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Flower and Fruit Production of Understory Shrubs in Western Washington and Oregon

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Abstract

We observed flower and fruit production for nine understory shrub species in western Washington and Oregon and examined the relationships between shrub reproductive output and plant size, plant age, site factors, and overstory density to determine the factors that control flowering or fruiting in understory shrubs. In Washington, 50 or more shrubs or microplots (for rhizomatous species) were sampled for each of eight species. The variables examined were more useful for explaining abundance of flowers or fruit on shrubs than they were for explaining the probability that a shrub would produce flowers or fruit. Plant size was consistently the most useful predictor of flower/fruit abundance in all species; plant age was also a good predictor of abundance and was strongly correlated with plant size. Site variables (e.g., slope) and overstory competition variables (e.g., presence/absence of a canopy gap) also helped explain flower/fruit abundance for some species. At two Oregon sites, the responses of five species to four levels of thinning were observed for 2-4 yr (15± shrubs or microplots per treatment per year). Thinning increased the probability and abundance of flowering/fruiting for two species, had no effect on one species, and responses for two other species were positive but inconsistent between sites or from year to year. We believe reducing overstory density or creating canopy gaps may be useful tools for enhancing shrub size and vigor, thus, increasing the probability and abundance of fruiting in some understory shrub species.

Introduction

Understory shrubs in Pacific Northwest conifer forests produce fruit and seeds that are consumed by birds and mammals or harvested by humans for medicinal use, floral greens, dyes, nuts or fruit (Vance et al. 2001). Understory shrubs also contribute to forest vertical structure, thereby increasing habitat complexity and food resource diversity, factors that are generally associated with high faunal species richness (Brokaw and Lent 1999). Despite their ecological and economic importance, there has been little investigation of the productivity or general ecology of special forest product species (Molina et al. 1997) or other understory shrubs in the northwest. By understanding the factors that affect shrub reproductive output, forest and wildlife managers could design management prescriptions to enhance fruiting for wildlife populations or human use.

Observed variation in plant reproductive output has been attributed to the effects of plant size in some perennial plants (Piper 1989, Herrera 1991,

1998), weather (Selås 2000), previous reproductive output (Samson and Werk 1986, Piper 1989), and the availability of pollen (Allen 1986), light (Niesenbaum 1993), and water (Herrera 1991) have also been cited as important variables that influence reproductive success. Recent studies in the Pacific Northwest suggest that overstory density or light availability, in particular, may strongly affect vegetative expansion, clone development, or reproduction from seed for Indian plum (*Oemleria cerasiformis*) (Antos and Allen 1999), Oregongrape (*Berberis nervosa*) (Huffman and Tappeiner 1997), Pacific yew (DiFazio et al. 1997), salal (*Gaultheria shallon*) (Bunnell 1990, Huffman et al. 1994, Tappeiner et al. 2001), salmonberry (*Rubus spectabilis*) (Tappeiner et al. 2001), and vine maple (*Acer circinatum*) (O'Dea et al. 1995). On the other hand, extrinsic factors (e.g., resource availability) may influence reproduction only indirectly through their effects on shrub size and vigor (Samson and Werk 1986, Piper 1989).

In a region with an active forest products industry, there is also a need to understand more about the effects of thinning and other silvicultural

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practices on understory shrub reproduction. Thinning encourages regeneration of shrub understories, either through clonal development and rhizome extension (Tappeiner et al. 2001, Huffman et al. 1994, O’Dea et al. 1995) or through seedling establishment (Tappeiner and Zasada 1993, Huffman et al. 1994). Less is known about the response of shrub fruit production following canopy manipulation. Scientists and forest managers have hypothesized that decreases in overstory density may promote fruit production (Molina et al. 1997, Brokaw and Lent 1999), presumably because of increased light and resource availability. Tests of this hypothesis are lacking.

To help determine important factors affecting sexual reproduction in northwest shrubs, we conducted two related observational studies on nine shrub species native to northwest lowland conifer forests: vine maple, Oregongrape, California hazelnut (*Corylus cornuta* ssp. *californica*), salal, oceanspray (*Holodiscus discolor*), Indian plum, red elderberry (*Sambucus racemosa* ssp. *pubens* var. *arborescens*), evergreen huckleberry (*Vaccinium ovatum*), and red huckleberry (*Vaccinium parvifolium*). We studied flower production for all nine species and in addition, we observed fruit production in three species. We concentrated our efforts on flower production because it is the prerequisite for fruit production and because it is less variable, and therefore easier to study, than fruiting patterns.

The first study, based in western Washington, provided descriptive data on the forest environments and plant characteristics for eight shrub species, and examined the relationships among those variables and flower or fruit production for a single year. We addressed two specific questions: (1) what factors influence the probability that plants will flower or fruit, and (2) which measured variables are useful for explaining the abundance of flowers or fruit produced?

The second study, conducted in western Oregon, examined (1) year-to-year variation in flower or fruit production for five shrub species, and (2) the effects of four overstory treatments on flower or fruit production. The Oregon study complements of the Washington study by extending the period of observation to multiple years and by examining shrub response to forest

management. By pairing these related studies into a single body of work, we aim to provide a more comprehensive discussion of the factors that influence flower and fruit production in understory shrubs common to conifer forests west of the Cascades in Oregon and Washington.

Washington Study Methods

Study Area

Washington study sites were located on the Olympic Peninsula and south Puget Sound region of western Washington. Shrubs were sampled primarily in Capitol State Forest, Olympic National Forest, Fort Lewis Military Reservation, and a private commercial forest on the Olympic Peninsula. Sites included a range of topographic, soil, precipitation, and forest conditions.

Shrub and Site Measurements

Differences in clonal vs. non-clonal growth-form required the use of two sampling approaches. Oregongrape and salal were treated as clonal patches and were sampled with a 0.5 m x 0.2 m microplot randomly placed within a patch of the target species. All stems of the target species in the microplot were assumed to be genetically identical. Subsequent shrub measurements applied to the collective stems within a microplot. Although vine maple also grows in clonal patches, a single basal clump was selected from a patch and treated as an individual plant. All other species were sampled as individual plants.

For both the microplot and individual shrub approach, samples were spaced a minimum of 25 m apart. Each species was sampled within its predicted flowering period (Table 1) in spring and summer 1999. Salal was sampled at one site while flowering and at several sites while fruiting. The data from the flowering and fruiting samples were analyzed separately.

Size and Age Factors

Plant size and age characteristics were measured for each selected shrub or clonal patch. Basal diameter (BSD), diameter at 1.3 m (DBH), total height (HT), and crown depth (CD) were measured in the field. Crown depth was measured as the distance between the lowest and highest live foliage or bud. Crown percent (CP) was the ratio of HT to CD. An index of stem volume (VOL) was calculated as $HT * BSD^2$. When multiple stems

TABLE 1. Comparison of plant, flower, and fruit characteristics for nine understory shrub species in Pacific Northwest conifer forests. Information compiled from Hitchcock and Cronquist (1973), Pojar and MacKinnon (1994), and USDA, Fire Effects Information System (2003).

