# Clonal expansion and seedling recruitment of Oregon grape (*Berberis nervosa*) in Douglas-fir (*Pseudotsuga menziesii*) forests: comparisons with salal (*Gaultheria shallon*)[1]

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**Abstract**: Seedling regeneration and morphology of Oregon grape (*Berberis nervosa* Pursh) and salal (*Gaultheria shallon* Pursh) were studied in thinned and unthinned Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands in the central Coast Range, Oregon. Above- and below-ground growth of both species were significantly and negatively correlated with stand density. Oregon grape appears to have less potential for vegetative spread than does salal. It produced two to three times fewer rhizome extensions, and rhizome extensions were only half as long as those of salal. Oregon grape seedlings were common in areas of moss ground cover among patches of the two species. Salal seedlings were restricted to decaying logs. Seedling densities of Oregon grape in thinned stands were more than six times those in unthinned stands. For Oregon grape, understory establishment is accomplished by seedling establishment and recruitment of new genets. In contrast, salal maintains itself in forest understories primarily through vegetative growth, since its seedling establishment is restricted mainly to decayed wood. Continual recruitment of new aerial stems or ramets enables Oregon grape to maintain a dense cover once it is established in the understory.

**Résumé** : La régénération et la morphologie des semis du vinettier nervuré (*Berberis nervosa* Pursh) et de la gaulthérie salal (*Gaultheria shallon* Pursh) ont été étudiées dans des peuplements éclaircis et non éclaircis du sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco), dans la chaîne côtière centrale de l'Oregon. La croissance épigée et hypogée des deux espèces était significativement et négativement corrélée avec la densité du peuplement. Le vinettier semble avoir moins de potentiel pour la propagation végétative que la gaulthérie. Il a produit de deux à trois fois moins d'extensions du rhizome et celles-ci représentaient seulement la moitié de la longueur de celles de la gaulthérie. Les semis du vinettier étaient communs dans les aires couvertes de mousses, situées entre les colonies des deux espèces. Les semis de la gaulthérie se limitaient aux billes en décomposition. La densité des semis du vinettier dans les peuplements éclaircis était six fois plus élevée que dans les peuplements non éclaircis. Dans le cas du vinettier, l'établissement en sous-étage se fait par des semis et le recrutement de nouveaux genets. Par contre, la gaulthérie se maintient en sous-étage de la forêt surtout par sa croissance végétative, puisque l'établissement de ses semis est limité principalement au bois en décomposition. Le recrutement continuel de nouvelles tiges ou ramets aériens permet au vinettier, une fois établi en sous-étage, de maintenir un couvert dense.
[Traduit par la Rédaction]

## Introduction

Oregon grape (*Berberis nervosa* Pursh) and salal (*Gaultheria shallon* Pursh) are evergreen, clonal shrubs common in the understory of conifer forests in the Pacific Northwest. Both occur in all stages of stand development (Long and Turner 1975), ranging from the stem initiation stage following fire or timber harvest through old-growth (Oliver 1981; Messier and Kimmins 1991; Messier 1992; Huffman et al. 1994*a*). These shrubs occur as small (1.0 × 1.0 m), sparse (≤20% cover), single-species patches in unthinned stands at the stem exclusion stage; however, in thinned stands, they may become dense (≥70% cover) patches from 1.0 to 1.5 m tall and from 2 to over 10 m across. Because of their frequency, extent, and cover, these species are likely to exert a major effect on understory development. For example, they inhibit the establishment of such shade-tolerant trees as western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (D.W. Huffman and J.C. Tappeiner, unpublished), bigleaf maple (*Acer macrophyllum* Pursh) (Fried et al. 1988), and probably shrubs and herbs as well. What is the method of invasion for each species, seedling recruitment or vegetative expansion, and how is invasion affected by thinning the overstory?

