

Salmonberry and salal annual aerial stem production: the maintenance of shrub cover in forest stands¹

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Abstract: Annual sprouting of aerial stems and ramets enables populations of salmonberry (*Rubus spectabilis* Pursh), salal (*Gaultheria shallon* Pursh), and probably other forest shrubs to maintain dense covers (>20 000 stems/ha). We studied annual stem production of salmonberry on cut (all stems cut within 15 cm of the ground) and uncut (stems were not treated) plots for 8 years and salal for 5 years in the understories of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), alder, and riparian stands, as well as clearcuts, which are all common stand types in western Oregon. Mean salmonberry stem production on uncut plots ranged from 4.7 stems·m⁻²·year⁻¹ (95% CI 2.9–7.4) in alder stands and clearcuts to 1.6 stems·m⁻²·year⁻¹ (95% CI 1.0–2.6) in conifer stands. Mean salal production was greater, ranging from 58 stems·m⁻²·year⁻¹ (95% CI 25–135) to 8.6 stems·m⁻²·year⁻¹ (95% CI 3.7–20.1) on uncut plots in clearcuts and unthinned Douglas-fir stands, respectively. Annual production of both species was somewhat greater on cut plots. Most stems produced in early spring die by December, but enough are recruited to replace mortality of older stems. Stem density was maintained for 8 years for salmonberry and 5 years for salal on both cut and uncut plots. Based on length of rhizomes and bud density we estimate that only 1–5% of the buds in the rhizomes are needed to support this annual stem production. Although these species sprout vigorously after their aerial stems are killed, disturbance is not necessary for maintaining a dense cover. It appears that, once established, salal, salmonberry, and probably other clonal forest shrubs can maintain a dense cover that can interfere with establishment of trees and other shrubs in canopy gaps or other openings.

Résumé : La production annuelle de repousses par les tiges aériennes et les ramets permet aux populations de ronce remarquable (*Rubus spectabilis* Pursh), de gaulthérie (*Gaultheria shallon* Pursh) et probablement d'autres arbustes forestiers de maintenir un couvert dense (>20 000 tiges/ha). Nous avons étudié la production annuelle de tiges de ronce remarquable et de gaulthérie pendant respectivement 8 et 5 ans dans des parcelles coupées (toutes les tiges étaient coupées à 15 cm du sol ou moins) et non coupées (les tiges n'étaient pas coupées) établies en sous-étage du douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco), de l'aulne, de peuplements ripicoles et dans des coupes à blanc; tous des types de peuplements communs dans l'Ouest de l'Oregon. La production moyenne de tiges de ronce remarquable dans les parcelles non coupées allait de 4,7 tiges·m⁻²·an⁻¹ (intervalle de 2,9 à 7,4 au seuil de confiance de 95%) dans les peuplements d'aulne et les coupes à blanc à 1,6 tiges·m⁻²·an⁻¹ (intervalle de 1,0 à 2,6 au seuil de confiance de 95%) dans les peuplements de conifères. Dans le cas de la gaulthérie, la production moyenne était plus élevée, allant respectivement de 58 tiges·m⁻²·an⁻¹ (intervalle de 25 à 135 au seuil de confiance de 95%) à 8,6 tiges·m⁻²·an⁻¹ (intervalle de 3,7 à 20,1 au seuil de confiance de 95%) dans les parcelles non coupées établies dans les coupes à blanc et dans les peuplements non éclaircis de douglas de Menzies. Les deux espèces avaient une production annuelle un peu plus élevée dans les parcelles coupées. La plupart des tiges produites tôt au printemps étaient mortes rendu au mois de décembre mais il y avait un nombre suffisant de recrues pour compenser la mortalité chez les plus vieilles tiges. La densité des tiges s'est maintenue pendant 8 ans dans le cas de la ronce remarquable et pendant 5 ans dans le cas de la gaulthérie tant dans les parcelles coupées que non coupées. En se basant sur la longueur des rhizomes et la densité des bourgeons, on estime que seulement 1–5% des bourgeons sur les rhizomes sont nécessaires pour supporter cette production annuelle de tiges. Bien que ces espèces rejettent abondamment après que leurs tiges aériennes aient été tuées, une perturbation n'est pas nécessaire pour maintenir un couvert dense. Il semble qu'une fois établis, la ronce remarquable, la gaulthérie et probablement d'autres arbustes forestiers qui forment des clones peuvent maintenir un couvert dense qui peut interférer avec l'établissement des arbres et d'autres arbustes dans les trouées et les autres ouvertures.

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Introduction

Clonal shrubs are important components of many forests. They form dense covers at early stages of forest succession just after a major disturbance and then later in stand development in the understory canopy of conifers or hardwoods (Tappeiner and John 1973; Whitney 1986; Balogh and Grigal 1987; Kurmis and Sucoff 1989; Tappeiner et al. 1991; Huffman et al. 1994a; O'Dea et al. 1995; Ricard and Messier 1996). Although these shrubs invade stands by seeding, rapid expansion of cover and site occupancy are more often determined by their ability to spread by clonal expansion from bud banks on roots and rhizomes (Whitney 1986; Tappeiner et al. 1991; Huffman et al. 1994a; Ricard and Messier 1996). Other forms of clonal expansion, like layering, can also result in extensive clones with numerous ramets (O'Dea et al. 1995).

Dense populations of shrubs, whether in an understory or open areas, affect availability of light and other resources, thus affecting the establishment and growth of other plants (Strothman 1967; Henderson 1970; Maguire and Forman 1983; Carlton 1988; Bailey and Tappeiner 1998). Thus, if the dense shrub populations persist, they may have a major effect on the development, structure, and species composition of forest stands.

It appears that clonal understory shrubs are persistent and may replace their aerial stems even in the absence of disturbance. For example, Kurmis and Sucoff (1989) found that the cover of beaked hazel (*Corylus cornuta* Marsh) in the understory of red pine (*Pinus resinosa* Ait.) stands was stable for the 19 years of their study. Although exact numbers of stems fluctuated during this period, the stem density at year 19 was essentially the same as at the beginning of the study. After 19 years, the oldest aerial stems were only about 15 years old; thus, recruitment of new stems maintained the stem density and cover during this period.