Name	Form	Flower	Fruit	Mode of reproduction	
				Normal	After damage
Vine maple	Erect to prostrate deciduous shrub to 9 m tall	Perfect in corymbs; April-June	Double samara; wind dispersed; Sept-Oct	Seed, layering	Sprouts
Oregongrape	Low-growing, rhizomatous, evergreen shrub; <1 m tall	Perfect; on racemes, up to 20 cm long; April-June	Berry; dispersed by birds, mammals; July-Sept	Rhizomes, seed secondary	Rhizomes
Hazelnut	Erect, deciduous shrub; to 6 m tall	Imperfect, monoecious; apetalous catkins; Jan-March	Nut; dispersed by birds, mammals; Aug -Oct	Seed, layering	Sprouts
Salal	Erect to spreading, rhizomatous, evergreen shrub; to 3 m tall	Perfect; on racemes; May-July	Fleshy capsule; dispersed by birds, mammals; Aug-Oct	Rhizomes, rarely seed	Rhizomes, sprouts
Oceanspray	Erect to spreading, deciduous shrub; to 6 m tall	Perfect on panicles, up to 30 cm; May-July	Achene; wind dispersed; Aug-Sept	Seed	Sprouts
Indian plum	Erect, deciduous shrub; to 3 m tall	Imperfect dioecious; on racemes; early spring	Drupe; dispersed by birds, mammals; June-July	Seed	Sprouts
Red elderberry	Erect, deciduous shrub; to 6 m tall	Perfect; on cymes; April-July	Drupe; dispersed by birds, mammals; July-Aug	Seed	Rhizomes, sprouts
Evergreen huckleberry	Erect, evergreen shrub; to 4.5 m tall	Perfect; clusters of 3-10 in leaf axils; April-Aug	Berry; dispersed by birds, mammals; July-Sept	Seed	Sprouts
Red huckleberry	Erect, rhizomatous, deciduous shrub; to 4.5 m tall	Perfect; solitary; April-June	Berry; dispersed by birds, mammals; July-Sept	Seed	Rhizomes, sprouts

were present on non-rhizomatous shrubs, all measurements except DBH were taken from a single stem that appeared typical for that shrub. Diameter was measured for both the typical and largest stem. Age was measured by counting growth rings on harvested typical stems.

For Oregongrape and salal, age and DBH were not measured. Basal diameter was measured for the largest stem per microplot. One HT and CD measurement was made of a visually determined typical shoot.

Flower or Fruit Abundance

The technique for counting or estimating flower or fruit production differed by species, according to shrub growth-form and flower or fruit abundance.

For hazelnut, evergreen huckleberry, and red huckleberry, each flower on the typical stem was counted, and the number of flowers per stem was multiplied by the number of stems per shrub to obtain a flower-per-shrub estimate. Because of the large number of flowers per stem for Indian plum and elderberry, flower abundance per stem was estimated by expanding mean number of flowers in a subsample of inflorescences by number of inflorescences per typical stem. Total flower abundance was calculated by multiplying estimated flowers per stem by number of stems per shrub. For vine maple, count of flowers on a typical stem per clump was used as an index of vine maple flower production. For Oregongrape and salal, flower or fruit counts were expanded

to reflect the number of flowers/fruits per microplot, rather than the number per stem. Flowers were counted in a subsample of inflorescences and the subsequent mean expanded by the number of inflorescences per microplot.

Site Factors

Slope, aspect, and percent light were recorded at each shrub or microplot. Available water capacity for each series was interpolated for the top 75 cm of soil using the MUIR database (USDA Natural Resources Conservation Service 1994). Site precipitation data were from the USDA NRCS PRISM model (Daly and Taylor 2000). Percent light was calculated as the amount of light reaching the target shrub divided by the total available light. Readings were taken on clear days within ± 2 hr of solar noon. For Oregongrape and salal, light readings were recorded using a Decagon AccuPAR positioned in each microplot at a height slightly greater than the tallest stem of the target species. For all other shrubs, a LiCor Quantum Line sensor and LI-1400 data recorder or Decagon AccuPAR (modified to permit elevating the sampling head), were similarly used to record light readings at the apex of each shrub's foliage. Total available light was measured in the nearest large opening using a Quantum Line sensor.

Growing season precipitation was also determined for four weather stations in western Washington close to the locations of the sampled shrubs (Western Regional Climate Center 2003). Monthly precipitation was evaluated for the year prior to and the year of the flower or fruit observations and compared to 10-yr average values.

Overstory Competition Factors

The local overstory competition around each shrub or microplot was characterized by measuring the relative position, canopy height, and total height for each competing tree. Trees were considered competitors when they were located at a distance less than their own height from the target shrub or microplot. Overstory density indices derived from these data included counts of total competitors (C 1), competitors that had driplines < 5 m away from the target shrub (C2), competitors that had crowns overlapping the target shrub (C3), competitors on the south side of the shrub (C4), and conifer competitors (C5). The presence/absence of a canopy gap (GAP) above each shrub or microplot was also

recorded. A canopy opening was only considered a gap when it was as large in diameter as the height of the dominant overstory surrounding the target shrub or microplot.

Data Analysis

Mean and range were generated by species using the MEANS and UNIVARIATE procedures of the Statistical Analysis System (SAS Institute, Inc. 1988). Summary statistics were generated separately for shrubs that produced flowers or fruit and shrubs that did not produce. Graphical analysis (i.e., scatter diagrams, boundary line analysis) was used to examine size and age thresholds to flowering.

We used linear regression to identify plant size, plant age, site, and competition factors that explained variability in square-root transformed flower or fruit counts. If plant size was the best predictor of flower/fruit abundance for a species, then we ran linear regression on residuals from that one-parameter size model, using site and competition factors as explanatory variables. In other words, we examined site and competition factors as predictors of flower/fruit abundance, after accounting for plant size. All models were fit using the REG procedure, STEPWISE selection option, in SAS (SAS Institute Inc. 1991). Following stepwise selection, models were improved by eliminating collinear variables and influential observations.

If the presence of canopy gaps proved significant in linear models for a species, then that relationship was further investigated using a Pearson chi-square test for association. Associations were tested between the binary variable, GAP, and size and flower production variables. New categorical size and flower variables were generated by reference coding each variable observation as 0 or 1, depending on whether the observation was above or below the variable's mean value. Because sample sizes were small, exact probability values were generated instead of asymptotic values. Tests were performed in SAS using the FREQ procedure, EXACT statement, PCHI option (SAS Institute, Inc. 1988).

Binary logistic regression models were fit to identify variables that were useful in explaining the probability of flower production (i.e., yes or no) in vine maple, Oregongrape, and evergreen huckleberry, and fruit production in salal. Again,

plant size and age, site, and overstory competition were entered as explanatory variables. Models could not be fit for hazelnut, salal (except fruit), Indian plum, elderberry, or red huckleberry, because of an insufficient sample size for plants that did not flower. The LOGISTIC procedure and STEPWISE option (SAS Institute, Inc. 1999) were used to generate models. The probability value associated with the Wald chi-square statistic was examined to determine the significance of model variable parameters. Odds ratios indicated the magnitude of likelihood that shrubs would flower relative to a significant explanatory variable. Significance levels for all model statistics were set at $P = 0.05$.

Washington Study Results

Shrub Characteristics

In all species, a majority (63-98%) of plants produced flowers or fruit (Table 2). Over 90% of salal, elderberry, and red huckleberry shrubs produced flowers. All species except Oregongrape, hazelnut, and salal produced, on average, more than 1000 flowers per shrub. Elderberry produced, on average, more than 10,000 flowers per shrub.

Shrubs flowered at a wide range of ages for most species, with no indication that production decreased beyond a threshold age. Indian plum, elderberry, and red huckleberry flowered on stems as young as 1-2 yr; however, because stems growing

TABLE 2. Mean (and range) of size characteristics by species for plants that produced or did not produce flowers in western Washington conifer forest understories.

