination of ten trees at two sites resulted in significantly increased rates of ovule development and a doubling of seed efficiency (ratio of seeds to ovules). However, seed efficiency still averaged <15% on branches receiving supplemental pollen, so pollination was not a primary factor limiting seed production. The number of developing ovules was positively associated with overstory openness, but seed production was not. Seed efficiency was negatively associated with overstory openness. Branches bagged to exclude vertebrate seed predators had higher seed production than unbagged branches at three of four sites for 2 yr. In contrast to unbagged branches, seed production on bagged branches was positively associated with overstory openness, as was the effectiveness of bagging. Therefore, both vertebrate predation and overstory were important in limiting seed production, and these factors interacted. Factors limiting seed production varied in importance among the four sites and between years, illustrating the importance of examining multiple limiting factors over several sites and years.

**Key words:** overstory; Pacific yew; pollen limitation; predation; seed; Taxaceae; *Taxus brevifolia*.

Plants commonly produce many more ovules than seeds (Sweet, 1973; Stephenson, 1981; Sutherland, 1986), and the mechanisms and patterns of flower and fruit abortion can provide insight into the evolutionary significance of low seed–ovule ratios. The major factors responsible for ovule attrition are inadequate pollination (reviewed by Bierzychudek, 1981; Young and Young, 1992; Burd, 1994), resource limitation (reviewed by Stephenson, 1981; Willson and Burley, 1983), genetic load (Charlesworth, 1989; Helenurm and Schaal, 1996), loss of seed to predators and pathogens (Janzen, 1971; De Steven, 1982; Louda, 1982; Rauf, Benjamin, and Cecich, 1985), and physical damage from abiotic factors such as frost (Sweet, 1973; Owens and Blake, 1985).

The relative importance of pollen limitation vs. resource limitation has been a recurring theme in reproductive biology research. A common way of experimentally testing for pollen limitation is by adding supplemental pollen to plants growing under natural conditions and determining whether there is an increase in seed production. However, several authors have pointed out shortcomings in this technique. Increased seed production might come at the expense of seed production in other portions of the same plant, or it might cause a reduction in future growth, reproduction, or survival of the manip-

ulated plant (Janzen et al., 1980; Bawa and Webb, 1984; Zimmerman and Pyke, 1988). Indeed, it appears that in some plants pollen limitation can occur over the short term, but lifetime reproduction of a plant is primarily limited by resource availability (Aker, 1982; Ackerman, 1989; Zimmerman and Aide, 1989; Ehrlén and Eriksson, 1995). Other authors have pointed out that many plants are likely to be limited by both resources and pollen (Haig and Westoby, 1988), and complex interactions between resource and pollen availability can occur. For example, plants can be limited by resources when pollen is abundant or limited by pollen when resources are abundant (Casper and Niesenbaum, 1993). Alternatively, resources and pollen might affect different components of reproduction, such as when resources primarily affect ovule production and pollination primarily affects the proportion of ovules that develop into seed (Campbell and Halama, 1993).

For many plants, the relative importance of resource or pollen limitation is likely to depend on resource levels. For understory plants, one source of variation in resource availability is the density of the overstory canopy. Seed production of many understory plants is limited by low light availability (Devlin, 1988; Lee, 1989; Bunnell, 1990; Dale and Causton, 1992; Niesenbaum, 1993), and successful sexual reproduction may occur only in the elevated light levels found beneath overstory gaps (Thompson and Willson, 1978).

Predispersal seed predation is another factor that can interact with pollen and resource availability in limiting seed production. For example, under high resource availability predation might limit seed production. Alternatively, when resources and predation are low, resources might limit seed production (Louda, 1982; Ehrlén, 1992). Therefore, it is necessary to take predispersal seed predation into account when considering the importance of resource and pollen limitation of seed production.

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TABLE 1. Study site characteristics. Values for overstory, slope, aspect and tree age are population means of values measured at individual trees. Values in parentheses are 1 SD.

Site <sup>a</sup>	Canopy group <sup>b</sup>	Elev. (m)	Vegetation association <sup>c</sup>	N	Overstory (DIFN) <sup>d</sup>	Slope (degrees) <sup>d</sup>	Aspect (degrees) <sup>d</sup>	Tree age (yr) <sup>d</sup>	Precip. (mm) <sup>e</sup>
HC1	OPN	1100	TSHE/RHMA/GASH	14	0.91 (0.02)	27 (5)	264 (20)	87 (41)	2569
	CAN	1200	TSBE/BENE/ACTR	14	0.21 (0.07)	27 (5)	192 (29)	122 (45)	
HC2	OPN	1150	ABAM/BENE	16	0.37 (0.24)	14 (4)	167 (161)	141 (36)	2143
	CAN	1035	ABAM/RHMA/XETE	14	0.11 (0.06)	8 (3)	40 (22)	153 (44)	
LC	OPN	850	TSHE/RHMA-BENE	14	0.47 (0.18)	11 (7)	192 (29)	151 (40)	2098
	CAN	850	TSHE/BENE/ACTR	14	0.16 (0.10)	8 (3)	211 (46)	132 (38)	
VAL	OPN	300	ABGR/RUUR-RHDI	15	0.83 (0.09)	19 (4)	206 (60)	88 (21)	1094
	CAN	200	ABGR/BRSY ABGR/DIHO-THOC	14	0.16 (0.12)	19 (5)	67 (40)	78 (18)	

<sup>a</sup> HC1, Higher Cascade 1; HC2, Higher Cascade 2; LC, Lower Cascade; VAL, Willamette Valley.