Previous studies have shown that salal has the potential for considerable rhizome expansion and development of a dense cover of aerial stems. Its clonal development and morphology (Bunnell 1990; Huffman et al. 1994*a*, 1994*b*), as well as aerial stem density and height (Messier 1992), are strongly related to overstory density. Seedling establishment of salal is higher on

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**Table 1.** Overstory stand characteristics (mean (range in parentheses)) for thinned (T) and unthinned (U) stands used in the study of Oregon grape and salal.

| Stand | Age (years) | Basal area ($m^2$/ha) | Density (trees/ha) | RD |
|---|---|---|---|---|
| T1 | 55 | 48 (25–62) | 278 (148–346) | 20 (11–25) |
| T2 | 55 | 43 (24–62) | 272 (148–346) | 20 (11–25) |
| T3 | 55 | 43 (26–61) | 253 (198–346) | 18 (14–25) |
| T4 | 55 | 46 (28–64) | 290 (148–395) | 21 (11–29) |
| T5 | 55 | 45 (26–56) | 272 (198–395) | 20 (14–29) |
| U1 | 35 | 47 (42–64) | 1433 (939–1680) | 105 (69–123) |
| U2 | 40 | 63 (40–77) | 803 (692–1038) | 59 (43–76) |
| U3 | 40 | 53 (45–62) | 704 (494–1137) | 52 (40–83) |
| U4 | 55 | 52 (36–65) | 370 (247–494) | 27 (18–36) |
| U5 | 55 | 63 (59–70) | 469 (445–494) | 34 (32–36) |

**Note**: Stands T5 and U5 were used for seedling surveys only. RD, Curtis's (1982) relative density.

decayed wood and disturbed soil than on undisturbed forest floor, and the rate of establishment on these substrates is greater in thinned stands than in unthinned stands (Tappeiner and Zasada 1993; Huffman et al. 1994*a*). Prior to this study, there was no information on clonal development and seedling reproduction of Oregon grape and no comparisons of these reproductive methods between Oregon grape and salal.

The objectives of this study were to (*a*) determine the importance of seedling and vegetative reproduction for the colonization and persistence of Oregon grape in thinned and unthinned Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands and compare them with salal and (*b*) provide information on the structure of Oregon grape clones and on the age structure and biomass of Oregon grape populations in those stand types.

## Methods

### Study sites

This study was conducted in Oregon's central Coast Range near Philomath, Oregon (approximately 305 m above sea level). Average annual precipitation is 178 cm, and summer and winter temperatures average 17 and 5°C, respectively (NOAA 1987). Soils are moderately well-drained clay loams derived from Flournoy sandstone with some isolated areas of basaltic material (Franklin and Dyrness 1973; Orr et al. 1992).

Forest overstories are composed primarily of Douglas-fir with a lesser component of western hemlock. Hardwoods present include red alder (*Alnus rubra* Bong.) and bigleaf maple. Common understory species include Oregon grape, salal, vine maple (*Acer circinatum* Pursh), salmonberry (*Rubus spectabilis* Pursh), oceanspray (*Holodiscus discolor* (Pursh) Maxim.), red huckleberry (*Vaccinium parvifolium* Sm.), western swordfern (*Polystichum munitum* (Kaulf.) L. Presl.), and bracken fern (*Pteridium aquilinum* (L.) Kuhn).

### Stand selection

Ten stands were selected on the basis of management history and overstory density (Table 1). Selected stands had developed from natural regeneration after timber harvest and ranged in age from 35 to 55 years. Five stands had been thinned 5–8 years previously (stands T1–T5) and five had not (stands U1–U5). Thinned and unthinned stands were the same age and were located within 1 km of one another, on similar soils and aspects. Stand understories contained patches of Oregon grape, salal, and other species. Mosses were the primary cover between shrub patches. Thinned stands had fewer and larger trees and slightly lower basal area than did unthinned stands (Table 1). Approximately 40% of the trees in stand U1 were western hemlock.

### Overstory measurements

Plots for overstory measurements were centered on each clonal fragment plot (T1–T4 and U1–U4) and on seedling plots in T5 and U5. In each of these plots (0.05 ha; 8-m radius), all live trees were tallied and their diameters measured at 1.5 m (breast height). These measurements were used to calculate overstory stand density indexes: basal area (BA, square metres per hectare), Curtis's (1982) relative density (RD), and trees per hectare (TPHa).