The studies by Balogh and Grigal (1987) of six shrub species in northern Minnesota and other circumstantial evidence (based on stem age or stem size density relationships) suggest that frequent stem recruitment is common in clonal shrubs like salal (*Gaultheria shallon* Pursh), salmonberry (*Rubus spectabilis* Pursh), and Oregon grape (*Berberis nervosa* Pursh) (Tappeiner et al. 1991; Huffman et al. 1994a; Huffman and Tappeiner 1997).

These studies provide indirect evidence for frequent recruitment of aerial stems and ramets in clonal forest shrubs. However, we found no documentation of recruitment rates and how rates might vary annually, among shrub species, or among forest stand types. Therefore, we annually monitored vegetative stem production of two shrubs that are common in Pacific Northwest forests.

Salmonberry, a deciduous shrub, is most common in the understory of riparian and upland red alder (*Alnus rubra* Bong.) stands (Henderson 1970; Carlton 1988). Salmonberry differs from other common *Rubus* species in having aerial stems (canes) that live for at least 15 years (Whitney 1986; Tappeiner et al. 1991; Ricard and Messier 1996). In addition, salmonberry clonal expansion occurs from rhizome extension; in other *Rubus* species it occurs from root suckers, stolons, and layering. On riparian sites salmonberry is often the principal cover (Nierenberg 1996), and on mesic sites, it

is common in the understory of red alder – Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands. Salmonberry stems are upright and 2.0–4.0 m tall.

Salal, an evergreen shrub, generally occurs on somewhat drier, more interior sites than salmonberry and is not common in alder stands. It produces a cover of dense, sprawling stems (0.5–1.5+ m tall) with two or three cohorts of evergreen leaves (Messier and Kimmins 1991; Huffman et al. 1994a). Like salmonberry, salal clonal expansion occurs from rhizome extension. Other species in this genus expand by layering of prostrate stems and develop lower (<20 cm), less dense covers.

Both species sprout vigorously from buds on their rhizomes and at bases of aerial stems. Both also form dense cover (>20 000 stems/ha) (Tappeiner et al. 1991; Huffman et al. 1994a) after fire or clear-cutting and in the understory of hardwood or conifer stands. Clones of both species have multiple-stemmed ramets of varying sizes and ages that coalesce to form dense populations of aerial stems.

We studied populations of salmonberry and salal to determine whether frequent aerial stem production was a factor in maintaining aerial stem density. To quantify how annual aerial stem production might vary by overstory composition, density, and disturbance to the shrubs, we monitored annual stem production of salmonberry populations in alder, conifer, and riparian stands and in clearcuts in which shrubs were (i) uncut and (ii) cut. Similarly, we monitored annual stem production of dense salal populations in thinned and unthinned conifer stands and in clearcuts. The shrub stems were cut to determine how severe disturbance to populations of these species might affect aerial stem reproduction and growth in these stand types.

Methods

Study areas

Salmonberry populations were monitored from 1988 to 1996 in an inland area in the vicinity of Marys Peak (44°33'N, 123°48'W) and near the coast at Cascade Head (45°03'N, 123°59'W) in the Coast Range of western Oregon. Salal populations were monitored at Marys Peak from 1992 to 1996 on two areas within 10 km of each other. The stands and areas were chosen to represent a range of stand types and overstory densities within the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) vegetation zone (Franklin and Dyrness 1973). They were not selected for testing differences among sites. Elevations ranged from 100 to 300 m. The maritime climate is cool and wet, with average winter temperatures of 9°C. Summer temperatures average 15°C near the coast and 17°C in the interior. Precipitation occurs mostly as winter rain and averages from about 175 (inland) to 215 (coastal) cm/year (NOAA 1987). Soils of the central Coast Range are generally derived from sandstone and range from moderately well-drained clay loams to slightly acidic, silty clay loams (Franklin and Dyrness 1973; Orr et al. 1992).

Stands

Dense salmonberry understory populations were studied in conifer, red alder, and riparian forests, as well as clearcuts, all stand types that are typical of western Oregon Coast Range forests (Table 1). Four stands of each type were selected in each area. Conifer stands were dominated by Douglas-fir and also contained some codominant western hemlock and western redcedar (*Thuja plicata* Donn.). Red alder stands were single species. Riparian forests were

Table 1. Overstory and understory characteristics at the beginning of the study.

Stand type	Overstory		Shrub population	
	Basal area (m ² /ha)	Age (years)	Stems/m ²	Basal area (cm ² /m ²)
Salmonberry				
Alder	26 (16–37)	58 (53–61)	5.3(3–7)	7.5 (6–11)
Conifer	46 (32–53)	130 (110–140+)	2.5(2–4)	6.8 (3–15)
Riparian	28 (14–47)	90 (58–120+)	2.8 (1–5)	5.7 (3–10)
Clearcut	—	5 (4–6)	5.0 (3–8)	12.4 (5–19)
Salal				
Conifer				
Thinned	33 (31–34)	56 (55–58)	61 (58–63)	15.7 (11–20)
Unthinned	46 (40–53)	69 (56–80)	30 (29–33)	7.1 (6–9)
Clearcut	—	6 (3–8)	116 (97–128)	8.7 (8–10)

Note: Values are means with ranges given in parentheses.

mixed age and species conifer–hardwood stands of Douglas-fir, western hemlock, red alder, and bigleaf maple (*Acer macrophyllum* Pursh). Stand ages were 110 to >140 years for conifer and 53–61 years for red alder; clearcuts were 4–6 years old. Salmonberry understories ranged from 2.0 to 8.0 stems/m².

Salal was studied in four nearly pure Douglas-fir stands and two clearcuts (Table 1). Two of the Douglas-fir stands were thinned, and two were not (Table 1). Overstory density in these stands ranged from 90 to 380 trees/ha. All stands had dense salal understories with 30–128 stems/m².