<sup>b</sup> OPN, populations occurring in clearcuts; CAN, populations occurring under overstory canopy.

<sup>c</sup> See Hemstrom, Logan, and Pavlat (1987) for HC1, HC2, and LC; Hubbard (1991) for VAL.

<sup>d</sup> See text for a description of methods.

<sup>e</sup> Average annual precipitation values derived from interpolations of 10-yr averages from nearby climate stations, using the PRISM climate model (Daly, Neilson, and Phillips, 1994).

The purpose of the present study was to determine the importance of pollen limitation, resource limitation, and predation in limiting seed production of the understory tree Pacific yew (*Taxus brevifolia* Nutt., Taxaceae). Pollen limitation was assessed through pollen supplementation experiments. Resource limitation was addressed by examining the relationship between overstory openness and seed production. A positive relationship would indicate resource limitation of seed production, because overstory openness provides an index of availability of resources such as light, water, and nutrients (Canham and Marks, 1985). Finally, predispersal seed predation was indexed through a predator exclusion experiment. Variability in the importance of pollen, resources, and predators was assessed for four different study sites over 2 yr.

## MATERIALS AND METHODS

**Study organism**—*T. brevifolia* occurs from northern California north to southeast Alaska and inland to western Montana (Bolsinger and Jaramillo, 1990). It is highly shade tolerant and is found most frequently in the understory of late seral forests, although it is not an obligate understory species (McCune and Allen, 1985; Busing, Halpern, and Spies, 1995).

*T. brevifolia* is dioecious and wind-pollinated. Mature female strobili consist of a single seed with a hard integument, surrounded by a bright-red cuplike aril. In western Oregon, pollination occurs in March and April and seed maturation begins in late July and continues through October (Rudolph, 1974; DiFazio, 1996). Seeds are consumed and dispersed by a variety of birds and rodents (DiFazio, 1996).

**Study design and tree selection**—This study was conducted on four sites in western Oregon (Table 1). The main criteria for site selection were the presence of at least ten sexually mature *T. brevifolia* trees per hectare and a range of canopy cover above the *T. brevifolia* trees. All sexually mature *T. brevifolia* trees were mapped. To ensure an adequate range of overstory canopy cover, trees were selected by stratified random sampling and subjectively assigned to two groups: those growing under open canopy (OPN) and those under canopy cover (CAN). Seven to eight female trees were randomly selected from each canopy grouping, for a total of 14–15 trees per site. For convenience, “site” will refer to an entire drainage and “plot” will refer to a canopy grouping within a site.

**Study sites**—The Higher Cascade 1 site (HC1) was in the Snow Creek drainage of the Willamette National Forest (44°23'N, 122°15'W). Overstory trees in the OPN plot were harvested in a 1990 clearcut. The CAN plot was ~1 km upslope from the OPN plot.

The Higher Cascade 2 site (HC2) was in the Hackleman Creek drainage of the Willamette National Forest (44°24'N, 122°02'W). Overstory trees for the OPN plot were harvested in a 1978 salvage logging operation, and substantial windthrow of remaining trees had occurred since that time. The CAN plot was ~1.5 km downslope from the OPN plot.

The Lower Cascade site (LC) was in the McCrae Creek drainage of the H. J. Andrews Experimental Forest (44°15'N, 122°11'W). Canopy gaps in the OPN plot were created by a 1981 clearcut and construction of a road in the 1950s. The CAN plot was contiguous with the OPN plot.

The Willamette Valley site (VAL) was located in the west fork of the Oak Creek drainage of the McDonald Research Forest in the foothills of the Oregon Coast Range (44°35'N, 123°35'W). Overstory trees in the OPN plot were harvested in a 1984 clearcut. The CAN plot was located ~2 km downslope from the OPN plot.

**Ovule and seed production**—Ovule production was determined on subsampled branches of each tree. In 1993, eight branch tips were randomly selected and the distal 30 cm was measured and marked with flagging. In May, June, and July of 1993 the number of ovules was counted and categorized as nondeveloping, developing, or mature, based on external morphology. Nondeveloping ovules were unexpanded and yellow, while developing ovules were green and expanding. From August until October 1993, the number of mature seeds per branch was counted at 2-wk intervals. Seeds with red arils covering the entire seed coat were considered mature; aborted seeds were misshapen and hollow. Estimates of seed production included the total number of mature seeds observed, the total number of empty receptacles (indicative of removal of mature seeds), and the number of healthy, developing seeds present at the final census. Mature seeds and empty receptacles were removed at each census in order to avoid duplication in counting. Ovule and seed production in 1994 was estimated in much the same way as in 1993, except trees were visited monthly rather than biweekly. Specific terms were defined to facilitate presentation of ovule and seed development data (Table 2).