### Oregon grape clonal fragments

In each of eight stands (T1–T4 and U1–U4), eight plots (4 $m^2$ each) were established to examine clonal fragments of Oregon grape (64 plots total). Plots (Fig. 1) were randomly selected to encompass from 5 to 22 aerial stems of Oregon grape and were established (4 plots/stand) (*i*) at the edges of dense populations (15–22 aerial stems/plot) of Oregon grape stems and (*ii*) in areas where the stems were less dense (5–10 aerial stems/plot).

Percent cover of Oregon grape was estimated in each plot. Stems within the plots were counted and mapped, and their current growth (most recent internodal length plus terminal bud) was measured. One-year-old stems were noted. We then excavated each stem and followed its rhizome connections until they ended, or were traced out of the plot. Rhizome networks were mapped and the following information was recorded: new rhizome extension lengths, number of connected ramets, and distance between ramets. Current rhizome extensions were identified by their bright yellow color and lack of suberized tissue.

### Salal rhizomes

Our objective for salal was to compare its rhizome development and growth with Oregon grape rhizomes. The above- and below-ground architecture of clonal fragments had been reported previously (Huffman et al. 1994*a*; Bunnell 1990). Salal rhizomes within 1–3 m of the Oregon grape plots were selected and their associated rhizomes (16/stand) were excavated. In unthinned stands (U1–U4) with small salal fragments (Huffman et al. 1994*a*), total rhizome length of clonal fragments ranged from 60 to 660 cm. Fragments ranging from 105 to 600 cm in total rhizome length were excavated in thinned stands. Total rhizome length, number of ramets, number of current rhizome extensions, and length of current rhizome extensions were measured. Definitions of ramets and current rhizome extensions followed Cook (1983) and Huffman et al. (1994*a*). All Oregon grape fragments with 60 cm or more total rhizome length were used for comparisons ($n$ = 60 in thinned stands; $n$ = 66 in unthinned stands) with salal fragments.

### Surveys of Oregon grape and salal seedlings

The number of seedlings was counted and recorded for each of the 64 plots where clonal fragments were excavated. They were easily identified on excavation by observable ortets and a lack of connected ramets. In addition, four large plots (15 × 15 m) were established in all 10 stands (Table 1) to inventory both Oregon grape and salal seedlings. Plots were located among the shrubs where the primary cover was moss. Seedlings were tallied according to the following height classes: 0–1, 2–5, and >5 cm. Because salal establishes preferentially on rotten logs and stumps (Huffman et al. 1994*a*), the number of decay class III, IV, and V (Sollins 1982) logs per plot was recorded.

### Ages and biomass of Oregon grape populations

In each of the eight stands, four plots (0.5 $m^2$ each) were established within dense Oregon grape stem populations (32 plots total). These plots were located 1 m from the edges of populations in which clonal fragments were sampled. Percent cover of Oregon grape was estimated for each plot. To determine the age structure of Oregon grape