Species	n	Production	Age	BSD (cm)	Height (m)	No. stems
Shrubs that produced flowers/fruit						
Vine maple	33	1565 (1-6834) ¹	30 (10-64)	5.5 (2.2-7.6)	6.2 (2.1-11.7)	9 (1-28)
Oregongrape	33	86 (1-252) ²	- ³	0.8 (0.4-1.4)	0.5 (0.2-0.9)	- ³
Hazelnut	44	705 (10-3744) ⁴	10 (4-26)	3.5 (2.0-7.8)	4.5 (2.2-10.4)	14 (2-52)
Salal (flower)	88	34 (1-149) ²	- ³	1.1 (0.4-3.0)	1.1 (0.3-2.5)	- ³
Salal (fruit)	95	22 (2-63) ²	- ³	0.7 (0.2-2.0)	0.6 (0.2-1.3)	- ³
Indian plum	38	2911 (12-13410) ⁴	8 (1-19)	2.3 (1.0-4.2)	3.2 (1.7-5.8)	4 (1-12)
Red elderberry	50	10875 (144-197064) ⁴	6 (2-13)	3.4 (1.1-9.4)	3.2 (1.5-5.8)	3 (1-7)
Evergreen huckleberry	32	1871 (3-14263) ⁴	10 (4-24)	1.8 (0.8-3.2)	1.8 (0.8-2.6)	8 (1-25)
Red huckleberry	51	1642 (8-8900) ⁴	8 (2-22)	1.9 (0.6-3.3)	1.9 (0.5-3.2)	4 (1-12)
Shrubs that did not produce flowers/fruit						
Vine maple	18	-	26 (14-49)	5.9 (2.9-10.2)	5.1 (2.2-10.1)	9 (1-35)
Oregongrape	19	-	- ³	0.8 (0.5-1.2)	0.5 (0.2-1.0)	- ³
Hazelnut	8	-	7 (3-16)	2.5 (0.9-3.9)	2.9 (1.3-5.0)	8 (2-12)
Salal (flower)	2	-	- ³	- ⁵	- ⁵	- ⁵
Salal (fruit)	29	-	- ³	0.5 (0.2-0.9)	0.5 (0.2-0.8)	- ³
Indian plum	8	-	7 (4-10)	2.1 (0.7-3.3)	3.0 (1.3-5.0)	4 (1-10)
Red elderberry	2	-	- ⁵	- ⁵	- ⁵	- ⁵
Evergreen huckleberry	18	-	8 (2-31)	1.5 (0.7-3.5)	1.5 (0.7-2.5)	8 (2-31)
Red huckleberry	4	-	4 (3-5)	1.9 (0.5-5.0)	1.1 (0.7-1.2)	3 (1-5)

¹ Flower index: number of flowers per selected "typical" stem.

² Number of flowers or fruits per 50 cm x 20 cm microplot.

³ Age and number of stems not measured for Oregongrape or salal.

⁴ Number of flowers per shrub.

⁵ Not enough non-flowering observations to calculate meaningful mean values.

from multi-stemmed shrubs can originate in different years, the plants may have been older than stem samples indicated. Vine maple exhibited a more obvious minimum age threshold to flowering; no flowering was observed on stems < 10 yr in age. Flowering was observed on vine maple stems up to 64 yr in age (the oldest in the sample). Hazelnut and both huckleberry species also flowered at ages > 20 yr.

Each species was capable of flowering at a wide range of plant diameters and heights, but some species exhibited minimum plant size thresholds for flowering. Examination of scatter diagram boundary lines was helpful in clarifying these relationships. For example, maximum production increased as hazelnut plants exceed BSD of 2.0 cm or heights of 2.5 m (Figure 1). In other species, similar minimum thresholds to flower production were also observed for basal diameter (Indian plum 1.5 cm), DBH (vine maple 3.0 cm; red elderberry 1.25 cm), height (red huckleberry 1.25 m), or crown depth (salal 0.5 m).

All of the non-rhizomatous species were observed in both single-stemmed and multi-stemmed forms, except for hazelnut, which was never observed as a single-stemmed shrub. Hazelnut shrubs consisted of up to 52 stems. Mean stem count was highest for hazelnut (14), followed by vine maple (9), and evergreen huckleberry (8).

Size and Age Effects

Probability of Flowering/Fruiting

For salal and evergreen huckleberry, size variables were useful predictors of the probability of fruiting or flowering. For salal, logistic model parameter estimates indicated that the probability of fruiting increased significantly with crown depth and height. For evergreen huckleberry, the probability of flowering increased significantly with largest stem diameter. No size variables were significant for vine maple or Oregon grape.

Flower/Fruit Abundance

Size variables were useful predictors of flower/fruit production for all species. Stepwise linear model selection, of size variables only, produced models that explained $\geq 30\%$ of the variability in production for hazelnut, Indian

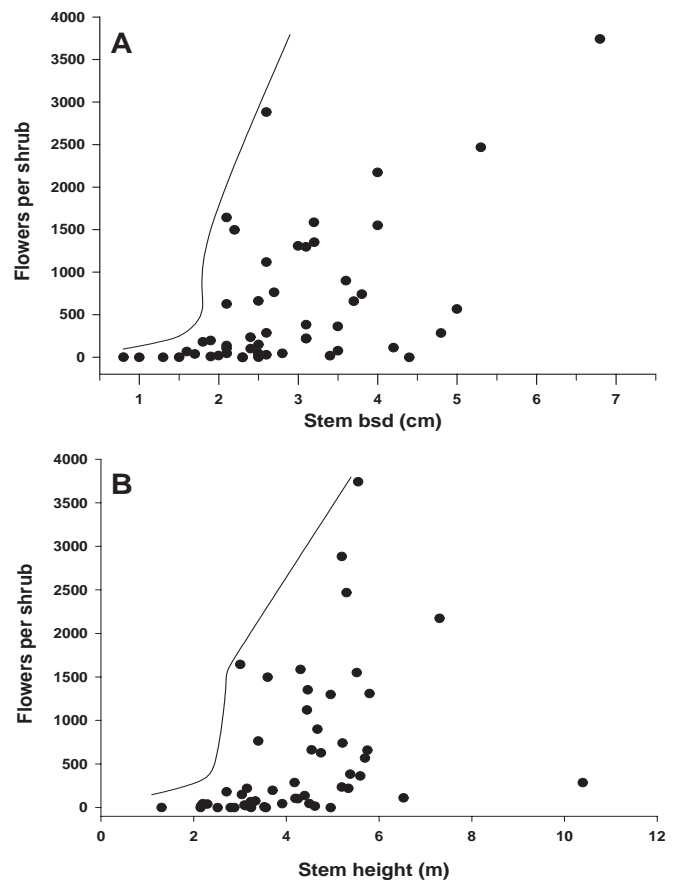


Figure 1. Flower abundance vs. average stem basal diameter (a) and mean stem height (b) for 44 hazelnut shrubs sampled in western Washington. Boundary lines show apparent minimum plant size thresholds to flower production.

plum, red elderberry, and red. Although significant for some species, age was dropped from linear models because of collinearity with shrub size. Age was never as strongly related to flower production ($r^2 = 0.06-0.26$) as the best size variable. However, there were strong correlations between shrub age and size indicating that age may influence production indirectly through its effect on shrub size. Age was most strongly correlated with stem diameter for hazelnut, salal (fruit), Indian plum, and red elderberry; with stem height for vine maple and red huckleberry; with crown depth for Oregon grape and salal (flowers); and with number of stems for evergreen huckleberry.

Site and Competition Effects

Probability of Flowering/Fruiting

Site variables were not good predictors of the probability of flowering or fruiting for most species. Overstory conifer density was the only

TABLE 3. Best statistically significant regression equations for the square root of fruit/flower production (\sqrt{P}) vs. plant size (one-parameter models) or vs. plant size, site factors, and overstory competition (multi-parameter models) for eight species in Washington study. Variable abbreviations are given in text. NS: No site or competition variables were significant.

Species	One-parameter model	r^2	Multi-parameter model	r^2
Vine maple	$\sqrt{P} = 14.6 + 3.1$ (HT)	0.16	$\sqrt{P} = 14.6 + 3.1$ (HT) - 0.5 (Slope)	0.24
Oregongrape	$\sqrt{P} = 2.2 + 0.1$ (CP)	0.15	$\sqrt{P} = 1.3 + 0.1$ (CP) + 0.1 (Slope)	0.21
Hazelnut	$\sqrt{P} = -5.1 + 7.7$ (BSD)	0.32	NS	--
Salal (flower)	$\sqrt{P} = 4.1 + 0.05$ (CP)	0.13	NS	--
Salal (fruit)	$\sqrt{P} = 3.6 + 1.3$ (BSD)	0.08	NS	-
Indian plum	$\sqrt{P} = -12.6 + 24.3$ (BSD)	0.30	$\sqrt{P} = -1.7 + 25.0$ (BSD) + 0.6 (Light%) - 6.6 (C2)	0.52
Red elderberry	$\sqrt{P} = 8.1 + 39.4$ (DBH)	0.40	$\sqrt{P} = 27.4 + 39.4$ (DBH) + 17.3 (DBH * GAP) - 3.4 (DBH * C1)	0.52
Evergreen				
huckleberry	$\sqrt{P} = 17.8 + 0.03$ (VOL)	0.23	$\sqrt{P} = 5.7 + 0.03$ (VOL) + 4.2 (C5) - 10.6 (C3)	0.41
Red huckleberry	$\sqrt{P} = -7.5 + 21.2$ (HT)	0.39	NS	--

significant site variable included in logistic regression models. Results for Oregongrape and evergreen huckleberry indicated a significant positive relationship between number of surrounding conifers (C5) and probability of flowering.