Shrub population sampling

Salmonberry

In summer 1987, six 4-m² plots were randomly located in pure populations of salmonberry in each stand (a total of 96 plots). Stem height and diameter (± 2 mm, at a height of 15 cm) were measured for each stem. In three of the six plots in each stand, all shrub stems were cut to ground level. Each June from 1988 through 1996, we tallied all new aerial stems that were initiated during the current year on each plot and marked each stem with a wire pin near the base. In December we counted the current-year stems that had died and removed their wire pins. We remeasured stem height and diameter in all plots in December 1996. We were not able to accurately age salmonberry, because annual rings are poorly defined.

Salal

Methods for salal measurement paralleled those for salmonberry. However, because salal stem density is much greater than that of salmonberry, we sampled stems on 1-m² plots. A total of 36 plots were established. In November 1992, six areas measuring 4 × 4 m were randomly located within nearly pure populations of salal in each stand. In three of the six areas, all aerial stems were clipped within 1–4 cm of the ground. Within these clipped areas, two 1-m² plots were established at random. In each unclipped 4 × 4 m area, two 1-m² plots were randomly located in which all stems were counted; height, diameter, and age were recorded for a sample of 30 stems within each plot. Stems were selected by placing a rod within the plot and sampling the first 30 stems it touched. Age was estimated by counting terminal bud scars (Huffman et al. 1994a). In these 1 × 1 m plots, aerial stems that initiated during the current year were loosely tied with colored flagging. Plots were remeasured every spring and late winter through 1996. Remeasurement consisted of examining previously marked stems, tallying surviving and dead stems, and tying the season's current stem cohort with a new color flagging. In 1996, all plots were remeasured for total numbers and heights of stems.

Effects of annual stem production on the bud bank

Both species have dense networks of rhizomes below ground that contain a bud bank from which the aerial stems sprout. Previous studies in the same stand types as in this study provided estimates of total rhizome length and new, annual rhizome elongation for salmonberry (Tappeiner et al. 1991) and salal (Huffman et al. 1994a). Other work estimated the potential bud bank on the rhizomes by growing rhizome segments in a greenhouse and counting the number of buds produced on 20-cm segments of salmonberry rhizomes and 30-cm segments of salal rhizomes (Zasada et al. 1994; Huffman et al. 1994b). Annual stem production (number of stems/m²) of both species was determined in this study. For both species and all stand types, the proportion of the bud bank on new and total rhizomes that produced stems annually was estimated as

$$[1] \quad \frac{\text{annual stem production/m}^2}{(\text{rhizome length/m}^2 \times \text{no. of buds/m of rhizome})}$$

Data analysis

We analyzed data for each species separately. For each plot, we calculated stem number and annual stem production per square metre and basal area (cm²/m²) from the beginning and ending inventories. We used the average of the cut or uncut plots in each stand in a split-plot design ANOVA to test the null hypothesis that, for each cutting treatment, there were no differences in annual stem production among stand types and no differences in numbers of stems at the beginning and end of the study. Stand type was the whole-plot factor; cutting treatment was the split-plot factor. Graphical analysis had indicated that the variation in annual stem production was not constant among treatments and stand types. Therefore, the analysis of stem production was carried out on log-transformed data for both species. Comparison of numbers of stems was done on untransformed data.

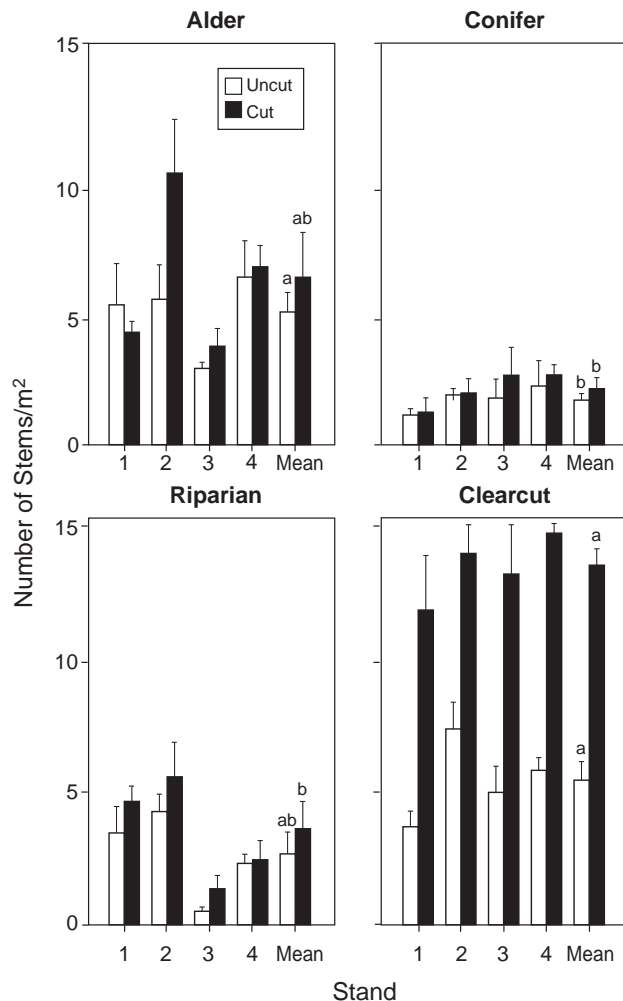
Using stand averages from all stand types and both transformed and untransformed data, we developed regression equations to relate numbers of new stems initiated to shrub stem basal area before cutting and to overstory tree basal area.

Results

Salmonberry

New aerial stems sprouted annually on both cut and uncut plots in all stands (Fig. 1). They arose from the bud bank at the base of the ramets, the large aerial stems on the ramets, and the rhizomes connecting the ramets. New stems were generally ≤ 5 mm in diameter; <10% of them reached 15 mm

Fig. 1. Mean annual salmonberry stem production on uncut and cut $1 \times 1 \text{ m}^2$ plots in each stand type. Error bars are SE. There were three cut and three uncut plots in each stand and four stands of each stand type. For each cutting treatment the 95% confidence intervals around the means with different letters do not overlap.



in diameter and $>2 \text{ m}$ in height and extended into the salmonberry canopy. Mean annual stem production on uncut plots ranged from 5.1 stems/m^2 in alder stands to 2.2 stems/m^2 in conifer stands (Fig. 1). On cut plots, production ranged from 13.0 stems/m^2 in clearcuts to 3.4 and 2.4 stems/m^2 in riparian and conifer stands, respectively (Fig. 1). There was a significant interaction between stand type and cutting treatments ($F = 10.39$; $df = 1, 12$; $p = 0.0012$). Sprouting in riparian stands, particularly in plots immediately adjoining streams, was likely reduced by invasion of stink currant (*Ribes bracteosum* Dougl.) the first year after cutting. In general, there was no invasion of other species. On one cut plot each in the densest conifer stands (3 and 4), salmonberry did not resprout. The greatest production occurred on cut plots in the clearcuts; the 95% confidence intervals for those plots (8.5 – 21.0) did not overlap the intervals for cut plots in the riparian (1.9 – 4.9) and conifer stands (1.3 – 3.4). Similarly, the 95% confidence intervals for

the uncut alder (3.0 – 7.5) and clear-cut (3.2 – 8.2) plots did not overlap those from the uncut conifer (1.0 – 2.6) plots.