**Pollination**—To determine whether ovules develop in the absence of pollination, pollen was completely excluded from 38 branch tips on 13 trees in 1993 and 1994. Before pollen shedding was observed at each site, branch tips were covered with paper pollen-exclusion bags. Cotton

TABLE 2. Terms defined to describe development and production of seeds and ovules.

Ovule production—maximum number of developing and nondeveloping ovules observed in May, June, and July censuses.
Ovule development—number of green and expanded ovules observed in July.
Ovule development efficiency—ovule development/ovule production.
Seed production—number of mature seeds, receptacles, and developing seeds observed at final census in late September.
Seed development efficiency—seed production/ovule development.
Seed efficiency—seed production/ovule production.

batting was wrapped around the branch and the bags were secured over the cotton with twist ties.

A pollen supplementation experiment was performed at the HC1 and VAL sites in 1994. These sites were chosen because considerable attrition of ovules was observed following pollination in 1993, possibly indicating pollen limitation.

Five female trees were randomly selected per site from all studied trees that produced at least two strobili per 30 cm branch that year. Twenty-one 30-cm branch segments were selected as described for ovule and seed production censuses. One branch per tree was covered with a pollen exclusion bag and received hand-pollination ("exclusion and pollination" treatment), ten open-pollinated branches were randomly chosen to receive hand-pollination ("supplemental pollination" treatment), and ten open-pollinated branches received no supplemental pollen ("control").

Pollen was collected by clipping branches from several male trees per site just before pollen began shedding. Cut branch ends were placed in water at room temperature overnight and pollen was collected on waxed paper. Viability was determined in a germination medium (Vance, 1995). Pollen used in hand-pollinations had >90% viability.

Hand-pollinations were performed in late March and April, at the time of peak receptivity of female trees. Criteria for receptivity were the emergence of the ovule from beneath bud scales and the presence of a pollination drop at the micropyle of the ovule (DiFazio, 1996). Receptivity was protracted at the VAL site, and there was much variability among trees; receptivity was more synchronized at the HC1 site (DiFazio, 1996). Therefore, hand-pollinations were performed on five dates at VAL and one at HC1.

At the time of hand-pollination all "control" branches were first covered with pollen exclusion bags, and "exclusion and pollination" branches were uncovered. A soft paintbrush was used to apply pollen directly to the micropyles of all visible ovules on "exclusion and pollination" and "supplemental pollination" branches. Bags were then removed from "control" branches and "bagged and pollinated" branches were rebagged.

The effect of supplemental pollination was assessed by comparing ovule development efficiency and seed efficiency between "supplemental pollination" and "control" branches (Table 2).

**Vertebrate exclusion**—A vertebrate predator exclusion study was conducted in 1993 for five trees per site, randomly selected from the trees used for assessing ovule and seed production. For each tree, four of the eight previously selected branch tips were randomly chosen and enclosed in 1-mm nylon mesh bags in July, following pollination. Seed production on bagged branches was assessed in late September. Seed production on the four unbagged control branches was assessed as described above.

In 1994, four randomly selected branches were bagged on all trees that had developing ovules as of July. On trees that had been bagged in 1993, branches bagged in 1994 included two branches that had also been bagged in 1993, and two branches that had not previously been bagged. This was done to equalize carryover effects from 1993 bagging between bagged and control groups in 1994.

Four trees were used both in the pollen addition and the vertebrate exclusion experiments. However, the timing of these experiments did not overlap, and branches that received supplemental pollination were not used for the vertebrate exclusion experiment. There was no evidence that ovule development efficiency or seed efficiency of unmanipulated branches were affected by supplemental pollination or bagging of other branches on the same tree (see below).

**Overstory**—Overstory canopy openness above and to the south of each study tree was estimated by using the model LAI-2000 plant canopy analyzer (LI-COR, Lincoln, NE, USA). The value used in this study was Diffuse Noninterceptance (DIFN), which is based on the ratio of diffuse light measured beneath the canopy to diffuse light in the open. DIFN ranges from 0 (completely closed canopy) to 1 (completely open canopy) (Welles and Norman, 1991). The southern aspect was measured for each tree on the assumption that this was the location of the most important canopy gaps at this latitude (i.e., those that resulted in the most significant increases in understory light levels: Gray, 1995).

**Statistical analyses**—Relationships among continuous variables such as DIFN, ovule development, seed efficiency, and treatment effects were assessed using the multiple linear regression procedure of SAS (SAS, 1987). Variables were transformed where appropriate to correct for heteroscedasticity. Separate slopes and intercepts were fitted for each site, and regression lines were compared among sites by systematically combining indicator variables and assessing the reduction in the regression sum of squares relative to the number of variables removed from the model (Neter and Wasserman, 1974). Final models were the most parsimonious models that yielded an *F* statistic greater than expected at the 95% confidence level when compared with the next simplest model.

