

VINE MAPLE CLONE GROWTH AND REPRODUCTION IN MANAGED AND UNMANAGED COASTAL OREGON DOUGLAS-FIR FORESTS¹

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Abstract. Vine maple (*Acer circinatum* Pursh.) clone development, expansion, and regeneration by seedling establishment were studied in 5–240 yr old managed and unmanaged Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands in coastal Oregon. Stem length, number of stems, and crown area were all significantly ($P \leq 0.01$) related to stand age, and clone development was most rapid during the first 50 yr of stand development. Following clear-cutting, clones were clumps of 1–3 m long upright stems. Fifty years after disturbance, clones consisted of 5–15 drooping aerial stems >10 m long and basal sprouts 1–2 m long; some stems had been pinned to the forest floor by fallen trees or branches and had layered. In stands >120 yr in age, clones were often quite complex, composed of several decumbent stems each of which connected the ramets of 1–10 new aerial stems.

Vine maple clone expansion occurs by the layering of long aerial stems. Over 95% of the layered stems we observed had been pinned to the forest floor by fallen debris. Unsevered stems that we artificially pinned to the forest floor initiated roots within 1 yr. Thinning may favor clonal expansion because fallen slash from thinning often causes entire clones to layer, not just individual stems.

Clonal vine maple seed production and seedling establishment occurred in all stages of stand development except dense, young stands following crown closure. There were more seedlings in thinned stands than in unthinned stands and in unburned clearcuts than in burned clearcuts.

Key words: basal sprouting; clonal architecture; clonal populations; clones; disturbance; coastal Douglas-fir forests; forest succession; layering; Pacific Northwest; ramets; silviculture; understory; vegetative reproduction; vine maple.

INTRODUCTION

Vine maple (*Acer circinatum* Pursh.) is common in the understory of the Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests of western Oregon and Washington. It is a deciduous, clonal shrub that grows on a variety of sites, ranging from relatively dry *Pseudotsuga-Holodiscus-Gaultheria* to moist *Tsuga-Polystichum-Oxalis* plant associations (Franklin and Dyrness 1973). Although relatively pure vine maple stands do exist, plants usually grow in combination with other understory species such as salal (*Gaultheria shallon* Pursh.), salmonberry (*Rubus spectabilis* Pursh.), hazel (*Corylus cornuta californica* (A. DC.) Sharp), ocean spray (*Holodiscus discolor* (Pursh.) Maxim.), elderberry (*Sambucus* sp.), sword fern (*Polystichum munitum*), and various huckleberries (*Vaccinium* sp.).

Vine maple has two modes of vegetative reproduc-

tion: layering and sprouting (Anderson 1967). The species layers when its stems contact the forest floor, root, and produce new ramets. When vine maple stems are killed by cutting or fire, basal sprouts, in clumps of from 10 to >50 stems ≤ 1 m long, are produced within 1 yr.

Vine maple clones persist through all stages of forest stand development (Schoonmaker and McKee 1988). They vigorously sprout basally in recent clearcuts and burns and, because they are shade tolerant, may survive complete canopy closure during the stem exclusion phase of stand development (Oliver and Larson 1990) in dense, young Douglas-fir stands 20–30 yr old. Consequently, vine maple may be a predominant understory species at the beginning of the stem reinitiation phase after self-thinning or prescribed thinning of the overstory. Vine maple clones are also common in old-growth Douglas-fir stands (Spies and Franklin 1989), frequently occurring in open areas created by the root disease caused by *Phellinus weirii*.

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TABLE 1. Characteristics of the four classes of Douglas-fir (*Pseudotsuga menziesii*) stands studied. Mean values are presented; values in parentheses are the range of averages.

Stand type	No. stands	Stand characteristics			Total no. of clones sampled
		Basal area (m ² /ha)	Tree density (no./ha)	Vine maple clone density (no./ha)	
Class 1 (5–20 yr)*					
Clear-cut (burned)	3	73 (25.9–168.4)	203
Clear-cut (unburned)	3	51.0 (16.2–220.2)	142
Class 2 (21–70 yr)*					
Unthinned	5	50.1 (20.7–56.0)	471 (237–628)	36 (13.0–51.8)	191
Thinned	5	30.0 (31.4–42.3)	248 (133–319)	41 (6.5–68.0)	168
Class 3 (71–120 yr)*					
Unthinned	3	40.8 (30.6–53.6)	131 (121–141)	47 (19.4–142.5)	120
Thinned	3	44.37 (38.2–50.5)	171 (148–213)	39 (32.4–55.0)	107
Class 4 (121–240 yr)*					
Unthinned	3	31.1 (30.5–32.1)	30 (20–49)	55 (32.4–93.9)	152

* Age of stand.