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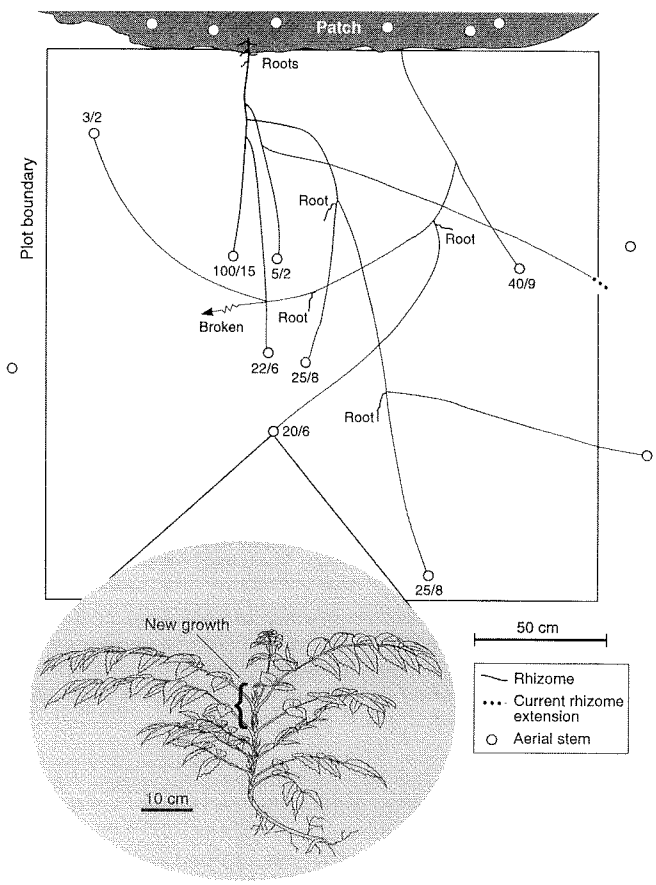
**Fig. 1.** Sample plot of Oregon grape clonal fragments. Numbers associated with aerial stems represent stem height (cm)/age (years). Enlargement illustrates aerial stem morphology and new growth.




populations, aerial stems rooted within the plots were counted and aged (by counting leaf scars) and their modal height was estimated. The stems were clipped at the base and returned to the laboratory, where they were dried (70°C for 48 h) and weighed; the aboveground biomass (g/m$^2$) was then calculated for each plot.

### Data analyses

One-way analysis of variance (ANOVA) was used to test for main effects of overstory stand condition on clonal fragment growth and morphology, population density and biomass, and seedling establishment parameters ($p \leq 0.05$). Data were normalized by square-root transformations when necessary. When main effects were found, least significant difference tests ($p \leq 0.05$) were used to test among groups.

Relationships among average overstory density values (BA, RD, and TPHa) and growth, morphology, and population parameters were tested by simple linear regression ($p \leq 0.05$). Natural log and square-root data transformations were used as needed in these tests.

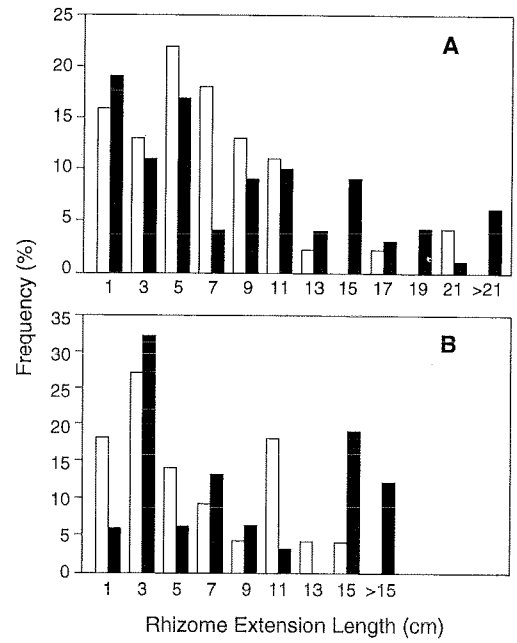
Contingency tables ($p \leq 0.05$) were used to test for differences in the proportions of plots with and without seedlings and in current rhizome extensions by stand condition. We found no significant differences in Oregon grape rhizome growth and clonal structure between dense and less dense populations. Data from these clonal fragments were, therefore, combined to compare salal and Oregon grape growth and to test for differences among stand types.

## Results

### Oregon grape and salal rhizome growth

Oregon grape appears to have less potential for vegetative spread than does salal. In both thinned and unthinned stands,

**Fig. 2.** Frequency distribution of current rhizome extension length for Oregon grape (open bars) and salal (solid bars) in (A) thinned and (B) unthinned stands.