Paired *t* tests were used for comparison of treatment effects in analyses where trees were the blocking factor (e.g., testing for the effect of vertebrate exclusion bags), and standard *t* tests were used for unpaired comparisons (e.g., comparing treated to untreated trees). For cases where transformations failed to correct for heteroscedasticity, the Wilcoxon signed-rank test was used for paired comparisons and the Wilcoxon rank-sum test was used for unpaired comparisons (Mosteller and Rourke, 1973).

## RESULTS

**Pollen limitation**—Of 380 ovules on bagged branches, only two developed. The two developing ovules could have arisen from pollen contamination or from apomixis (Orr-Ewing, 1957; Allison, 1993).

Open pollination in 1994 resulted in mean ovule development efficiencies of 0.59 at site HC1 and 0.17 at VAL. Seed efficiencies were 0.20 and 0.05 at HC1 and VAL respectively (Table 3). Hand-pollination on bagged branches resulted in ODE ranging between 0.5 and 0.8 (mean = 0.7) at HC1 and 0.6 and 0.9 (mean = 0.7) at VAL.

Ovule development efficiency was significantly higher on branches receiving supplemental pollination than on control (open-pollinated) branches for two of five trees at the HC1 site and for four of five trees at the VAL site (Table 4). Seed efficiency on supplementally pollinated branches was greater than that of control branches for all trees at both sites, but the differences were only significant for two trees at VAL (Table 4). If trees were considered the experimental units rather than branches, ovule development efficiency was significantly greater with supplemental pollination at the VAL site but not at the HC1 site, while seed efficiency was significantly improved at both sites (Table 4).

TABLE 3. Mean ovule development efficiency (ODE) and seed efficiency (SEF) by year and site. Superscript numbers indicate homogeneous groups within years as determined by Duncan's multiple range test (SAS, 1987).

	1993				1994				<i>N</i>	1993 vs. 1994 <sup>a</sup>			
	HC1	HC2	LC	VAL	HC1	HC2	LC	VAL		HC1	HC2	LC	VAL
<i>N</i> <sup>b</sup>	14	16	14	14	14	15	14	15		14	15	14	14
ODE	0.51 <sup>2</sup>	0.76 <sup>1</sup>	0.20 <sup>3</sup>	0.09 <sup>4</sup>	0.59 <sup>2</sup>	0.71 <sup>1</sup>	0.45 <sup>3</sup>	0.17 <sup>4</sup>	<i>P</i>	0.28	0.01	0.001	0.03
SEF	0.15 <sup>12</sup>	0.24 <sup>1</sup>	0.11 <sup>2</sup>	0.05 <sup>3</sup>	0.20 <sup>2</sup>	0.34 <sup>1</sup>	0.21 <sup>2</sup>	0.05 <sup>3</sup>	<i>P</i>	0.35	0.15	0.001	0.90

<sup>a</sup> Wilcoxon signed-rank test for differences between years in tree means.

<sup>b</sup> *N* = number of trees.

Seed efficiency on control branches in the year of pollen supplementation was not significantly different from seed efficiency on the same trees in the previous year (paired  $T = 1.17$ ,  $P = 0.27$ ). Similarly, seed efficiency on control branches for trees receiving supplemental pollination was not significantly different from seed efficiency on unmanipulated trees at the same site in the same year ( $T = 0.48$ ,  $P = 0.64$  at HC1; and  $T = 1.15$ ,  $P = 0.27$  at VAL).

**Predation**—Branches bagged to exclude vertebrates had significantly higher mean seed development efficiency than unbagged branches at the HC1, HC2, and LC sites in both 1993 and 1994 (Table 5). Seed development efficiencies were also higher for bagged branches at VAL, but the difference was not significant (Table 5). No carryover effect of bagging was detected: branches bagged in 1993 did not differ significantly from unbagged branches in 1994 ovule production or seed development efficiency (Wilcoxon two-tailed signed rank test,  $P = 0.60$  and  $0.50$ , respectively).

**Overstory**—Overstory openness (DIFN) was positively associated with ovule development at all sites in 1993 and at three of four sites in 1994 (Figs. 1, 2). Overstory openness accounted for 68% of the observed variation in ovule development in 1993 and 45% in 1994. There was no significant difference in the slope of ovule development vs. DIFN among sites within years, with the excep-

tion of site HC1 in 1994, for which the slope was not significantly different from zero. *Y*-intercepts did vary among sites within years, mainly because the higher Cascade sites had greater ovule development than the lower elevation sites (Figs. 1, 2).

No significant association was detected between DIFN and seed production in either year (Figs. 3, 4). This lack of a significant relationship was due to higher attrition of developing ovules under open-canopy conditions, as illustrated by the negative relationship between overstory openness and seed efficiency for HC1, HC2, and LC in 1993 and all four sites in 1994 (Figs. 5, 6).