For 2 or 3 years after cutting, stem production on cut plots was generally two to three times greater than on uncut plots, after which annual stem production was nearly identical for both cutting treatments. Mean stem initiation on uncut plots was significantly related ($p < 0.001$) to salmonberry basal area:

$$[2] \quad y = 1.40x^{0.815}, \quad r^2 = 0.77, \quad \text{SE of estimate} = \pm 0.63$$

where y is the number stems initiated per square metre, and x is the salmonberry basal area (cm^2/m^2). Standard errors were ± 0.53 for the coefficient and ± 0.115 for the exponent. Both new salmonberry stem production and older stem density were inversely related to overstory basal area ($p \leq 0.01$), but these relationships explained less than 40% of the variation.

Stem density in the uncut plots in 1996, after eight growing seasons, was nearly the same as it was in 1988 (Fig. 2), and on uncut plots there were no significant differences in total numbers of stems for these two dates for any stand type ($p = 0.11$ to 0.91) (Fig. 2). For example, the number of salmonberry stems in alder stands averaged $4.9/\text{m}^2$ (range 3.2 – 7.1) in 1988, and $4.6/\text{m}^2$ (3.7 – 7.0) in 1996. On cut plots, stem density in 1996 was slightly lower than in 1988, but significantly lower ($p \leq 0.02$) only in clear-cut stands (6.6 ± 0.54 (mean \pm SE) vs. $4.5 \pm 1.7 \text{ stems/m}^2$). There was evidence of a significant difference in stem density ($p \leq 0.08$) in alder stands (5.0 ± 1.1 vs. $3.3 \pm 10.7 \text{ stems/m}^2$) (Fig. 2).

Few stems in diameter class 3 (11–15 mm) and larger died during the 8 years of this study. Total mortality during this period on uncut plots averaged 1.5, 1.9, 2.7, and 5.7 stems/m^2 in the conifer, riparian, alder, and clear-cut stands, respectively. Mean mortality of stems in diameter classes 3 and above for all stand types was $<1 \text{ stem} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$. The mean annual production of new stems (2.2 – $5.1 \text{ stems} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) on uncut plots and 2.1 – $13 \text{ stems} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$ on cut plots; Fig. 1) far exceeded the number needed to replace mortality of large stems, and 85–95% of the new stems died. On the cut plots, total average mortality of stems in classes 1 and 2 for 8 years ranged from 1.1 to 3.2 stems/m^2 , and 84–98% of the new stems died.

It appears that the annual production of aerial stems occurs from a relatively small proportion of the bud bank. Rhizome lengths of 2.6, 4.2, 5.5, and 15.5 m^2 were reported for salmonberry populations in conifer, riparian, alder, and clear-cut stands, respectively (Tappeiner et al. 1991) (Table 2). We estimate that the rhizomes supported bud banks of 65, 105, 138, and 387 buds/ m^2 in these same stands; and that from 1 to 4% of the buds produced stems on uncut plots (Table 2).

The distribution of salmonberry stems among diameter classes was similar for all stand types and cutting treatments (Fig. 3). Although the numbers of stems in classes changed during the study, the overall distribution remained about the same. For example, in alder stands there were generally fewer stems in diameter classes 4 and above in 1996 than there were in 1988; however, there were more stems in classes 1 and 2.

Numbers of stems in the smallest class, and sometimes the second smallest, varied with the time of year. In the

spring after stem sprouting, stem density in the first class was often two to three times greater in uncut plots and three to four times greater in the cut plots than it was in the winter. For example, on uncut alder plots there were an average of 5.1 ± 0.6 new stems present in the spring, mostly in the first diameter class. However, at the winter inventory, there was only about one stem in this diameter class (Fig. 3). There was also considerable year-to-year variation; in one alder stand, numbers of stems in diameter class 1 in the spring varied from 4 to 18/m² over the study period.

Two growing seasons after cutting, over 90% of the salmonberry stems were in the first two diameter classes (1–10 mm); the remainder were in the third (11–15 mm). However, by 1996, the diameter distributions were similar to those for uncut plots, although there were fewer stems in the larger size classes (Fig. 3).

Salal

Like salmonberry, new stems sprouted annually on both cut and uncut plots, and average stem production was quite variable. However, salal produced two to five times more stems than salmonberry (Fig. 4). Stems were initiated both at the base of aerial stems and from rhizomes and were usually ≤ 2 mm in diameter. There was no significant relationship between annual salal stem initiation and salal basal area or stem density.

ANOVA showed no significant interaction between cutting treatment and stand type ($p = 0.27$). Annual production was greater in clearcuts than in thinned and unthinned stands ($p \leq 0.04$). Mean annual production on uncut plots ranged from 8.7 stems/m² (95% CI 3.7–20.1) in unthinned stands to 58 stems/m² (95% CI 25.1–135.3) in clearcuts ($p \leq 0.04$). On cut plots, mean stem production ranged from 18 stems/m² (8.0 to 42.8) in unthinned stands to 77 stems/m² (33.4 to 179.2; 95% CI) in clearcuts ($p \leq 0.04$). Confidence intervals from the cut and uncut clear-cut plots did not overlap with those from the unthinned stands ($F = 11.90$; $df = 2, 3$; $p = 0.027$).