Flower/Fruit Abundance

Inclusion of site variables (e.g., slope, aspect, soil texture, moisture index) into linear models rarely improved model fit for explaining production. The exceptions were in vine maple and Oregongrape, where the addition of slope improved models modestly (Table 3). The regression coefficient for slope for vine maple was negative, but for Oregongrape, the coefficient was positive.

Overstory density indices or other overstory variables further improved linear model fit for Indian plum, elderberry, and evergreen huckleberry (Table 3). For Indian plum, flowering increased with percent light and decreased with the number of competitors within 5 m of the measured shrub (C2).

Elderberry flower production was related to DBH, GAP, and overstory density (Table 3). Linear regression indicated a positive relationship between DBH and GAP. The chi-square test for association confirmed a significant relationship. The linear regression model also indicates a negative relationship between elderberry DBH and the number of surrounding trees (C 1). Heavy-flowering shrubs were present more frequently in gaps than under intact canopy (Figure 2).

Evergreen huckleberry flower production increased

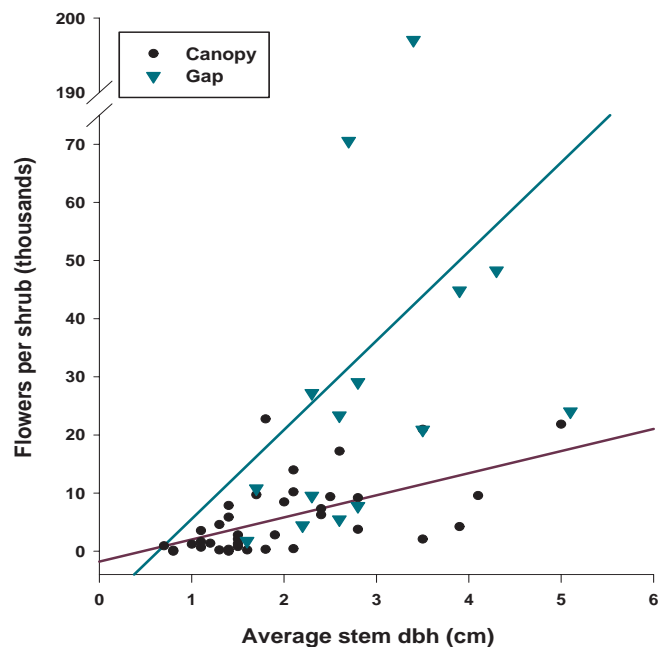


Figure 2. Flower abundance vs. average stem diameter for 50 red elderberry shrubs under intact canopy and canopy gaps in western Washington. The solid line indicates the regression relationship for shrubs under intact canopy and the dashed line indicates the relationship in canopy gaps.

as conifer overstory density (C5) increased. Conversely, evergreen huckleberry flower production decreased as more tree crowns overlapped (C3) huckleberry shrubs.

Regression on residuals revealed that site and competition explained additional variability in flower/fruit abundance after accounting for plant size. Accounting for HT in vine maple, C5 ($r^2 = 0.19$), GAP ($r^2 = 0.16$), and slope ($r^2 = 0.13$) were useful predictors of flower/fruit abundance. Moisture ($r^2 = 0.13$) was significant in hazelnut, after accounting for BSD. Percent light ($r^2 = 0.16$) and

of competitors < 5 m away (C2) ($r^2 = 0.15$) were significant for Indian plum, after accounting for BSD. For red elderberry, GAP ($r^2 = 0.18$) and C5 ($r^2 = 0.11$) were significant, after accounting for DBH. No site or competition variables were significant for Oregongrape, salal, evergreen huckleberry, or red huckleberry.

Oregon Study Methods

Study Area

The two Oregon study sites, Bottom Line (BL) and O. M. Hubbard (OM), were located in the low coastal mountains that drain to the Umpqua River. Each 80-ha site consisted of relatively homogeneous Douglas-fir (*Pseudotsuga menziesii*) stands of age 40-50 yr. The sites were divided into four 20-ha stands randomly assigned to one of four operational thinning treatments: (1) unthinned with ≥ 375 or more trees per ha (tph), (2) light thinning to 300 tph, (3) moderate thinning to 200 tph, and (4) heavy thinning to 100 tph or 0.4-ha openings. Treatments were applied in 1996-1997.

Shrub Measurements

Within each site, suitable patches of Oregongrape and salal, or individual hazelnut, oceanspray, or red huckleberry shrubs were identified and ≥ 15 of the patches/shrubs were randomly selected per treatment unit. Fewer than 15 patches of salal and Oregongrape were available for some treatment units, particularly at OM. For Oregongrape and salal, a suitable patch was a minimum 3 m x 3 m area, having $\geq 50\%$ of cover in the target species. Oregongrape and salal were sampled in 4 m² microplots. The unit of observation for hazelnut, oceanspray, and red huckleberry was an individual shrub. Logging damage was minimal on sampled shrubs or patches.

Plant size and growth characteristics were measured in 1998 and 1999 at BL and OM for Oregongrape and salal. Size and growth were measured only in 1998 and 1999 at OM for oceanspray and red huckleberry. Flower/fruit production was sampled from 1998-2001 for Oregongrape, salal, and hazelnut but only in 2000-2001 for oceanspray and red huckleberry.

For Oregongrape and salal, percent cover of the target species within a microplot was estimated by two

observers and recorded as an average. Mean HT of cover and the number of target shrub stems were also recorded. The number of new growth whorls was counted for Oregongrape and the number of new stems originating from underground rhizomes or the base of aerial stems was counted for salal. All flower racemes inside a microplot were counted.

For hazelnut, oceanspray, and red huckleberry, shrub measurements included mean HT and BSD of the three largest stems, crown diameter, and number of stems. Crown diameter was recorded as the average of two perpendicular diameter measurements. Total fruits per shrub were counted.

For each site, monthly precipitation during the growing season was determined from the closest weather station for years 1997-2001 (i.e., the year prior to and the years of flower/fruit observations) (Western Regional Climate Center 2003).

Data Analysis

Using the same process described for the Washington study, explanatory linear models of flower or fruit abundance were generated. Models were generated separately for each year and site. Sample sizes were small for some species-site-year combinations. Data from BL and OM were combined to increase sample sizes for Oregongrape and salal. For oceanspray and red huckleberry, size data were only available from 1999 and were used to explain flower or fruit production in 2000 and 2001.

Binary logistic regression models were fit to identify variables that were useful in explaining the probability of flower production (i.e., yes or no) by species, year, and site. The LOGISTIC procedure and STEPWISE option (SAS Institute Inc. 1999) were used to generate models. The probability value associated with the Wald chi-square statistic was examined to determine the significance of model variable parameters. Odds ratios indicated the magnitude of likelihood that shrubs would flower relative to a significant explanatory variable. In addition to plant size, thinning intensity was included as an explanatory variable. Because a given species may have had few plants that actually produced flowers or fruits in a particular year or site, models could not be fit for all species/year/site combinations. The number of observations used in a model was also restricted because size variables were only measured on a subset of observations, and only in certain years.