**Overstory and predation**—Seed production on branches bagged to exclude predators was positively associated with DIFN at sites HC1, HC2, and LC in both years (Figs. 7, 8), whereas there was no significant relationship on unbagged branches (Figs. 3, 4). The effect of bagging (difference in seed development efficiency between bagged and unbagged branches) was also positively associated with DIFN in 1994 at all sites, but not in 1993 (Figs. 9, 10). The VAL site was excluded from these analyses due to insufficient ovule production on shaded trees.

**Variation among sites and years**—Early abortion (due at least in part to unsuccessful pollination) was significantly different among all four sites in both years of the study, accounting for the majority of ovule attrition at

TABLE 4. Effect of supplemental hand-pollination at sites HC1 and VAL in 1994. "Supplemented" branches were open-pollinated branches receiving supplemental hand-pollination; "Control" branches were open-pollinated.

Tree	Ovule development efficiency			Seed development efficiency		
	Supplemented branches	Control branches	<i>P</i> <sup>a</sup>	Supplemented branches	Control branches	<i>P</i>
Higher Cascade 1 (HC1)						
1	0.74 (0.054)	0.61 (0.035)	0.05	0.058 (0.018)	0.025 (0.012)	0.18
2	0.73 (0.057)	0.65 (0.073)	0.27	0.068 (0.035)	0.033 (0.017)	0.45
6	0.73 (0.034)	0.61 (0.064)	0.15	0.073 (0.057)	0.028 (0.012)	0.30
14	0.70 (0.070)	0.79 (0.038)	0.45	0.024 (0.014)	0.017 (0.007)	0.77
26	0.72 (0.064)	0.53 (0.055)	0.04	0.091 (0.030)	0.057 (0.022)	0.45
Mean	0.72 (0.006)	0.64 (0.042)	0.14	0.062 (0.011)	0.032 (0.007)	0.008
Willamette Valley (VAL)						
12	0.60 (0.039)	0.27 (0.037)	0.0002	0.14 (0.043)	0.051 (0.021)	0.14
17	0.65 (0.042)	0.13 (0.027)	0.0002	0.15 (0.027)	0.040 (0.014)	0.005
20	0.78 (0.028)	0.44 (0.028)	0.0002	0.33 (0.016)	0.20 (0.043)	0.007
134	0.17 (0.105)	0 (0)	—	0 (0)	0 (0)	—
153	0.69 (0.042)	0.076 (0.051)	0.0006	0.14 (0.056)	0 (0)	—
Mean	0.58 (0.006)	0.19 (0.079)	0.013	0.15 (0.052)	0.057 (0.036)	0.012

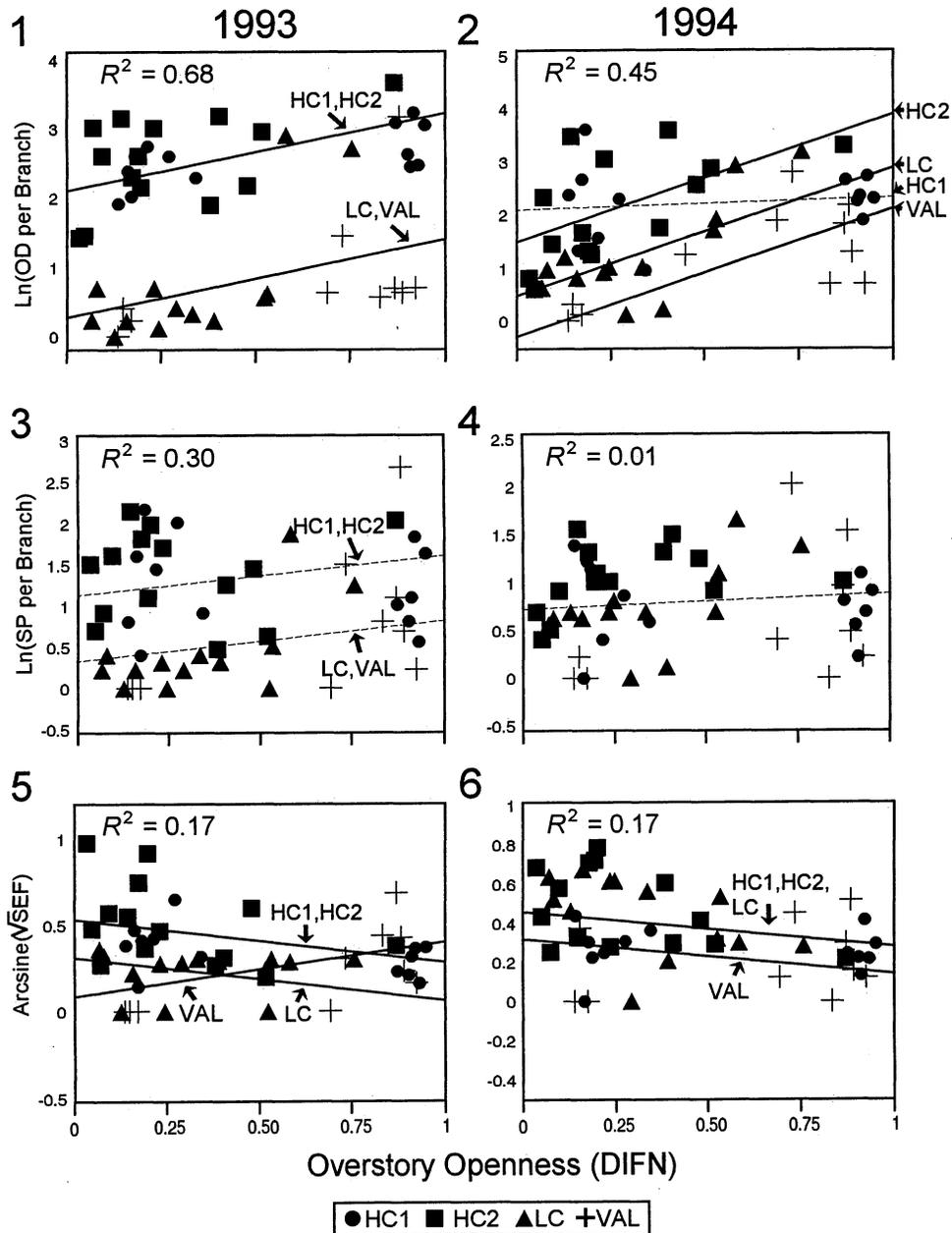
<sup>a</sup> *P* values for differences in means calculated by Wilcoxon rank sum test for comparisons within trees, and the Wilcoxon signed-rank test for overall comparisons within sites.