There was no significant ($p = 0.21$ – 0.61) difference in stems per square metre in 1992 and 1996 in the cut or the uncut plots (Fig. 5). However, on cut plots there were more stems in 1996 than before cutting in 1992. There was also evidence on the cut plots of significant difference in the thinned stands ($p = 0.064$; 61 ± 6 vs. 71 ± 5) and in the clearcuts ($p = 0.11$; 45 ± 6 vs. 78 ± 10) (Fig. 5).

Many more stems were produced than were needed to maintain stem density, and there was high mortality of young stems. Annual mean stem mortality during the 5-year period was significantly greater in the clearcuts: 58 stems versus 19 and 20 stems in the thinned and unthinned stands, respectively. In the uncut plots, from 75 to 93% of the new stems produced died; on the cut plots, mortality ranged from 71 to 91%.

Rhizome lengths of 11, 43, and 135 m/m² were reported for salal populations in unthinned, thinned, and clear-cut stands, respectively, on these same sites (Huffman et al. 1994a) (Table 2). We estimate bud banks on the rhizomes of 165, 1120, and 2835 buds/m² in these same stand types and that 2–5% of these buds produced stems (Table 2).

Although there were many more stems in clearcuts than in thinned and unthinned stands, the stem distributions were

Fig. 2. Number of salmonberry stems in 1988 and 1996 in cut and uncut plots, by stand type. Values are means of four stands; data are untransformed. Error bars are SE. There were three cut and three uncut plots in each stand and four stands in each stand type. The p values are for the differences between the 1988 and 1996 means.

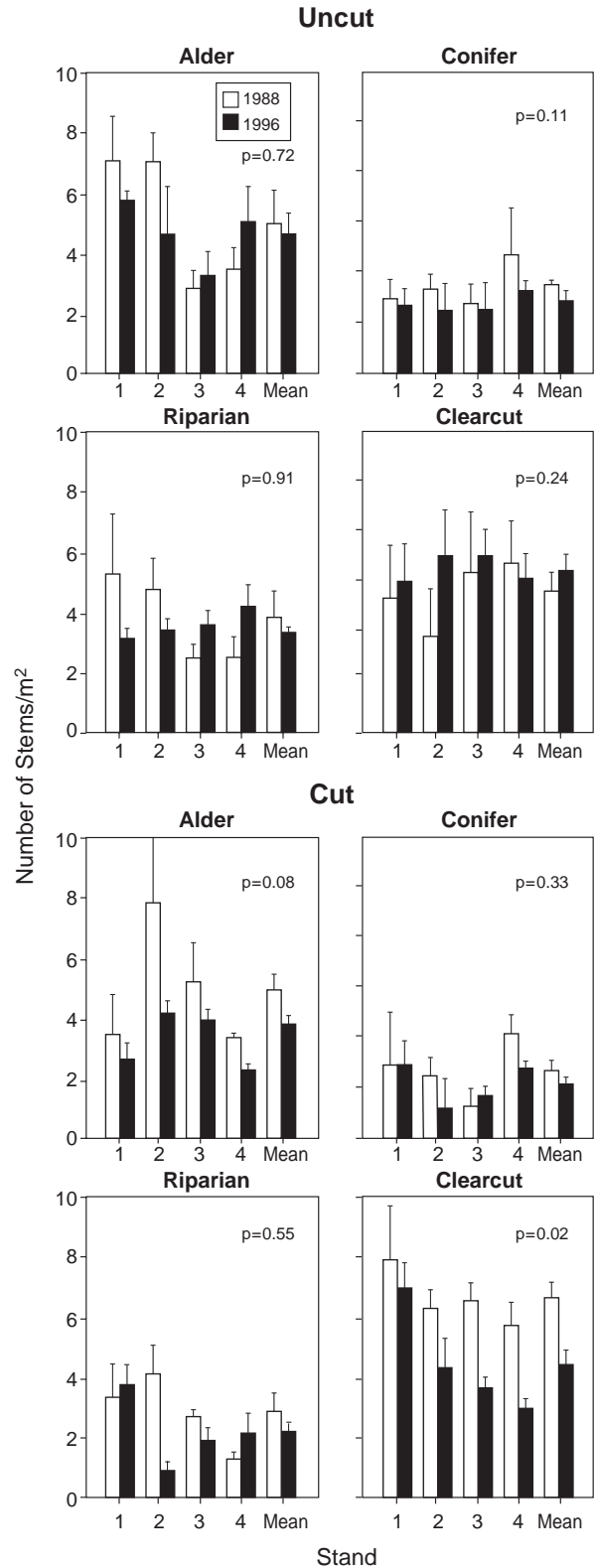


Table 2. Estimates of the proportion of the bud bank on uncut plots that annually produced stems for salmonberry and salal by stand type.

Stand type	Rhizome length (m/m ²)*	Buds (m ²) [†]	Annual stem production/m ² [‡]	Buds producing stems (%) [§]
Salmonberry				
Alder	5.5 (0.6)	138	5.0	4
Conifer	2.6 (0.4)	65	2.2	3
Riparian	4.2 (0.4)	105	3.5	3
Clearcut	15.5 (2.0)	387	5.1	1
Salal				
Thinned	43 (3.9)	1120	20	2
Unthinned	11 (0.6)	165	9	5
Clearcuts	135 (12)	2835	53	2

*Means (with SE given in parentheses) are from Tappeiner et al. (1991) and Huffman et al. (1994a).

[†]Assume 25 buds/m of rhizome for salmonberry (Zasada et al. 1994) and 26, 15, and 21 buds/m of rhizome for salal for thinned, unthinned, and clearcuts, respectively (Huffman et al. 1994b).

[‡]This study.

[§]Values are buds per square metre.

similar in all stand types (Fig. 6). Mean ages of salal stems in the conifer stands ranged from 1 year in the 2- and 4-mm diameter classes to 28 years in the 12- and 16-mm classes. However, size-age relationships are quite variable. For example, we found 1- and 2-year-old stems in classes 4 and 5 along with 6- to 8-year-old stems. Most stems were in diameter classes 1–6. In the conifer stands, where there had been little disturbance, there were 1–3 stems/m² in classes 10 and above, while the clearcuts had none in these classes. In the clearcuts, however, there were three to six times as many stems in the smaller diameter classes as there were in the conifer stands (Fig. 6).