Information on the growth and regeneration of vine maple clones in relation to stand age is important for understanding forest stand development, particularly understory growth and dynamics, and also the effects of forest management practices. In the future, forest stand management practices will be more concerned with total ecosystem values, and understory species such as vine maple will be given increased consideration for values such as aesthetics, structure, forage for wildlife habitat, and maintenance of understory herbaceous species. Knowledge of vine maple's reproductive biology is essential for determining how the species is affected by practices such as thinning and prescribed burning, which reduce overstory density and competition and also have a physical impact on clones.

In this study, we investigated the potential for vine maple clonal development and expansion via layering in different stages of forest succession. We also examined the relative importance of layering vs. seedling regeneration for vine maple regeneration. Vine maple regeneration from seed is reportedly infrequent in the understory of undisturbed Douglas-fir stands (Russell 1974). However, Roach (1952) found seedling regeneration but no layering on rocky lava flows in the Cascade Mountains.

The objectives of this study were: (1) to quantify clonal development and vegetative and seedling regeneration in a chronosequence of Douglas-fir stands; (2) to determine the effects of commercial thinning and prescribed fire on clone growth and regeneration; and (3) to determine patterns of layering in relation to stem size and forest floor conditions.

METHODS

Study sites

Twenty-five 5–240 yr old Douglas-fir stands, located in the Oregon Coast Range from Mist south to Mapleton, were selected for this study (Table 1). These stands represent plant associations ranging from relatively moist *Tsuga–Polystichum–Oxalis* to much drier *Pseudotsuga–Holodiscus–Gaultheria* (Franklin and Dyrness 1973) and comprise four broad age classes (Table 1) that generally correspond to the stages of forest stand development described by Oliver and Larson (1990). Class 1 stands (age 5–20 yr) corresponded to the stem initiation stage; class 2 stands (age 21–70 yr) corresponded to the stem exclusion stage; in class 3 stands (age 71–120 yr), understory reinitiation was underway; and class 4 stands (age 121–240 yr) had a well-developed understory and corresponded to the old-growth stage. Half of the class 1 stands had been burned for site preparation and planted with Douglas-fir; the other half had been planted but not burned. Half of the class 2 and 3 stands had been commercially thinned from below (Smith 1986) with ≈25% of the total basal area removed at least 5 yr previously. No thinning had been done in any of the class 4 stands, and no stand >20 yr old showed any evidence of major disturbance (by wind or fire, for example).

Clone and overstory measurements

Within each stand we located three 0.05-ha plots under a uniform overstory canopy; each plot contained at least 10 vine maple clones. We excavated all vine

maple clones on the plots, obtaining a total of 1083 clones for all sites. We define vine maple clones as aggregations of aerial stems originating from a common base, including ramets that have resulted from layered aerial stems, with no evidence of connection to other such aggregations. For each clone we recorded: (1) stem age of the smallest and largest stems (by counting xylem rings on discs cut from the stem base); (2) number of stems; (3) diameter (to the nearest 0.1 cm), length (to the nearest 0.1 m), and 5-yr shoot growth (to the nearest 0.1 cm) of each stem; and (4) crown area (the circular area the diameter of which equaled the average of two edge-to-edge crown measurements taken at right angles through the center of the clone). In addition, on at least one clone per plot, we aged all stems and, in stands aged ≥ 70 yr, we mapped one or more representative clones to gain information on their spatial distribution and to determine how clones developed their present structure. We aged all stems of the mapped clones.

For each clone, we also examined all stems in contact with the forest floor to determine whether stems had layered. A total of 1911 layered stems was found. At each point of layering, we measured: (1) distance of layering (to the nearest 0.1 m) from the center of the clone, (2) stem diameter (to the nearest 0.1 cm) at the point of layering, and (3) 5-yr shoot growth (to the nearest 0.1 cm) of ramets formed at the point of layering. We also noted whether the layered stem had died in the forest floor and the ramet was independent from its progenitor. We examined all clones for seed production. We also searched each plot for vine maple seedlings and measured total height, age (by counting terminal bud scale scars), and 5-yr height growth of all seedlings found.