Oregon grape produced two to three times fewer current rhizome extensions per unit rhizome length than did salal (Table 2). Further, salal's current rhizome extensions were about 1.5 times longer than those of Oregon grape (Table 2). Only 8% of Oregon grape's current rhizome extensions were >12 cm in length in thinned and unthinned stands; for salal, 27 and 31% of current extensions were >12 cm in length under these respective stand types (Fig. 2). Current rhizome proportions of total fragment length reflect Oregon grape's fewer and shorter new rhizomes (Table 2).

Number of ramets per unit of rhizome length did not differ between the two species (Table 2). There were, however, somewhat more ramets per unit rhizome length for salal in thinned stands (0.020/cm) than in unthinned stands (0.016/cm) ($p \leq 0.10$). This parameter for salal was negatively correlated with RD at $p = 0.10$ ($r^2 = 0.39$).

### Seedling density

Seedling densities of both species were significantly greater in thinned stands (Fig. 3). For Oregon grape, this was true for each size class, as well as for all size classes combined. For salal, this was true only for combined size classes. Although 90% of all seedling plots in thinned stands contained one or more Oregon grape seedlings, only 45% did so in unthinned stands. Oregon grape seedlings were found in 31% of the clonal fragment plots in thinned stands whereas no seedlings were found among fragments in unthinned stands. Salal seedlings were found in 40% of the seedling plots in thinned stands and in 20% of these plots in unthinned stands ($p = 0.10$). No salal seedlings were found where rhizomes were excavated.

Significantly more Oregon grape than salal seedlings of every size class were found in thinned stands (Fig. 3). When all sizes are combined, Oregon grape seedling density in thinned stands (374/ha) was more than three times that of salal (114/ha). In unthinned stands, there were no significant differences

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**Table 2.** Morphological characteristics (means (with SE in parentheses)) of Oregon grape and salal rhizomes in thinned and unthinned stands.

| Characteristic | Species | Stand condition | |
|---|---|---|---|
| | | Thinned | Unthinned |
| Ramets/fragment length (no./cm) | Oregon grape | 0.017 (0.002) | 0.015 (0.001) |
| | Salal | 0.020 (0.001) | 0.016 (0.001) |
| Current extensions/rhizome length (no./m) | Oregon grape | 0.4 (0.08) | 0.1 (0.04) |
| | Salal | 0.8 (0.1) | 0.3 (0.07) |
| Current extensions/fragment (%) | Oregon grape | 2.9 (0.7) | 0.8 (0.4) |
| | Salal | 7.2 (0.9) | 2.5 (0.6) |
| Length of current extensions (cm) | Oregon grape | 7.0 (0.6) | 6.4 (0.9) |
| | Salal | 10.7 (0.9) | 9.4 (1.2) |

**Fig. 3.** Density of Oregon grape and salal seedlings by size class in thinned (open bars, Oregon grape; hatched bars, salal) and unthinned (cross-hatched bars, Oregon grape; solid bars, salal) stands. Bars with the same letter in size class groupings denote statistically similar means at a 95% significance level.

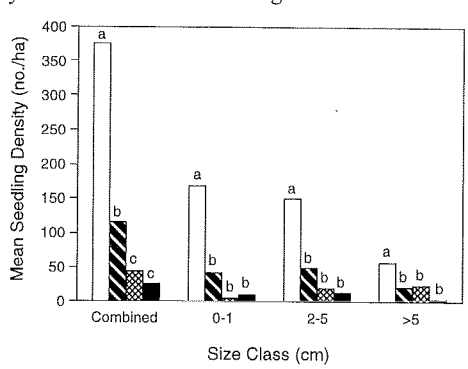
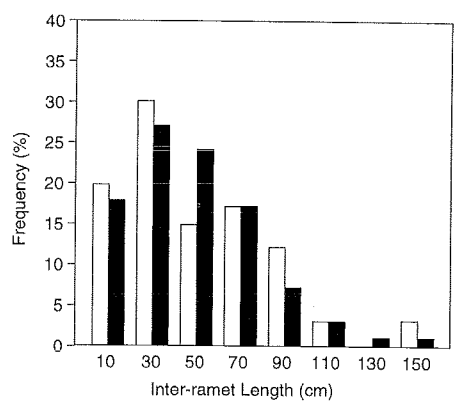



**Fig. 4.** Frequency distribution of inter-ramet lengths measured in Oregon grape clonal fragments in thinned (open bars) and unthinned (solid bars) stands.




between seedling density of the two species. However, Oregon grape seedlings occurred in a greater proportion ($p = 0.10$) of the plots (45%) than did salal seedlings (20%).