In the cut plots, most salal stems were only 2–4 mm in diameter. Like salmonberry, the numbers of stems in the smallest diameter class varied considerably from spring to winter. In the spring the number of stems in class 1 was often two to four times greater than it was in the winter.

Discussion

The results of this study suggest that rhizomatous shrubs in the understories of forest stands and on recent clearcuts produce many aerial stems annually (often >10/m²) and that this annual production may maintain dense, uneven-age or -size populations of aerial stems that may persist for many years.

Over 8 years, salmonberry populations maintained similar size-class distributions (Fig. 3); salal did the same for 5 years (Fig. 6). The number of stems at the end of these periods was nearly the same as at the beginning (Figs. 2 and 5), although stems died in all size classes. Both species produced more than twice as many stems as were needed to replace those that died. Both species immediately produced new stems when older stems were cut. The changes in stem numbers by size class and the maintenance of diameter distributions that we observed for both species in this study were very similar to those reported by Kurmis and Sucoff (1989) for beaked hazel over a 19-year period.

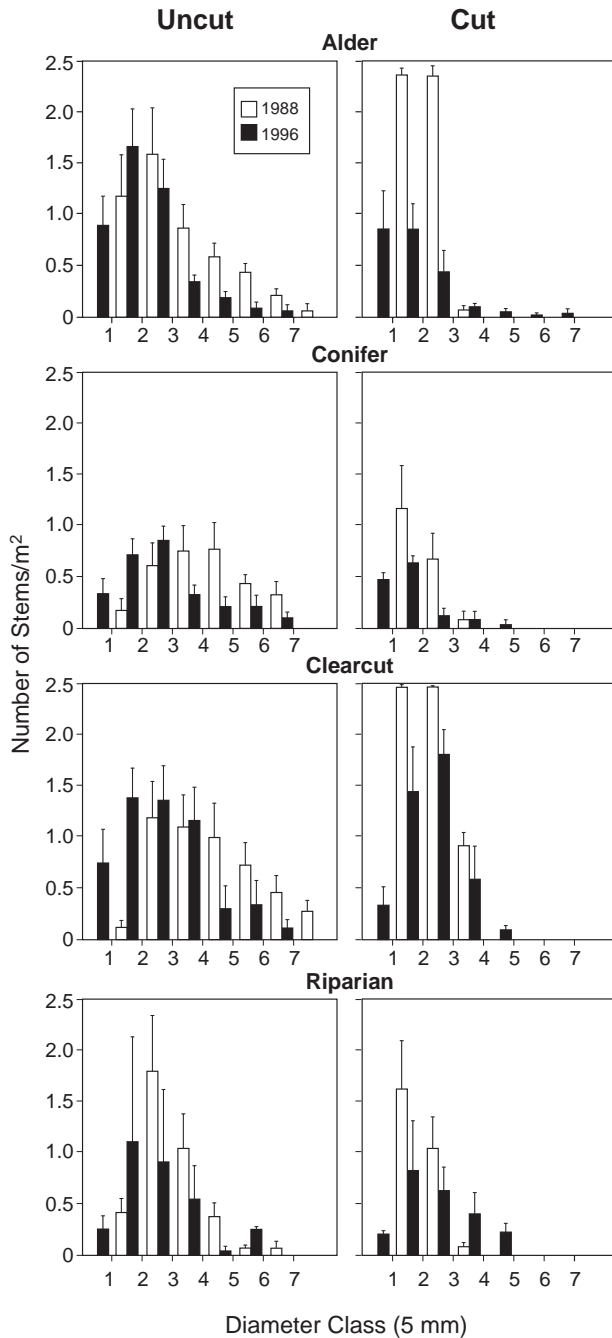
It appears that severe disturbance that kills the aerial stems and causes many new sprouts to occur is not needed

to maintain a dense cover of salmonberry or salal. The alder and unthinned conifer stands had apparently been undisturbed for 50 to >130 years; however, annual production maintained stem density in these stands just as it did in the recently thinned and clear-cut stands. Thus, both shrub species are able to initiate stems even during long disturbance-free periods. Although stem production for both species occurred each year even on undisturbed sites, cutting aerial stems of either species stimulated accelerated production for 2 or 3 years.

Our results confirm those of Balogh and Grigal (1987), who found similar size-density relationships for six shrub species in northern Minnesota as we found for salmonberry and salal (Figs. 3 and 6). However, our results suggest that the relationships vary not only among shrub species but also among stand types and stand density. Different size-density relationships might be expected for shrub populations growing in the understory compared with those growing in the open (Figs. 3 and 6). Balogh and Grigal (1987) suggest that the intercepts of their negative exponential equations may represent new stem production, and the large percentage of stems that they found in the small age or size classes also suggests frequent production of new stems. However, our results indicate that stem numbers in the small size classes vary considerably from year to year and within years, as most stems produced in the spring die by winter. It appears that many more stems are produced than would be needed to maintain shrub cover. For example, in salmonberry populations in alder stands, an average of 4.7 stems·m⁻²·year⁻¹ were produced during our study; only 2.7 stems/m² died during the study, an average of just over 0.3 stems·m⁻²·year⁻¹. The size-density distribution will also change following disturbance, as the young, small stems gradually grow into larger size classes.