Within each 0.05-ha plot we counted all trees and measured their diameters at breast height (dbh; 1.4 m). Stand age was estimated from increment cores taken at dbh from two or three dominant trees.

Artificial layering study

In three class 2 stands, both thinned and unthinned, we conducted a study to determine the time and pattern of vine maple layering and whether forest floor conditions affected layering. Also, to determine whether vine maple stems would layer, we selected 20 pairs of similar stems 1.76–2.41 cm in diameter and 2.3–3.9 m long, from five or more clones within each of the three stands. These stems were still attached to the clones. In September 1990, we pinned these stems to the forest floor with wooden or metal pegs driven into the soil at an angle of $\approx 30^\circ$. The stems were pinned to the soil surface without damaging the bark in the continuous layering method described by McMillan (1969). Prior to pinning, the litter layer was removed from the forest floor so that all pinned stems would be in contact with the A-1 soil horizon. One stem in each pair was then covered with the removed litter; the other stem re-

mained uncovered. In addition, 12 pairs of stems were severed from various clones and pinned to mineral soil as with the unsevered stems. One stem of each severed pair was covered with litter; the other was not.

One year later (September 1991), we lifted the stems and recorded: (1) the number and location (node or internode) of roots, (2) whether shoots had been initiated, and (3) stem age (by counting xylem rings on a disc cut from the stem's widest point). Half of the stems were randomly selected for measurement of stem diameter at the point(s) of rooting and for root length. In addition, in July, August, and September 1991, we measured soil moisture gravimetrically in each of the three stands. Samples were taken from the top 5 cm of mineral soil within 10 cm of three pinned stems that we covered by litter and three that were exposed. Samples were weighed, dried for 24 h at 90°C , and reweighed; percentage moisture was calculated on a dry mass basis.

Data analysis

We used regression analysis to examine the relationship between stand age and several clone characteristics: stem number, stem length, stem diameter, and crown area. Lines were fit using residual analysis and coefficients of determination, R^2 . We used one-way analysis of variance to test the null hypothesis that neither prescribed fire (in class 1 stands) nor thinning (in class 2 and 3 stands) affected clone size, number of layered stems per clone, total area of layering, numbers of clones producing seed, or stocking of vine maple seedlings in that age class.

Data from the artificial layering study were analyzed to test the null hypothesis that number of roots per stem and root density per stem did not differ for covered and uncovered stems. For this analysis, we used analysis of variance and a randomized complete block design with the three experimental sites as blocks. Linear regression on a data set pooled over all sites was used to determine whether a relationship existed between stem diameter and number of roots.

RESULTS

The character of vine maple clones and potential for vine maple seedling establishment vary markedly at different stages of Douglas-fir stand development (Fig. 1). In addition, both vegetative and seedling reproduction of vine maple are strongly affected by silvicultural practices such as clear-cutting, prescribed fire, and commercial thinning.

Clone characteristics at different stages of natural development

In class 1 stands, an average clone comprised 39 monopodial stems that were ≈ 1.4 m tall and 0.9 cm in diameter and had a crown area of ≈ 4.6 m². In unthinned class 2 and 3 stands, clones were structurally quite different from clones in unburned class 1 stands,