TABLE 5. The effect of bagging to exclude vertebrates on seed development efficiency. Four branches per tree were covered with nylon mesh bags in July, and four control branches were not bagged. Values in parentheses are 1 SE.

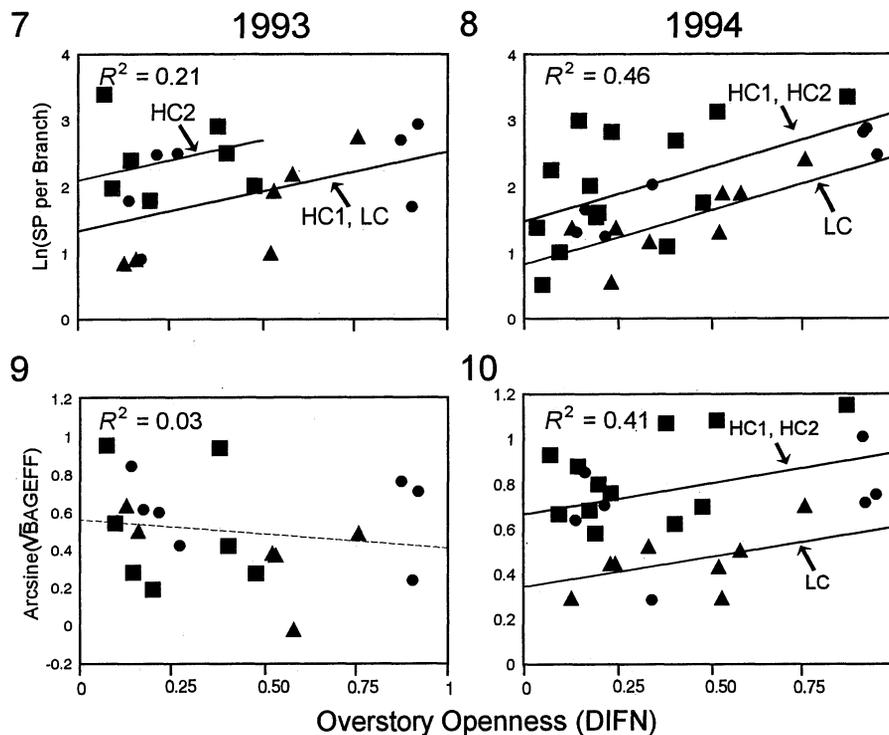
Site	N <sup>a</sup>	1993			N	1994		
		Bagged	Control	P <sup>b</sup>		Bagged	Control	P
HC1	7	0.65 (0.090)	0.17 (0.057)	0.0005	9	0.64 (0.034)	0.11 (0.029)	0.0001
HC2	7	0.69 (0.059)	0.27 (0.081)	0.0049	15	0.70 (0.040)	0.10 (0.022)	0.0001
LC	7	0.46 (0.057)	0.19 (0.064)	0.0056	10	0.46 (0.051)	0.17 (0.033)	0.0001
VAL	3	0.30 (0.110)	0.22 (0.076)	0.29	5	0.29 (0.078)	0.14 (0.055)	0.078

<sup>a</sup> N = number of trees.

<sup>b</sup> P values for differences in means calculated by paired t test.