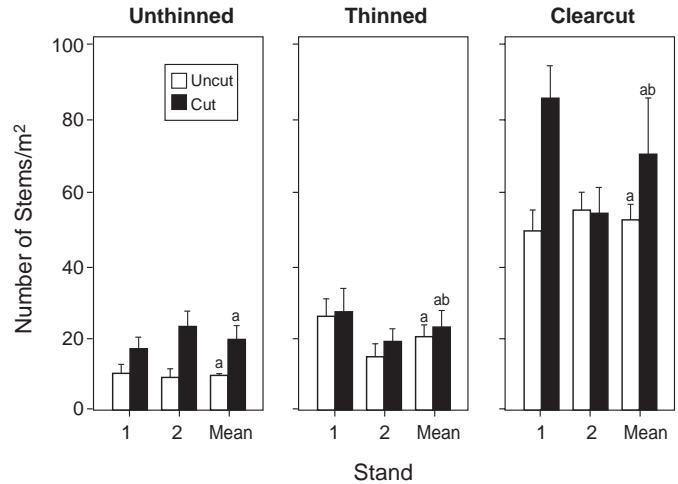
Different stem-size relationships can be expected for different species of the same genus. For instance, *Rubus* spp. are all clonal and exhibit a variety of methods for clonal expansion (Hudson 1959; Ryynanen 1973; Whitney 1986; Suzuki 1987; Jennings 1988; Tappeiner et al. 1991). All of the *Rubus* species produce new aboveground stems each

Fig. 3. Numbers of salmonberry stems per square metre by 5-mm diameter class and by stand type for cut and uncut salmonberry in the winters of 1988 and 1996. Error bars are SE. Numbers of stems in classes 1 and 2 are greater in the spring just after sprouting of new stems (see Fig. 1). There were three cut and three uncut plots in each stand and four stands in each stand type.



year, although the potential longevity of the stems varies; salmonberry is perennial, *Rubus arcticus* L. and *Rubus chamaemorus* L. are annual, and *Rubus idaeus* L. is biennial. *Rubus pubescens* Raf. has a prostrate stem that remains intact for several years and roots at the nodes as it expands. Thus, there is a common theme, characterized by annual shoot production from a buried bud bank, throughout the ge-

Fig. 4. Mean annual salal stem production in unthinned, thinned, and clear-cut stands and means for each stand. Data are untransformed. Error bars are SE. There were three cut and three uncut plots in each stand and two stands in each stand type. For each cutting treatment the 95% confidence intervals around means with different letters do not overlap.

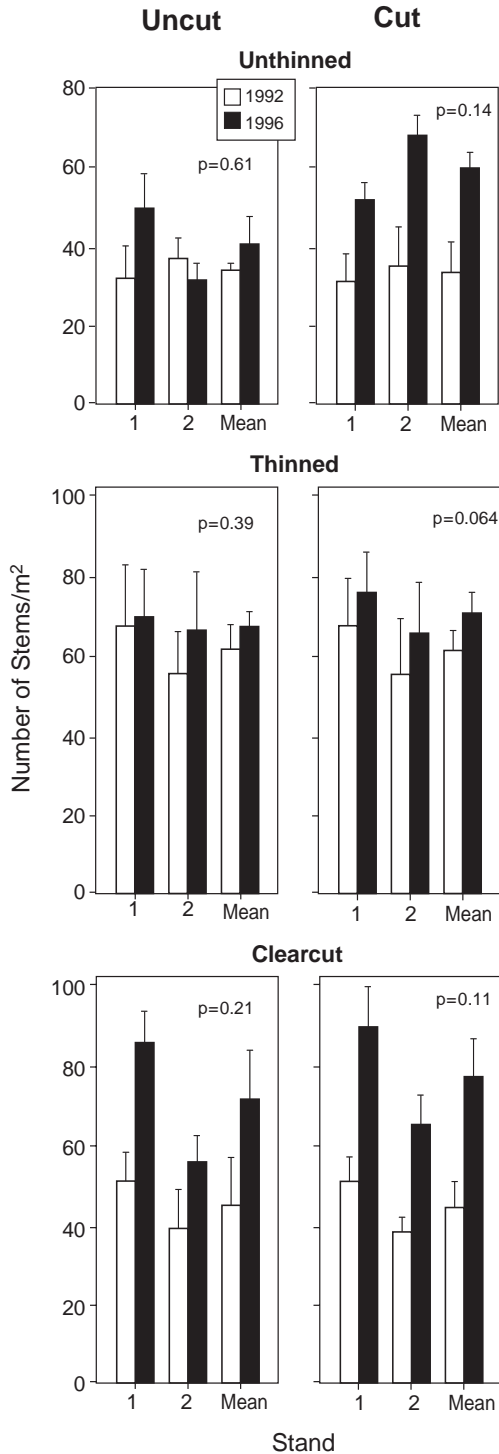


nus *Rubus* for those species that have well-developed root and rhizome systems. Similarly, salal differs from other species in the genus *Gaultheria* in that it produces new stems from rhizomes, while other species (e.g., *Gaultheria procumbens* L. and *Gaultheria hispidula* L. (Bigel)) have prostrate stems and expand above ground by layering.

Aerial stem population dynamics similar to those reported here may be a common characteristic of clonal forest shrubs in many forest stand types. Additional evidence is the maintenance of stem density and turnover of hazel stems reported by Kurmis and Sucoff (1989), which probably required frequent stem initiation. Also, Oregon grape (Huffman and Tappeiner 1997), a rhizomatous shrub that grows on sites adjoining the salal sites in this study, has a stem age–density or size–density distribution like those of salal and salmonberry, as do the six species studied by Balogh and Grigal (1987). Vine maple (*Acer circinatum* Pursh) (O’Dea et al. 1995) and devils club (*Oplopanax horridum* (Smith) Miq.), which grow on sites similar to those in this study but reproduce by layering, have similar uneven age or size distributions. The frequent production of new stems has also been reported for clonal tree populations of understory of tanoak (*Lithocarpus densiflorus* (Hook and Arn. Rehd.)) (Tappeiner and McDonald 1984) and for trembling aspen (*Populus tremuloides* Michx.) (Tappeiner 1982) and northern prickly ash (*Xanthoxylum americanum* Mill.) (Reinartz and Popp 1987), which reproduce from root sprouts. Thus, maintenance of an uneven-age population of ramets and aerial stems may be characteristic of many clonal plant populations (Cook 1984).