The relationship between thinning intensity and whether or not shrubs flowered was also investigated using a Pearson chi-square test for association. The association was tested by species, site, and year, but was precluded in certain species-site-year combinations by insufficient observations for years in which shrubs rarely produced. Tests were performed in SAS using the FREQ procedure, EXACT statement, PCHI option (SAS Institute, Inc. 1988). Significant chi-square statistics only indicate that an association exists between thinning intensity and percentage of shrubs that produced flowers/fruit and, therefore, do not yield as much information as logistic regression models. However, because logistic regression models were fit only for the data subsets for which size variables were measured, logistic regression did not always detect associations that were significant according to chi-square tests. Significance levels for all model statistics were set at $P = 0.05$.

Oregon Study Results

Precipitation

Precipitation during May and June near each site was much greater in 1998 than in 1997, 1999, or 2000 (186 mm vs. 90-108 mm for BL and 140 mm vs. 60-

94 mm for OM) (Western Regional Climate Center 2003). Precipitation from July through September did not differ much from year to year.

Shrub Characteristics

The percent of shrubs that produced flowers or fruit varied substantially between sites and from year to year. In 1998, fewer than 20% of Oregongrape or salal shrubs produced racemes at either site. The percent of producers peaked in 1999 for Oregongrape (BL = 58%, OM = 21%) and declined in 2000 and 2001. Most salal shrubs produced in 1999 and 2000 at both sites (69-84%) and at BL in 2001 (84%). Fewer salal shrubs produced in 2001 at OM (39%). The percent of oceanspray shrubs that produced flowers ranged from 46-73% at the two sites in 2000 and 2001, the only years sampled for oceanspray and red huckleberry. The percent of red huckleberry shrubs that produced fruit ranged from 50-96%. A higher percentage of shrubs produced at BL compared to OM for all species in all years.

Size and growth differences in 1999, between shrubs that produced flowers/fruits and those that did not, were minor for red huckleberry, but more notable for Oregongrape, salal, and oceanspray (Table 4). Salal and Oregongrape microplots with raceme-bearing stems had a greater total number of stems than microplots with stems that produced

TABLE 4. Mean (and range) of size characteristics for plants that produced or did not produce flowers by site for four shrub species sampled in western Oregon conifer forest understories.

Species	Site	n	BSD (cm)	HT (m)	Crown diam. (m)	No. stems	Whorls	New Stems
Shrubs that produced flowers/fruit								
Oregongrape	BL	33	—	0.5 (0.3-0.9)	—	34 (7-67)	1 (0-5)	—
	OM	9	—	0.3 (0.2-0.4)	—	23 (5-58)	1 (0-5)	—
Salal	BL	58	—	0.4 (0.1-0.8)	—	59 (13-146)	—	2 (0-28)
	OM	41	—	0.3 (0.1-0.6)	—	87 (11-210)	—	10 (0-50)
Oceanspray	OM	41	2.4 (0.9-5.8)	2.4 (1.0-4.5)	2.6 (0.9-6.6)	8 (1-17)	—	—
Red huckleberry	OM	20	1.5 (0.4-3.1)	1.2 (0.2-2.5)	1.5 (0.6-4.4)	10 (2-49)	—	—
Shrubs that did not produce								
Oregongrape	BL	33	—	0.4 (0.2-0.6)	—	21 (1-48)	1 (0-3)	—
	OM	35	—	0.3 (0.1-0.6)	—	17 (1-76)	1 (0-7)	—
Salal	BL	11	—	0.4 (0.2-0.8)	—	42 (1-65)	—	3 (0-12)
	OM	20	—	0.2 (0.1-0.5)	—	45 (1-250)	—	8 (0-75)
Oceanspray	OM	27	1.5 (0.5-5.1)	1.7 (0.4-5.3)	1.9 (0.4-6.4)	5 (1-18)	—	—
Red huckleberry	OM	18	1.5 (0.4-4.6)	1.3 (0.4-2.3)	1.1 (0.5-3.2)	6 (1-19)	—	—

no racemes. Oceanspray shrubs that flowered had greater basal diameter, height, crown diameter, and number of stems than those that did not.

Size and Age Effects

Probability of Flowering/Fruiting

Size and growth variables were significant in some years for Oregongrape and salal, but in no years for oceanspray and red huckleberry. For Oregongrape, height, cover, and the number of new whorls were positively associated with the probability of producing racemes at BL in 1999. At OM, none of the variables was significant for Oregongrape in any year. For salal the probability of flowering increased significantly with cover at BL in 1998 and OM in 1999 and 2000. A significant positive relationship was also observed with new salal stems at BL in 1998 and 1999.

Flower/Fruit Abundance

Salal flower/fruit production increased significantly as average stem height increased in 1999 ($r^2 = 0.11$) and 2000 ($r^2 = 0.34$), for heavy thinning only. When data from all thinning treatments were combined, no size variables were significant. No size variables were significant for Oregongrape in any year, for any treatment or for thinning treatments combined. Oceanspray and red huckleberry size characteristics were measured only at OM and only in 1999. Oceanspray flower production increased significantly with crown diameter in 1999 ($r^2 = 0.43$), but no size variables were significant in 2000 or 2001. No size variables were significant predictors of fruit abundance for red huckleberry.

Thinning Effects

Probability of Flowering/Fruiting

Chi-square tests showed significant associations between thinning intensity and production outcome for Oregongrape, salal, oceanspray, and red huckleberry for some sites and years. The percentage was usually lowest in the unthinned and highest in the moderate or heavy thinning. The response was most apparent in salal (Figure 3). In 1998, the total percent of microplots with raceme-bearing stems for salal was low and there was no significant association between the four levels of thinning and presence of racemes. In 1999 and 2000, salal responded significantly to thinning at BL and OM. Thinning effects persisted at both sites for salal through 2001. A similar pattern was observed for Oregongrape,

except that flowering production in 2001 was low, as in 1998 (Figure 4). Oceanspray exhibited a significant association between thinning intensity and flowering in 2000 and 2001 at both sites. A significant association was observed for red huckleberry only at OM in 2001. Hazelnut did not produce flowers, regardless of overstory density. Only five hazelnut fruits were observed at BL, in 4 yr combined and no fruits were found at OM in any year.

Thinning treatment was also a significant variable for predicting flower/fruit production in logistic regression models in 1999 at BL for salal and Oregongrape. Moderate and heavy thinning treatments, but not light thinning, were statistically different from the unthinned for both species. Odds ratio estimates showed that probability of producing increased with thinning intensity. Thinning treatment was also a significant explanatory variable for oceanspray at BL in 2001. Light, moderate, and heavy thinning treatments were all significantly different from the unthinned treatment. Odds ratio estimates indicated that the greatest increase in probability of flowering occurred in moderate, followed by heavy, then light thinning (compared to the unthinned). Thinning treatment was not significant for the probability of flowering for red huckleberry in any year.

Flower/Fruit Abundance

The abundance of racemes produced by salal was affected by thinning (Figure 5). Raceme production was low in the unthinned stand at both sites in all years. Production increased in thinned stands at both sites in 1999. At both sites and in all treatments except the unthinned, raceme abundance was ranked 1999 > 2000 > 2001 > 1998. Although there were more Oregongrape racemes per microplot in the thinned treatments than the unthinned in 1999, the response was not consistent for all years for both sites, or even among the thinning treatments (Figure 6). For both species, years of higher mean production in thinned stands were not a consequence of prolific flowering in a couple of microplots; instead, a flattening of the shrub frequency distribution for racemes per microplot was observed (salal, Figure 7).