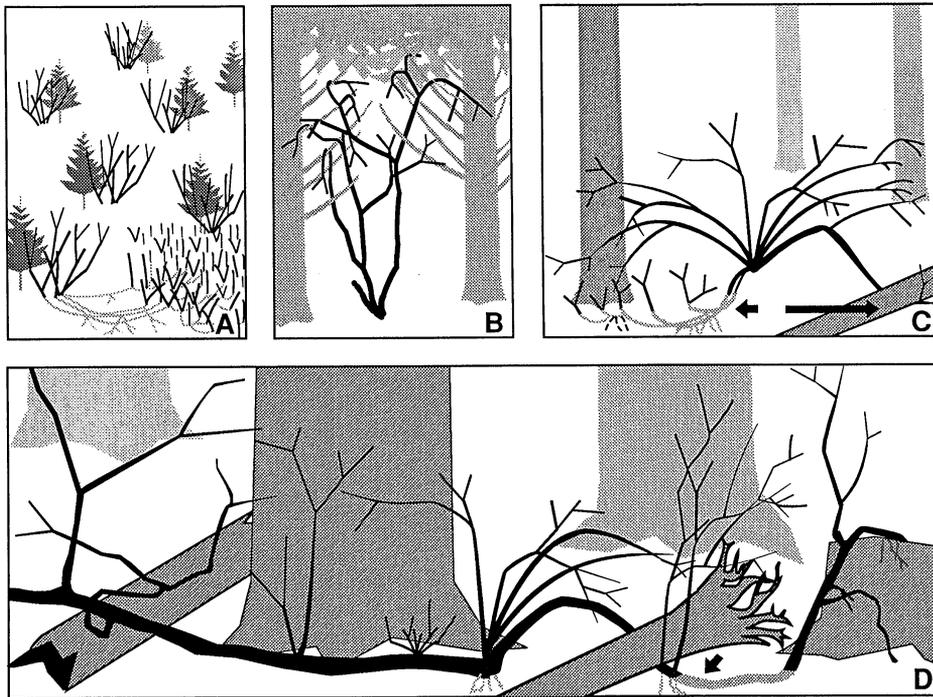


FIG. 1. A general life history of the vine maple clone in Douglas-fir stands: (A) Vine maple produces shoots from basal buds after stem removal because of fire or logging. Often, if live stems remain after the disturbance, they can become pinned to the forest floor and form a matted area of rooted stems (lower right corner). (B) The vine maple stems continue to grow and become overtopped by the Douglas-fir, becoming significantly fewer in number. They are often intertwined in the conifer branches. As the conifers self-thin and discard branches, the vine maple stems fall to the ground. (C) Later, as the Douglas-fir crowns grow well above the clones, the latter assume a characteristic "convex" shape. During this phase, clones often layer and form mats as conifer limbs or trees fall and pin the vine maple stems to the ground (arrows). (D) In stands greater than ≈ 120 yr old, clones consist of aggregations of upright stems connected by decumbent stems. Secondary or tertiary layering may occur in dead logs or stumps, as well as in the soil. Independent ramets are also prevalent in these stands as the connections between layered stems and the progenitor decompose (arrow).

but there was little difference in clone structure between unthinned class 2 and 3 stands (Fig. 2). For example, unthinned class 2 and 3 stands, respectively, had an average of 8.0 and 3.9 stems per clone, average stem lengths of 6.4 and 7.6 m, average stem diameters of 4.5 and 5.0 cm, and average crown areas of 44.9 and 48.5 m². Stem growth was sympodial, and second- and third-order branches grew an average of ≈ 10 cm/yr. Also, in class 1 stands, vine maple stems were stiff and upright, while in class 2 and 3 stands, stems generally had a characteristic convex shape and their tips often touched the forest floor (Fig. 1A–C). In class 2 stands, stems of vine maple clones were often intertwined with the lower branches of nearby Douglas-fir trees, which supported the stems in an upright position (Fig. 1B). Occasionally, stems supported in this manner rooted in the Douglas-fir bark or dead branches 4–8 m above the forest floor, indicating the relative ease with which vine maple stems root when they contact suitable substrate.

Layering of stems pinned to the forest floor by fallen branches and trees was common in class 2 and 3 stands, in which we counted an average of 1.2 new ramets per clone and 37–59 independent ramets/ha. In addition,

these stands produced new stems from the buds at the base of the clone, even when older stems were undamaged. For example, in a clone growing in a 40-yr-old stand, the oldest stem (undamaged) was 40 yr old, and two others were 28 yr old.

The structure of clones in class 4 stands (all undisturbed) was much more variable than in younger stands. Clones ranged in form from treelike clumps to decumbent and rambling stems, no longer having the characteristic multistem clump form of younger clones (Fig. 1D). Upright stem diameters ranged from 2.4 to 9.0 cm with average stem lengths of 5.3–7.7 m (Fig. 2). Class 4 stands contained considerable amounts of debris from branch mortality and self-thinning of Douglas-fir. There was an average of 2.2 layered stems per clone, about twice the number in the younger stands (which had 1.2 layered stems per clone) (Fig. 2E). Consequently, clones were often a series of spatially separated ramets of one to five upright stems with merged crowns (Figs. 1D and 2B). We found no evidence of connections among clones in any of the 25 stands. However, within stands, what we have defined as clones may be ramets of the same clone that were produced by layering in the understory of a previous stand.