In thinned stands, salal seedling density was positively correlated ($p = 0.006$; $r = 0.59$) with the number of decaying logs per plot. This relationship was weaker for unthinned stands ($p = 0.06$; $r = 0.43$). No correlation existed between number of seedlings of either species and overstory density indexes.

### Morphology of Oregon grape clones

Aerial stems of Oregon grape clones are produced as rhizomes turn upward. As stems grow, monopodially elongating from a terminal meristem, new compound leaves with 9–19 coriaceous, evergreen leaflets (Pojar and MacKinnon 1994) are produced (Fig. 1). Leaves can persist for up to 5 years before being shed. Over 80% of the sampled stems ($n = 458$) were <30 cm in height.

Below ground, rhizomes branched at angles of <90° to the direction of the parent rhizome's growth. On clones, rhizome branches are generally located distally from ramets; few rhizomes appeared to be initiated from buds near ramet bases. Apparently, rhizomes branch during extension and continue to elongate prior to aerial stem and ramet formation. We found rhizomes growing at soil depths of up to 45 cm and estimated that 75% of all rhizomes excavated ($n > 420$) were growing within the mineral soil. Rhizome networks can be extensive (Fig. 1). Although no attempt was made to excavate entire clones, the largest clonal fragment sampled consisted of 5 m of rhizome and 15 ramets.

### Effects of overstory on Oregon grape morphology

Morphology of Oregon grape clones was not obviously affected by overstory stand density. There was no significant difference in mean inter-ramet length (length of rhizome connecting two or more ramets) in thinned stands (51.2 cm) and unthinned stands (49.7 cm) (Fig. 4). In addition, there was no difference in average maximum inter-ramet length in thinned stands (150 cm) and unthinned stands (160 cm). Inter-ramet length was not significantly correlated with overstory stand density.

Mean length of Oregon grape current rhizome extensions did not differ between stand conditions (Table 2), and it was not significantly correlated with overstory stand density. Further, there was no difference in mean number of ramets per 100 cm of length of rhizome for fragments in thinned (1.7 ramets) and unthinned (1.5 ramets) stands.

### Overstory effects on aerial stem and rhizome growth

Aerial stem elongation (new growth) was negatively correlated with overstory RD and TPHa ($p < 0.0001$; $r = -0.53$). Average annual stem elongation (±SE) was nearly 30% greater in thinned stands (4.0 ± 0.15 cm) than in unthinned stands (3.1 ± 0.1 cm), and maximum current height increment for all stems sampled was 13.0 cm (stand T2). Elongation was also

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**Fig. 5.** Biomass of Oregon grape populations estimated from measurements of cover and aerial stem height.

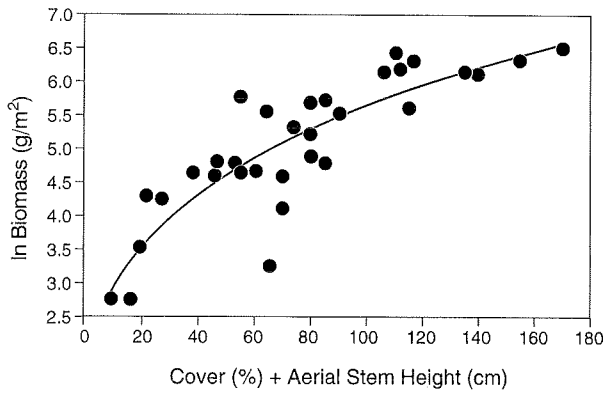
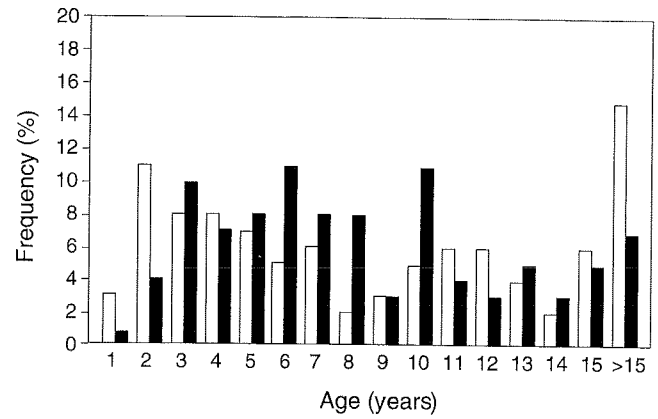