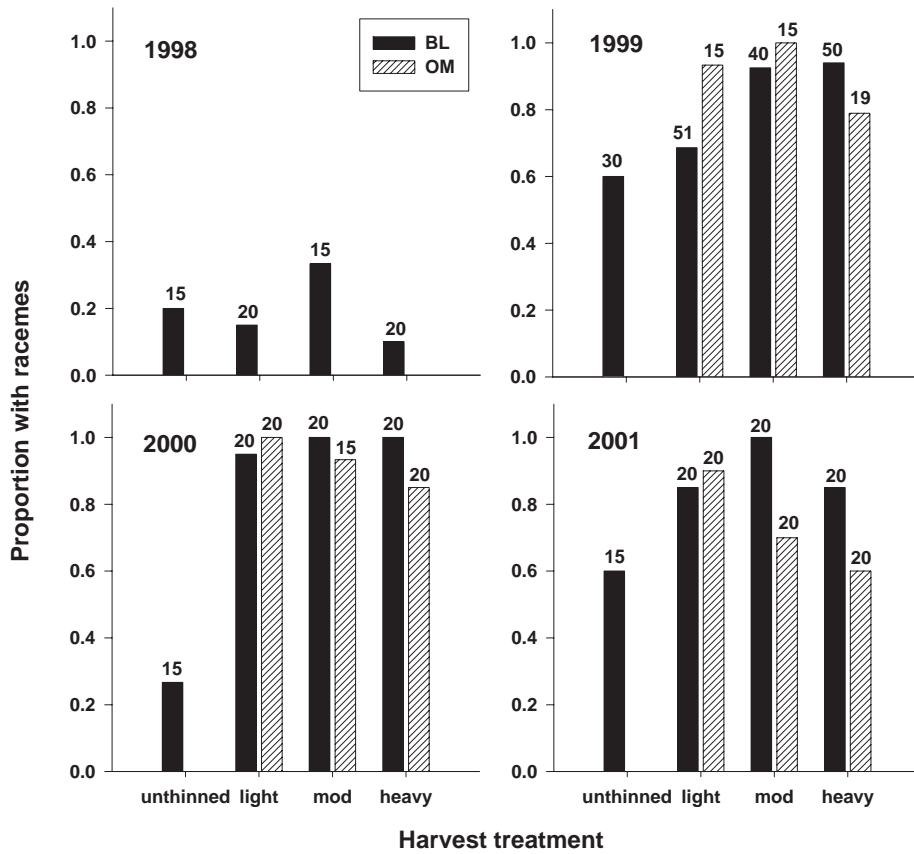


Figure 3. Effects of four levels of thinning on the probability of flowering in salal at two sites in western Oregon from 1998 to 2001. Vertical bars represent the proportion of microplots that had raceme-bearing stems to total number of microplots for a site-year-treatment combination. Values above bars are the total number of micro-plots sampled for each combination.

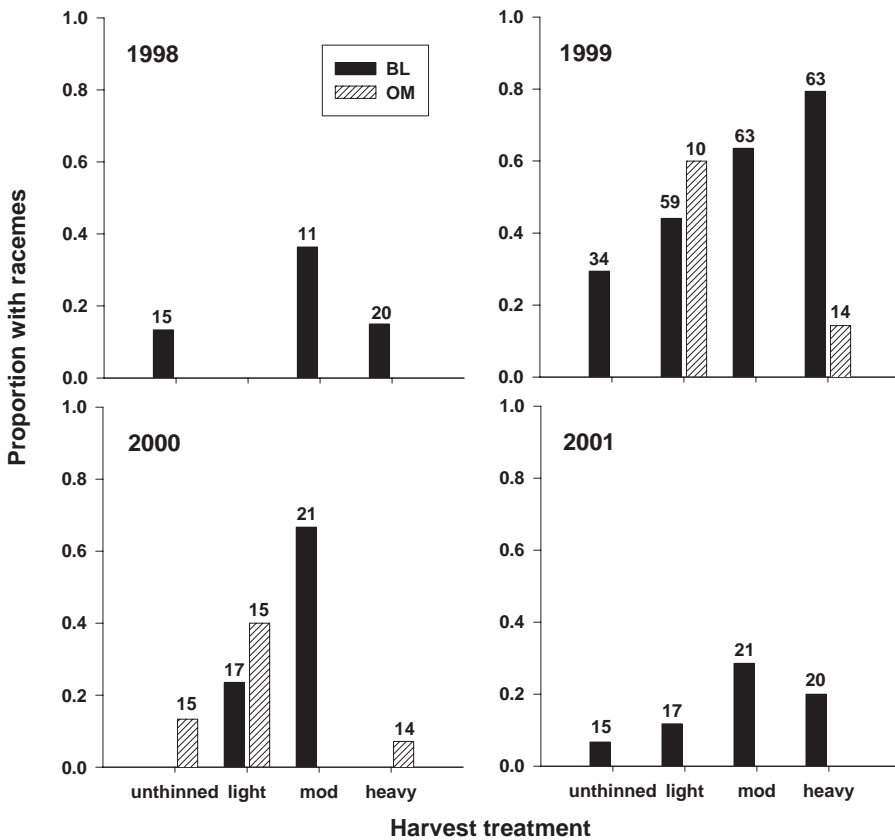


Figure 4. Effects of four levels of thinning on the probability of flowering in Oregon-grape at two sites in western Oregon from 1998 to 2001. Vertical bars represent the proportion of microplots that had raceme-bearing stems to total number of microplots for a site-year-treatment combination. Values above bars are the total number of microplots sampled for each combination.

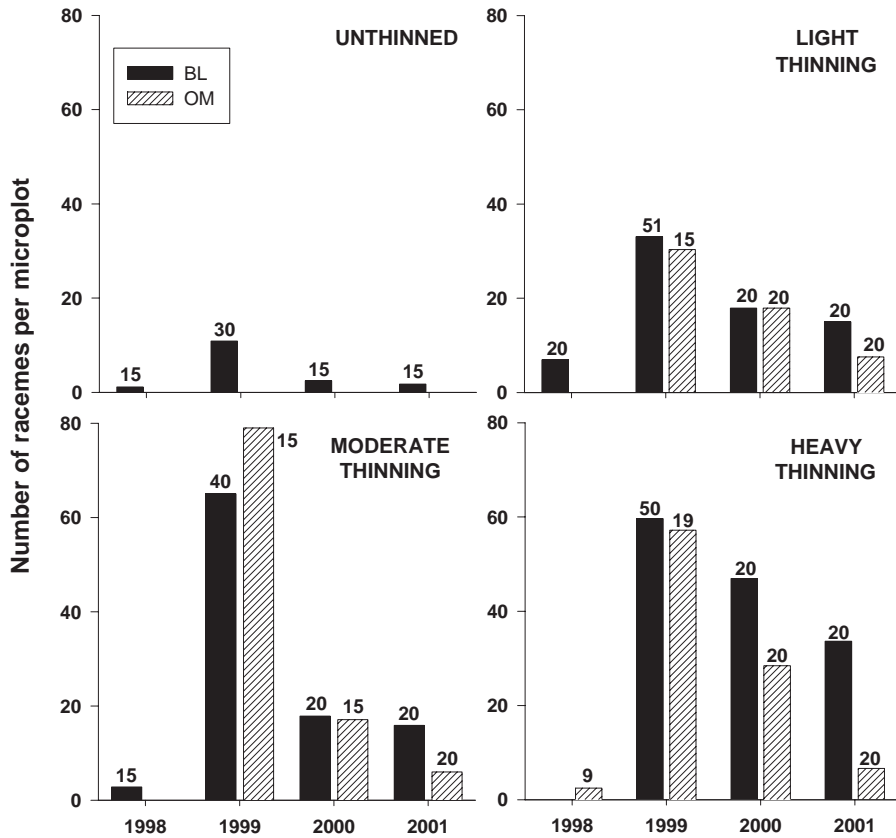


Figure 5. Effects of four levels of thinning on raceme abundance for salal at two sites in western Oregon from 1998 to 2001. The bars represent the mean number of racemes sampled per 4 m² microplot for a site-year-treatment combination. Values above bars are number of each combination.