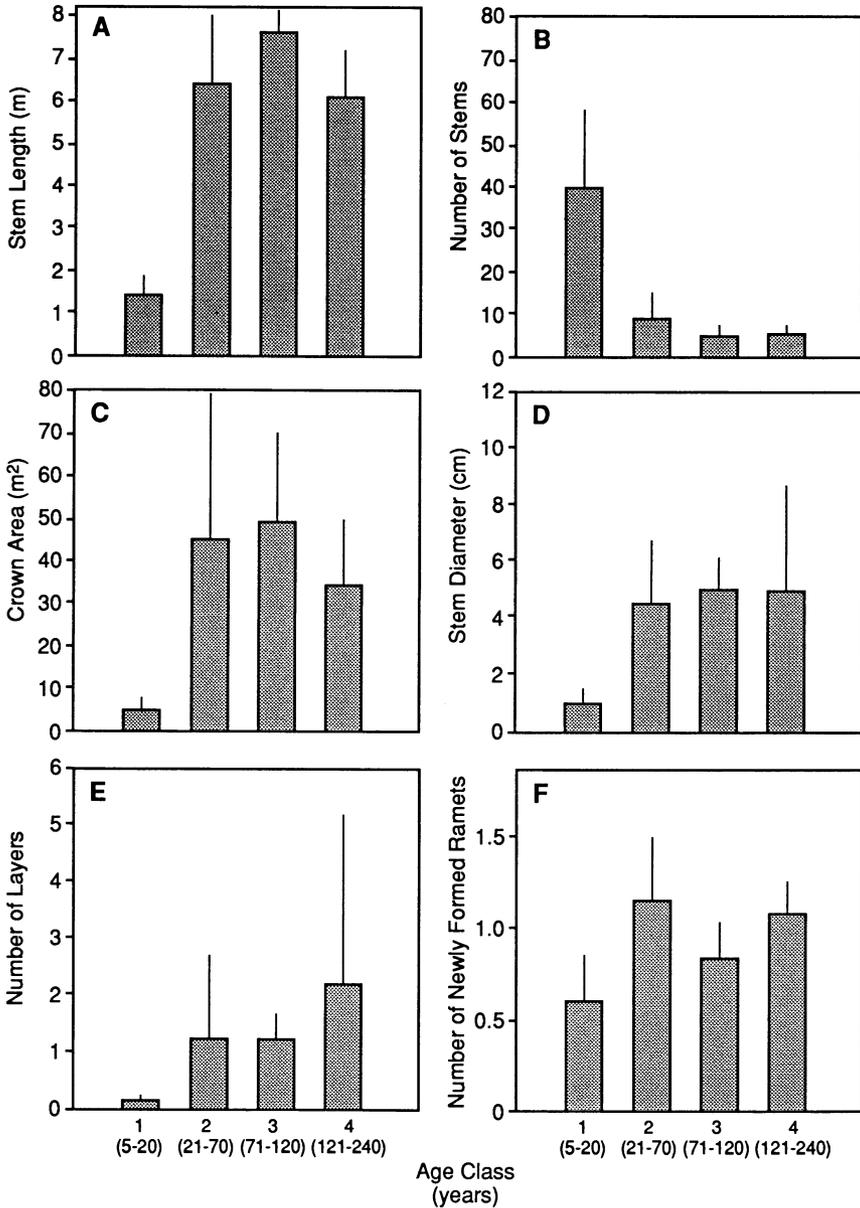


FIG. 2. Clone characteristics in unthinned stands by stand age class. Unburned clones in class 1 stands are not included. Data are mean; error bars represent 1 SE.

The clone diagrammed in Fig. 3 represents a relatively complex structure and illustrates what may develop in older stands. The area covered by the clone was $\approx 210 \text{ m}^2$, while the cumulative crown area of all ramets combined was 80 m^2 (data not shown). Three logs had fallen on previously upright stems, pinning them to the forest floor. As a result, there were well-developed taproots in 18 locations and several clumps of aerial stems connected by formerly aerial but now decumbent stems partially buried in the forest floor. The 40 upright stems (not shown) ranged from 18 to 125 yr old, from 0.5 to 8.0 m in length, and from 1.1 to 15.9 cm in diameter. The oldest stem was 125 yr

old, and although a 45-yr-old stem was slightly larger in diameter (15.9 vs. 15.0 cm), the 125-yr-old stem was only about half the length of the 45-yr-old stem. This illustrates that stem sizes within clones are not closely related to age and that there is considerable variation in growth rates within clones.