**Fig. 6.** Age distribution of aerial stems in populations of Oregon grape in thinned (open bars) and unthinned (solid bars) stands.




positively correlated with stem height ($p < 0.0001$; $r = 0.76$ and 0.57 for thinned and unthinned stands, respectively).

In thinned stands, more than twice the number of current rhizome extensions were found per plot than in unthinned stands. This parameter was negatively correlated with overstory stand density ($p = 0.002$; and $r^2 = 0.81$ for RD). Further, current extensions were found in 72% of the thinned stand plots, a significantly ($p = 0.006$) greater proportion than the 41% found in unthinned stands. Current rhizome extension made up a significantly larger percentage of clonal fragment rhizome systems in thinned stands (2.9% of total rhizome length) than in unthinned stands (0.8% of total rhizome length). Percent new rhizome per fragment was significantly ($p \leq 0.001$) negatively correlated ($r^2 = 0.62$) with overstory density. We detected no differences in morphology or growth of clones at the edges of dense populations (Fig. 1) and of those not associated with dense populations.

### Clonal populations

Oregon grape patches in thinned stands had significantly greater biomass, stem density, stem height, and average cover than did those in unthinned stands (Table 3). Biomass and cover were negatively correlated ($r^2 = 0.87$ and 0.86, respectively) with overstory RD. Stem density in populations was also negatively correlated with overstory density, but only at $p = 0.10$ ($r^2 = 0.46$ for tests with RD).

Biomass of Oregon grape populations was positively correlated ($p < 0.0001$) with plot percent cover and modal stem height (Fig. 5). Dry mass of stems can be predicted ($r^2 = 0.74$) for 1-m$^2$ plots by the following equation:

$$[1] \quad \ln \text{biomass (g/m}^2) = 1.504[\text{cover (\%)} + \text{modal stem height (cm)}]^{0.287}$$

Biomass ranged from 16 to 100 g/m$^2$ in unthinned stands and from 148 to 665 g/m$^2$ in thinned stands.

Stem age distribution in populations followed an all-age pattern (Fig. 6). Populations in thinned stands had proportionally more young (first- and second-year) aerial stems than did those in unthinned stands. We noted new ramets sprouting beneath established ones in both stand types.

Aerial stems also appear to be long-lived. Although estimations became more difficult with increasing stem age, we sampled stems in all stands that had 20 height growth increments. The oldest living stem was estimated to be 30 years old (stand U2).

**Table 3.** Characteristics (means (with SE in parentheses)) of Oregon grape clonal populations in thinned and unthinned stands.

| | Stand condition | |
|---|---|---|
| Characteristic | Thinned | Unthinned |
| Biomass (g/m$^2$) | 368.0 (48.8)*a* | 120.0 (24.4)*b* |
| Aerial stem density (no./m$^2$) | 26.3 (4.2)*a* | 10.9 (1.3)*b* |
| Height (cm) | 38.4 (5.8)*a* | 22.3 (2.5)*b* |
| Cover (%) | 64.4 (4.9)*a* | 28.1 (4.5)*b* |

**Note**: Means followed by the same letter across rows are statistically similar at a 95% significance level.

## Discussion

Oregon grape and salal colonize the understory of Douglas-fir forests by different methods. On our study sites, seedling establishment was Oregon grape's principal means of colonization whereas salal was much more dependent on rhizome expansion and vegetative regeneration than on seedling establishment. Once they establish dense covers, however, both species maintain them by vegetative recruitment of aerial stems and ramets.