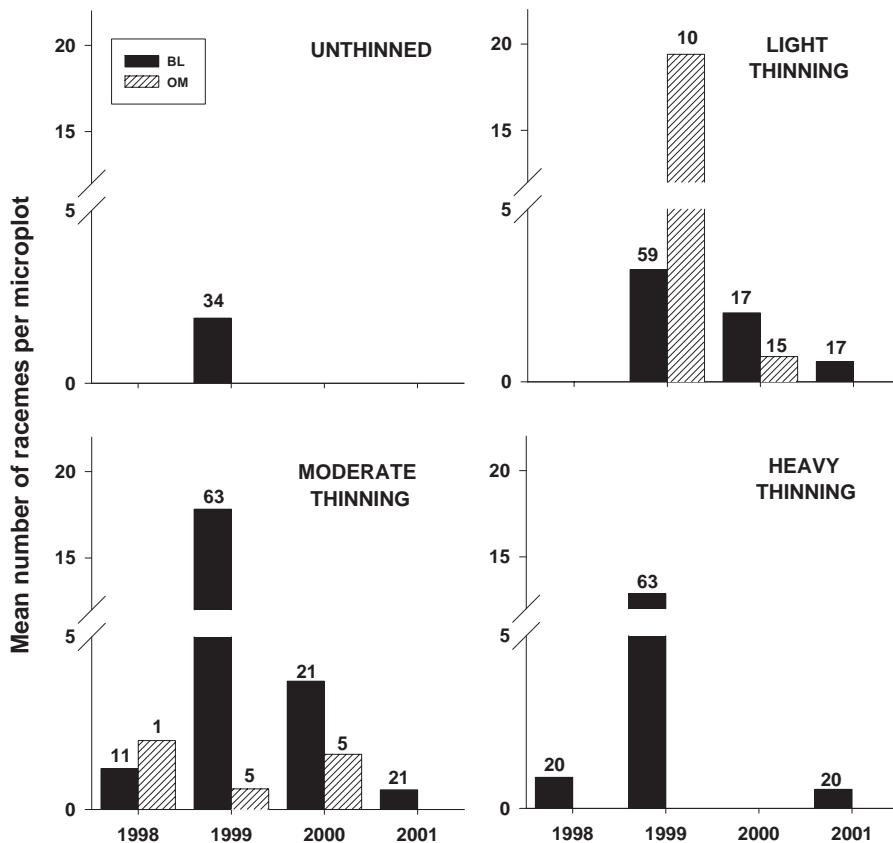


Figure 6. Effects of four levels of thinning on raceme abundance for Oregon grape at two sites in western Oregon from 1998 to 2001. The bars represent the mean number of racemes sampled per 4 m² microplot for a site-year-treatment combination. Values above bars are number of microplots sampled for each combination.

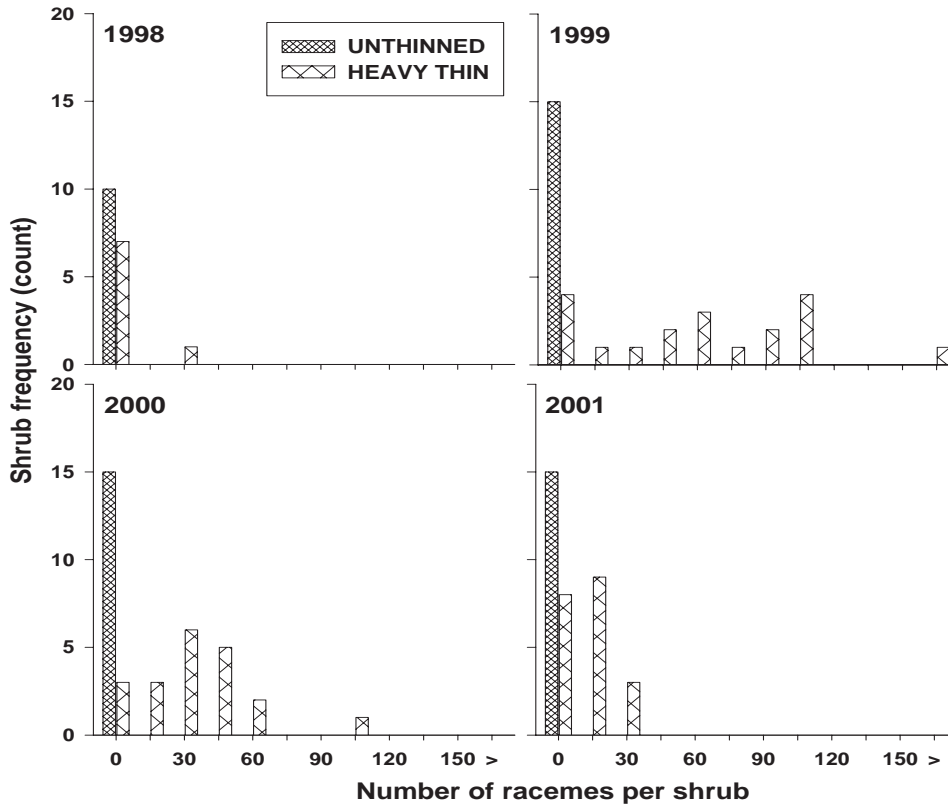


Figure 7. Comparison of frequency distribution of raceme abundance in salal for unthinned control and heavily thinned stands from 1998-2001 at one site (OM) in western Oregon.

Oceanspray flower production was limited in unthinned stands at both sites in 2000-2001. Thinning treatments did not appear to have much effect on production at OM. At BL, flower production was highest after moderate and heavy thinning.

Red huckleberry showed a greater tendency to produce fruit in unthinned stands than other shrub species. Production was higher in moderately or heavily thinned stands than in unthinned or lightly thinned stands. Shrub frequency distributions flattened out slightly, but displayed no major shifts (Figure 8).

Discussion

Our research suggests that plant size and age are the primary determinants of flower and fruit production in nine northwest understory shrub species. In addition, for most of the species we studied, the resource environment also directly affects production, or otherwise controls production indirectly by influencing plant size.

Thinning or creating canopy gaps will improve the resource environment, and therefore, increase shrub size and flower/fruit production.

Plant size characteristics were consistently the best predictors of flower/fruit abundance (Table 3). Plant age was important for most species, but was more strongly related to plant size than to fruit or flower production. Previous studies showed that resource availability influences perennial plant reproduction indirectly through its effect on plant size and growth (Samson and Werk 1986, Piper 1989) and our results support this for some species. For example, in red elderberry, DBH was a primary determinant of flower abundance and was also positively related to the presence of canopy gaps. Large elderberry shrubs produced the most flowers, and large shrubs were more common in canopy gaps than under intact canopy (Figure 2). After accounting for plant size (through regression on residuals from flower/fruit abundance vs. plant size models), the resource and competitive environment still proved to have significant effects