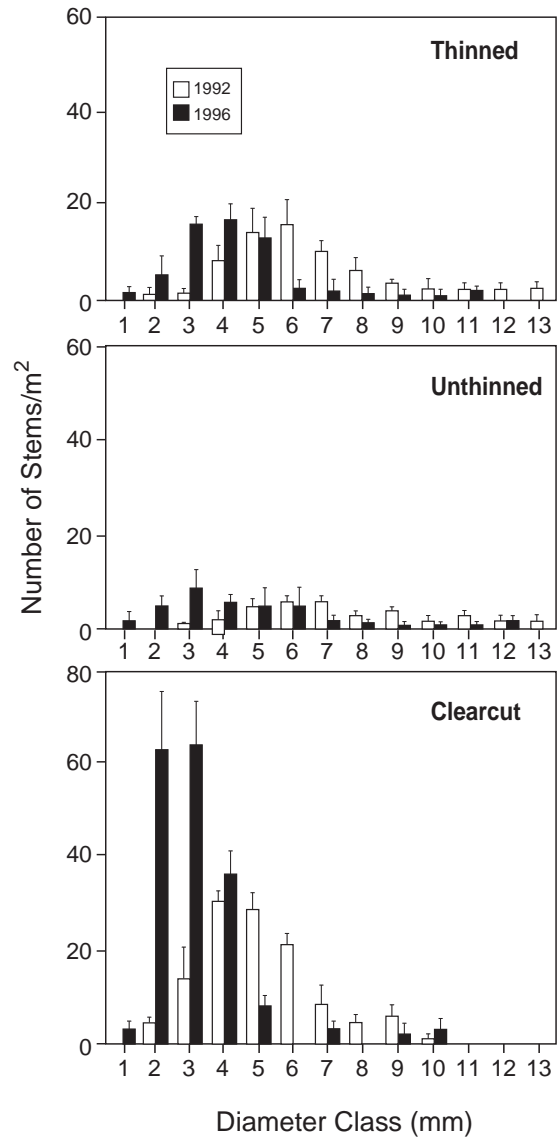
The results of this study and others suggest that these species have a very active bud bank below ground (Table 2). The estimates made by Zasada et al. (1994) and Huffman et al. (1994b) of the numbers of the buds in the bud bank are only a first approximation, but combined with the data presented here, they indicate that for both species, annual “investment in new stems” occurs from only a very small proportion of the bud bank. This bud bank is likely main-

Fig. 5. Mean stem density for salal in 1992 (at the beginning of the study) and in 1996 (at the end) for each stand and for both stands combined; data are untransformed. Error bars are SE. There were three cut and three uncut plots in each stand and two stands in each stand type. The *p* values are for the differences between the 1992 and 1996 means.



tained or increased each year by the production of new rhizomes, and it may decrease as rhizome density decreases with increasing overstory density (Huffman et al. 1994a; Tappeiner et al. 1991) or if pathogens or insects infect the

Fig. 6. Number of salal stems per square metre by 2-mm diameter class and by stand type on uncut plots in the winters of 1992 and 1996. (On cut plots all stems were in classes 1 and 2; data not shown.) Error bars are SE. Numbers of stems in classes 1 and 2 were greater in the spring just after sprouting of new stems (see Fig. 4). There were three uncut plots in each stand and two stands in each stand type.



rhizomes. Furthermore, the growth of these new stems is limited; most of them do not grow beyond the smallest diameter classes before they die. Therefore, stem production represents little cost to the vigor of the clones of these species. In addition to the bud bank below ground, there are also buds in the stems above ground, which are activated when these stems are broken or browsed, that are not included in our estimates.

The size of the bud bank and its potential for producing new stems is likely related to the vigor of the clones growing in different environments. Rhizome density and growth have been shown to be negatively related to overstory density (Tappeiner et al. 1991; Huffman et al. 1994a, 1994b). Zasada et al. (1994) found that stem production from the

salmonberry bud bank was correlated with levels of non-structural carbohydrates: Stem production was highest in the spring when nonstructural carbohydrate levels were the highest. The lower annual stem production of both species in the denser conifer stands (Table 2), compared with the more open clear-cut, thinned, and alder stands, and salmonberry clone mortality after cutting in two conifer stands are likely to be the consequence of lower rhizome density, as well as lower carbohydrate levels in the rhizomes, in the dense conifer stands.

A common trait of forest understory plants appears to be the ability to maintain a large population of young or small individuals. The annual initiation of aerial stems is analogous to ongoing seedling recruitment of *Acer* spp. (Hett 1971; Hett and Loucks 1971; Hibbs 1979) and tanoak (Tappeiner and McDonald 1984). In tree seedling populations, frequent germination of new seedlings is balanced by mortality of older ones (Hibbs 1979; Fried et al. 1988), thus maintaining a size–density or age–density relationship similar to those of salal, salmonberry, and other shrubs (Balogh and Grigal 1987; Kurmis and Sucoff 1989). In the case of the clonal forest shrubs, this relationship is maintained by input of stems from an active bud bank in the rhizome and at the base of older aerial stems, rather than germination of seed.

Implications

The ability of forest shrubs to maintain a dense stable cover, once they are established, has important implications for forest succession and stand development. Continued stem recruitment may allow dense covers of shrub to preclude or greatly limit establishment of trees and other plants in the understory of forest stands and in the open (Strothman 1967; Maguire and Forman 1983; Ishikawa et al. 1999). Like others, we observed no tree regeneration in our plots under either salmonberry (Schrader 1998; Carlton 1988; Henderson 1970) or salal (Bailey and Tappeiner 1998). Forests with dense populations of salmonberry and salal may follow Connell and Slatyer's (1977) inhibition model of succession at the scale of the shrub populations. When gaps occur in the canopy of Douglas-fir or red alder stands, as a result of windthrow or root disease (Oren et al. 1985), for example, they can be readily occupied entirely by salal or salmonberry (Schrader 1998). Even intense disturbance that kills the aerial stems may not substantially affect the stability of these populations, because a new cover of aerial stems will sprout immediately if the bud bank at the base of aerial stems and in the rhizomes is not damaged (Zasada et al. 1994).

However, increasing overstory density may reduce the cover and sprouting potential of these shrubs. Conifers established immediately after disturbance among resprouting shrubs will overtop them in 15–20+ years. Shrub density and vigor may decline to very low levels as the conifer canopy closes, and may remain low for 50+ years if high overstory density is maintained. Similarly, shade-tolerant species like western hemlock often become established in the understory, so that shrub cover is reduced throughout the stand or in patches as their crowns develop. If trees become established and overtop the shrubs, the cover and rhizome density of those shrubs may be reduced (Table 2).

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