Figs. 1–6. Regressions of ovule development (OD), seed production (SP), and seed efficiency (SEF) vs. overstory openness (DIFN). Each point represents mean values for individual trees. Slopes of broken lines are not significantly different from 0. Lines were combined for different sites if slopes and intercepts were not significantly different. Terms are defined in Table 2.



Figs. 7–10. Regressions of seed production (SP) of branches bagged to exclude predators and bagging effect (BAGEFF, difference in seed development efficiency between bagged and unbagged branches) vs. overstory openness. Each point represents average values for individual trees. Broken lines have slopes that are not significantly different from 0. Lines were combined for different sites if slopes and intercepts were not significantly different. Site VAL was excluded from this analysis because of insufficient data (see text).

VAL and LC, but for less than half of the observed ovule attrition at HC1 and HC2 (Table 3, Fig. 11). In contrast, predation was a relatively minor source of ovule attrition at LC and VAL in both years, while it accounted for approximately half of the mortality at HC2 (Table 3, Fig. 11).

The patterns also varied somewhat between years. For example, ovule development efficiency was significantly higher in 1994 than in 1993 at LC and VAL but higher in 1993 at HC2 and not significantly different between years at HC1 (Table 3). However, seed efficiency did not differ between years except at site LC (Table 3), indicating that significant improvements in ovule development did not consistently translate into large improvements in seed production.

## DISCUSSION

Attrition of ovules for *T. brevifolia* trees in western Oregon was due to a variety of causes. Pollination success, the amount of available resources (as indexed by overstory canopy), and predation of ovules by vertebrates were some of the factors responsible for limiting seed production. There was an interaction between predation and overstory. Furthermore, the importance of each factor varied at different sites and in different years.

**Pollination**—Lack of pollination may be responsible for much of the early season attrition of ovules. Exclusion of pollen almost always resulted in failure of ovules to develop, and the morphology of ovules from which pol-

len was excluded was indistinguishable from that of the majority of undeveloped ovules on unbagged branches during the same period (personal observation).

Supplemental pollination resulted in approximately doubled mean seed efficiency per tree at both sites. These results agree with those of Allison (1990), who found a significant increase in *Taxus canadensis* Marsh. seed production due to pollen supplementation. Increased seed efficiency apparently did not come at the expense of seed efficiency on control branches, as these did not differ from seed efficiency of untreated trees, or from seed efficiency on the same branches in the previous year.

Ovule development efficiency in the present study was not increased beyond 80% by hand-pollination, even with five hand-pollinations over a 3-wk period. Furthermore, ovule development efficiency was not significantly improved by supplemental pollination on four of ten trees. This suggests that other factors, such as resource limitation, genetic load, or damage by insects, frost, or pathogens were also important in causing early attrition. Methodological problems might also explain the failure of some supplementally pollinated ovules to develop. These include lack of receptivity at the time of pollen application, incompatibility with pollen used in pollen supplementation, clogging of the micropyles with heavy pollen loads, or physical damage to the ovules resulting from pollen application (Young and Young, 1992). Finally, damage by phytophagous mites [principally *Cecidophyopsis psilaspis* Nalepa (Acari: Eriophyidae) and *Pentamerismus taxi* Haller (Acari: Tenuipalpidae)] caused

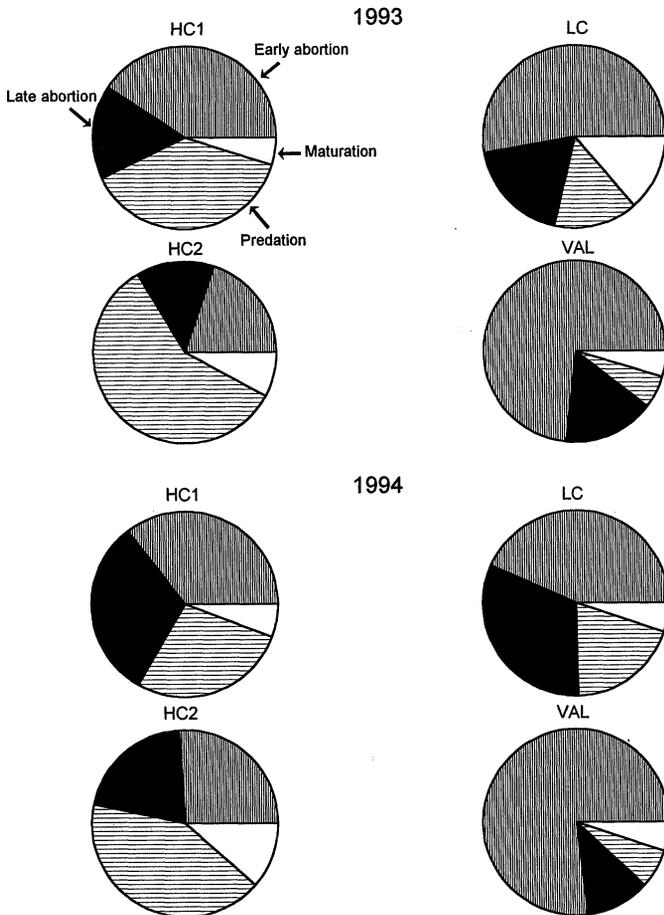


Fig. 11. Fates of ovules: early abortion, ovules that did not begin expanding by July; late abortion, ovules that aborted after July; predation, developing ovules that were removed by vertebrates; maturation, ovules that developed into mature seed.

swelling of immature ovules and may have caused non-developing ovules to be confounded with developing ovules. This problem was particularly severe for tree 14 at the HC1 site.