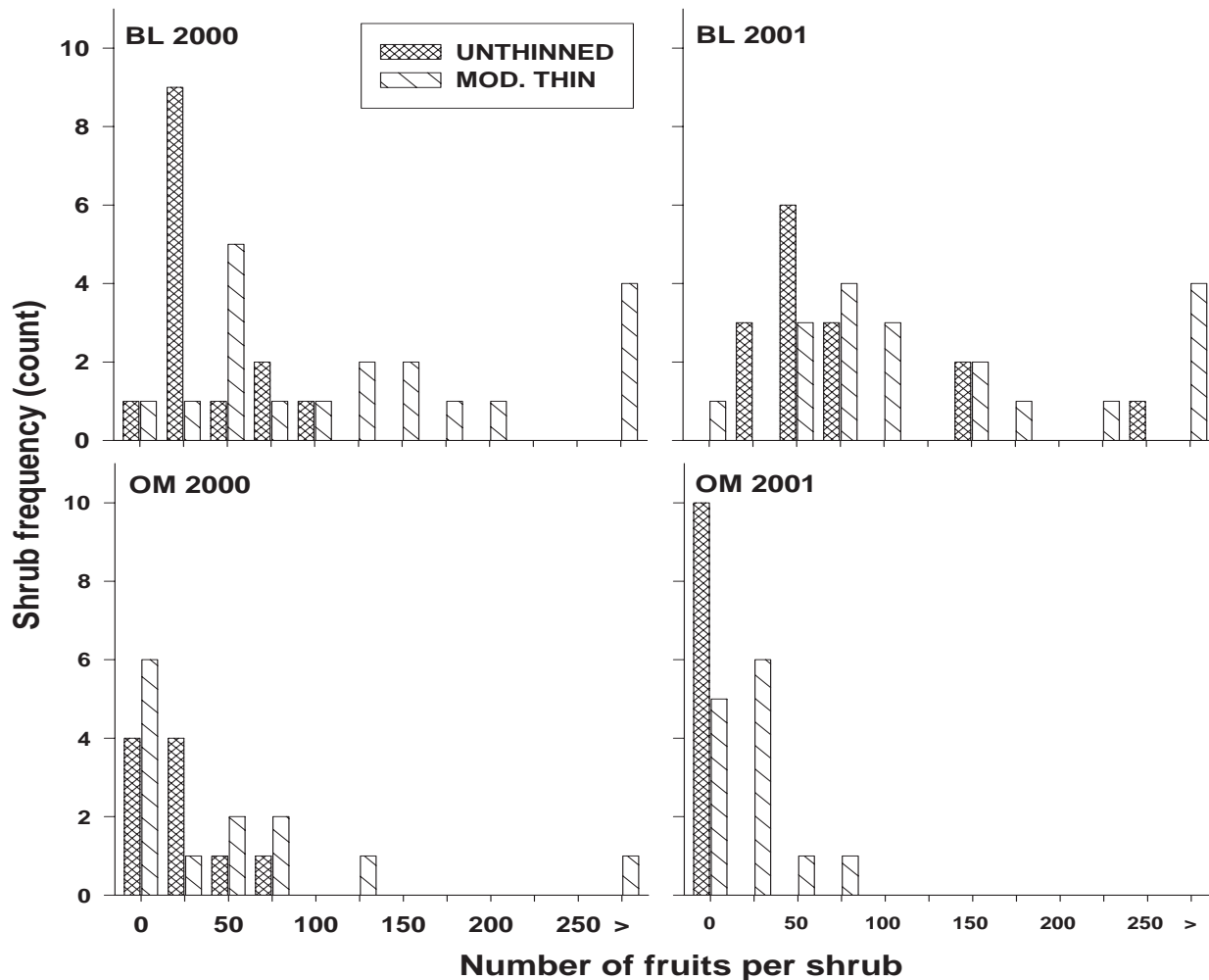


Figure 8. Comparison of frequency distributions of fruit abundance in red huckleberry for unthinned control and moderately thinned stands from 2000-2001 at two sites in western Oregon.

on flower/fruit production. Site factors or overstory density also controlled flower/fruit abundance, independent of size effects, for hazelnut, Indian plum, and vine maple.

We detected a response to gaps only in red elderberry and vine maple; however, the potential effect of canopy gaps on flower or fruit production should not be dismissed for the other shrub species that we studied. We recorded the presence of large canopy gaps, but did not consider the effects of smaller gaps. Small canopy gaps are ephemeral and may close quickly because of lateral expansion of surrounding canopy trees and the growth of subcanopy plants within gaps (Runkle 1982). Previous stand disturbance and gap formation may have consequences for sexual production even after gaps appear closed. The ability of woody perennials to store resources for long time periods (Antos and Allen 1999, Selås 2000) means

consequence of gap-induced plant growth may be hard to predict. Perennials may accumulate energy over several growing seasons and then fruit prolifically when a reserve threshold is reached (Selås 2000). The effects of small canopy gaps on flower/fruit production may be delayed until after the gap has closed.

The effects of canopy gaps and resource availability are further confounded by differences in vegetative reproduction among species. Effects of plant size on flower/fruit production were small or undetectable for Oregon grape and salal, species that can expand by horizontal rhizomes. Rhizomatous plants are more capable of quickly exploiting the flush of resources that might accompany a tree-fall gap than plants that depend solely on sexual reproduction. Rhizomatous plants also may have the ability to transfer resources

among ramets, meaning the health or vigor of an individual ramet depends less on local resource space (Piper 1989). A ramet growing in a nutrient-poor environment might flower vigorously because of the resource contribution from ramets growing in more favorable conditions. Presumably, vine maple has a similar ability to share resources among multiple stems in clonal mats produced by stem layering (O'Dea 1995).

Although understory shrubs are adapted to grow and reproduce in low light forest conditions, the flowering potential of some species may not be reached under dense forest canopies. Thinning increased the abundance and probability of flowering/fruitletting in four shrub species, but had no effect on another (Table 5). Generally, higher intensities of thinning resulted in a higher likelihood and abundance of flowering/fruitletting. Production in unthinned stands was consistently lower than in thinned stands. Bunnell (1990) observed a similar trend for salal; plants rarely flowered in dense canopies, relying instead on vegetative reproduction. Huffman et al. (1994) demonstrated that salal growth is reduced in low-light environments. These authors also reported that in high light environments, salal plants favored rhizome expansion over aerial stem production. Results from our study, however, indicate no adverse affect of heavy thinning on salal raceme production.

In some years, increases in flower/fruit production

for thinned stands were accompanied by increases in unthinned stands, which may have been because of natural year-to-year variation in production. Precipitation patterns also provide some explanation for year-to-year variation in flower/fruit production. During May and June 1998, the year prior to the maximum flower abundance at the Oregon study sites, precipitation was much greater than the 10-yr average and substantially above the precipitation in the three other years preceding our observations. Flowers would have been initiated the spring prior to their observation; thus, the greater precipitation early in the 1998 growing season may have been a contributing factor in the high 1999 flower production.

We observed substantial year-to-year and between-site variation in flower/fruit production. Other long-term studies of flower/fruit production in understory shrubs also suggest that factors limiting production may differ among sites and between years (DiFazio et al. 1998). Results of such studies highlight the danger of making conclusions when data are collected for a single year or under uniform conditions (DiFazio et al. 1998). The Washington study observations were made in the year the Oregon study had the greatest amount of flowering (and precipitation during all summer months in the year prior to our observations was above the 10-yr average); therefore, our results may not be typical of what we would have observed in a long-term study

TABLE 5. Comparison of thinning effects on flower or fruit production for five species sampled at two sites in western Oregon.

Species	Percent of plants producing			Amount produced per plant			Comments
	Response to thinning	Consistency		Response to thinning	Consistency		
		Annual	Between sites		Annual	Between sites	
Oregongrape ¹	Small increase	No	No	Small increase	No	No	Production peaked in 1999 in thinned stands, but returned to 1998 levels by 2001
Hazelnut ¹	None	—	—	None	—	—	Only 5 nuts observed in 4 yrs at both sites combined
Salal ¹	Large increase	Yes	Yes	Large increase	Yes	Yes	Production peaked in 1999 and remained above 1998 levels through 2001
Oceanspray ²	Large increase	Yes	Yes	Large increase	Yes	Yes	Production highest after moderate and heavy thinning; minimal response to light thinning
Red huckleberry ²	Small increase	Yes	No	Small increase	Yes	No	Consistently produced fruit at BL, regardless of treatment

¹ Flower/fruit production observed for 4 yrs.

² Flower/fruit production observed for 2 yrs.

As maintaining ecosystem components and function become more prominent objectives for some forest managers, information about shrub reproduction will be useful for habitat development and species conservation applications. Reducing overstory density or creating canopy gaps by thinning may provide a flush of resources to understory shrubs. Subsequent plant growth and enhanced vigor should increase the probability and amount of flowering and fruiting for at least some species. Responses to thinning or gap creation may be delayed if environmental conditions such as growing season precipitation are unfavorable.

Forest operations could have negative or positive consequences for shrub flower and fruit production. Large, older shrubs are valuable components in forest ecosystems because they provide cover and vertical structures important for wildlife habitat, host bryophyte colonies, are bird nesting and perching sites, and are also the plants most likely to produce large amounts of fruit. Thus, the largest shrubs may be the most valuable from a wildlife habitat viewpoint. Standard forest harvesting operations will not protect these plants and many will be damaged. Although most shrubs will resprout after injury, it may take many years for the aerial portions of the plants to regain their pre-disturbance size. Injury to large

shrubs could limit the potential increase in fruiting that would otherwise occur after thinning. Forest managers should consider the legacy value of older shrubs of desired species when planning forest operations (Harrington et al. 2002). Depending on the management objectives for a stand, it may be warranted to protect some individuals or portions of a stand during thinning or other forest operations to ensure that some large individuals are maintained.

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