Above ground, Oregon grape aerial stem growth, density, cover, and consequent biomass were greatest in thinned stands (Fig. 5). Below ground, the density of new rhizomes per clonal fragment and per plot was also greater in thinned stands than in unthinned stands for both species. We found no increase in mean rhizome extension in Oregon grape in thinned stands; however, salal mean rhizome extension was greater in thinned stands, and the frequency of rhizome extensions ≤12 cm was two to three times that of Oregon grape in both stand types (Fig. 2). The values for salal rhizome extension and numbers and the relationships of salal growth to overstory density in this study are similar to those reported by Huffman et al. (1994*a*). Bailey's (1996) survey of 32 pairs of thinned and unthinned Douglas-fir stands in western Oregon supports the results of this study. He reported only slightly greater Oregon grape cover in thinned stands whereas cover of salal in thinned stands was nearly double that in unthinned stands.

Differences in rhizome growth between Oregon grape and salal may be related to the soil environment in which their

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rhizomes occur. Oregon grape rhizomes grew in mineral soil from 10 to 45 cm below ground whereas salal rhizomes were generally only 1–5 cm below the mineral soil surface or in organic layers (Huffman et al. 1994*a*). Similarly, extensive salmonberry clones (Tappeiner et al. 1991) with rapid rhizome growth occur in the forest floor or 1–5 cm below the mineral soil surface.

Oregon grape seedling density was three times greater than salal's in both thinned and unthinned stands. In thinned stands, its density was greater than salal's in all three size classes. This suggests that seedling recruitment is an ongoing process, and not an infrequent occurrence. As reported in other studies (Sabhasri 1961; Huffman et al. 1994*a*), salal seedlings were mainly restricted to decaying logs or stumps, and their density was low, especially in unthinned stands. Oregon grape, on the other hand, was found throughout the 15 × 15 m plots that we examined and on the plots from which we extracted rhizomes. Thus, Oregon grape apparently colonizes a wider range of microsites by seeding than does salal in both thinned and unthinned stands. Seedling recruitment enables Oregon grape to expand the perimeter and density of established patches, as well as to establish new patches.

Seed availability was not determined for either species, and it could have affected the number of Oregon grape and salal we found, as could predation and dispersal. However, our observations of fruit production indicate that there was considerable seed of both species, especially in the thinned stands.

The greater seedling recruitment of Oregon grape is perhaps related to seed size. Oregon grape averages 58 890 seeds/kg (Rudolph 1974), and salal averages 7.1 million seeds/kg (Dimock et al. 1974). Other work on similar sites showed that species with large seed, e.g., vine maple and bigleaf maple, had higher rates of seedling establishment than did salal (Tappeiner and Zasada 1993). Also, high rates of seedling recruitment have been reported for *Berberis darwinii* Hoak (Allen 1991). Density of Oregon grape seedlings in this study was much higher than that of vine maple, a large-seed species, on similar sites (O'Dea et al. 1995).

Oregon grape aerial stem density and growth increased with decreasing overstory density. Thus, new aerial stems and ramets (Cook 1983) become established among older ones. As older stems die, they are replaced by younger ones (Fig. 6) and a dense cover is maintained (Kurmis and Sucoff 1989). Similar population size and age structures and apparent persistence have been reported for salal (Huffman et al. 1994*a*) and salmonberry (Tappeiner et al. 1991) on similar sites. Salal appears to be able to maintain considerably more biomass in the understory than does Oregon grape. The Oregon grape aboveground biomass was only 5–15 and 18–27% of salal's biomass in unthinned and thinned stands, respectively, on similar sites (Huffman et al. 1994*a*).

Thinning can be expected to increase density or cover of established patches of Oregon grape and to increase the establishment of seedlings in open areas among shrubs. For salal, however, both patch density and size are likely to increase vegetatively by rhizome growth.

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