Because of inadequate replication, it was not possible to examine interactions between the effects of supplemental pollination and overstory canopy. However, ovule development efficiency was not associated with overstory canopy in either year (data not shown). Furthermore, the density of males and average pollen production in the vicinity of each female were not consistently associated with ovule development efficiency (DiFazio, 1996). Pollination success can be affected by many factors, including weather, microclimate, prevailing wind, genetic load, and maternal effects (Charlesworth, 1989; Whitehead, 1983; Roach and Wulff, 1987). However, seed efficiency was low for all trees examined, even with supplemental pollination. Therefore, because pollen limitation was not the primary factor limiting seed production at these sites, detailed characterization of pollination success was beyond the scope of this study.

**Predation**—Bagging of branches to exclude vertebrates resulted in increased seed development efficiency,

indicating that predation was a significant source of ovule attrition. The main predator of ovules observed in this study was Townsend's chipmunk (*Tamias townsendii*). It was common throughout the study area and was observed to destroy ovules at all sites. *T. townsendii* forages by hanging from the underside of branches and removing ovules, biting a hole in the poisonous integument, and removing the ovule contents. Large numbers of ovule and seed integuments with bite holes were found beneath all productive trees in this study. There is also substantial rodent predation of seeds of other yew species, including *Taxus baccata* L. (Hulme, 1996) and *T. canadensis* (Wilson, Buonopane, and Allison, 1996).

Removal and dispersal of mature seeds might also have accounted for some of the difference in seed development efficiency between bagged and unbagged branches. However, errors in estimates of seed production were minimized by including empty receptacles in estimates of seed production. Receptacles persisted for up to several weeks following seed removal (personal observation), and spontaneous abscission of the strobilus at the base of the receptacle was relatively rare: 82% of 754 seeds produced on bagged branches in July 1993 were still attached to the branches in October.

**Overstory**—Ovule development was positively associated with DIFN at all sites in both years except for HC1 in 1994. Ovule production followed the same pattern (DiFazio, Vance, and Wilson, 1997). This positive relationship suggests that resource availability was important in setting the upper limit on seed production in these *T. brevifolia* populations. Differences in DIFN arose from past removal of overstory canopy. In addition to increased light levels, canopy removal can also lead to decreased competition for soil nutrients and water (Horn, 1971). Controlled experiments would be required to elucidate the mechanisms of increases in ovule production.

Shading limits seed production in a number of species (Silen, 1973; Owens and Blake, 1985; Schutte Dahlem and Boerner, 1987; Devlin, 1988; Dale and Causton, 1992; Niesenbaum, 1993), yet seed production in this study did not significantly vary with DIFN. *T. brevifolia* trees in clearcuts in Idaho had lower seed production than trees under intact canopy (Crawford, 1983). A possible explanation for these discrepancies is that *T. brevifolia* requires several years of acclimation following overstory removal. Crawford (1983) examined trees in the year following overstory removal; trees were examined 3–30 yr after overstory removal in the present study. However, ovule production, ovule development, and growth were all positively correlated with overstory openness for trees used in this study, suggesting that tree vigor increased with overstory openness (DiFazio, Vance, and Wilson, 1997).

A more likely explanation for the lack of relationship between DIFN and seed production is that there was an interaction between DIFN and predation rates. In fact, seed production on bagged branches was positively associated with DIFN, and regressions of bagging effect vs. DIFN were significant and positive in 1994. This indicates that predation rates increased under open conditions. A similar phenomenon might account for the negative association between overstory and seed production

observed by Crawford (1983). Increased predation for open-grown trees might be due to the presence of a greater number of predators on open sites, or greater attractiveness of open-grown trees to predators due to greater visibility or larger fruit crops (Thompson and Willson, 1978; Ehrlén, 1996).

This study points out the importance of simultaneously examining several potential sources of attrition at different sites over several years. Few studies have taken the effects of predation into account when examining the importance of pollen and resource limitation. A common practice has been to exclude from consideration all fruits or seeds that showed evidence of predation (e.g., Gorchov, 1988; Zimmerman and Pyke, 1988; Vaughton, 1991; Campbell and Halama, 1993; but see Ehrlén, 1992). It is important to be cautious in drawing broad conclusions from narrowly focused studies performed at a few sites under relatively uniform conditions. Limitations to seed production can vary markedly among sites and years. For example, if the present study had been performed solely at site HC2, conclusions about the relative importance of pollen vs. predation in accounting for low seed-ovule ratios would have been quite different than if the study had been performed only at VAL.

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