Relationship of clone characteristics to stand age

Although the relationships between stand age and number of stems per clone, stem length and diameter, and crown area were all nonlinear and significant ($P \leq 0.01$), most were quite weak (Fig. 4). The strongest

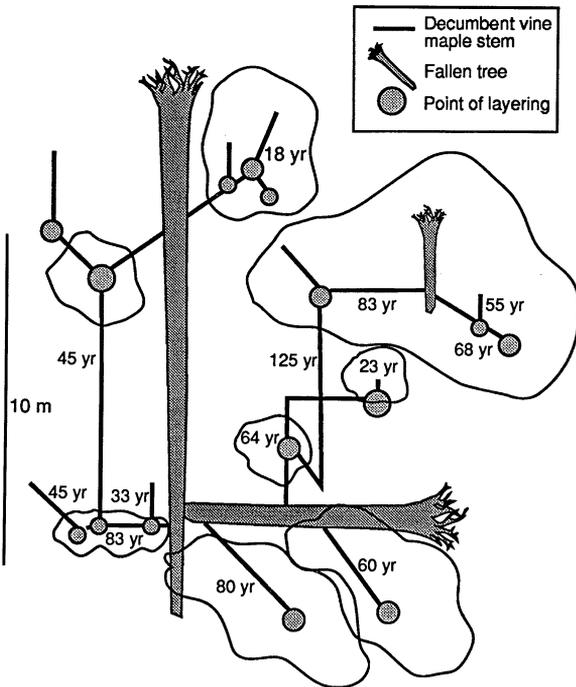


FIG. 3. Horizontal view of a vine maple clone in a 130-yr-old Douglas-fir stand, showing decumbent stems and points of layering. Aerial stems are not shown. Open areas indicate vine maple crown dimensions. Ages were estimated by counting the rings in the vine maple stems.

relationship was between stand age and average number of stems per clone ($R^2 = 0.085$); the relationships of other variables to stand age were weaker ($R^2 = 0.18$ – 0.41). Little stem growth and crown development occurred in stands older than 50 yr; upright stems in 50-yr-old and 100-yr-old stands, respectively, were an average of 5.5 and 6.0 m long. Regressions of stem diameter and length on stands ≤ 50 yr old were linear, highly significant ($P \leq 0.01$), and much less variable ($R^2 = 0.74$ and 0.70 , respectively; O'Dea 1992).

There was a significant linear relationship between stand age and average ages of the oldest vine maple stems ($P \leq 0.01$; $R^2 = 0.81$). Thus, the clone characteristics we measured, for the most part, developed following disturbances that initiated the present Douglas-fir stands. It was not uncommon, however, to find vine maple stems older than the Douglas-fir stand in which they were growing. For example, in a 51-yr-old stand we found an 86-yr-old vine maple stem, indicating that individual stems can survive from one stand of conifers to the next, providing a legacy of structure between forest generations. This legacy was also apparent in recent unburned clearcuts, where some older, larger stems survived disturbance and would be a component of the next stand.

Layering

Natural layering.—Natural vine maple layering was closely associated with fallen trees and branches of the

overstory Douglas-fir. Of the 1911 layered stems we examined, only two were not pinned by fallen debris. When formerly aerial stems layered, buds in the bud bank were released and produced new upright stems. Tap or dense fibrous roots usually emerged beneath these stems. After rooting of new upright stems, the distal portion of layered stems thickened but the portion closest to the new stems appeared to grow little (Fig. 5). The layered stems rotted in this proximal area, creating independent ramets. Class 2–4 stands had, on average, 0.83–1.14 independent ramets per clone. Some layered stems remained alive on the forest floor and continued to grow in diameter. When entire branches or crowns of clones were pinned by fallen debris to the forest floor, the result was the production of rooted stems arising from second- and higher order branches that contained buds activated after layering. These rooted “mats of stems” produced a dense clone comprising 1–3 aerial stems/m² with taproots beneath them (Fig. 6).

Artificial layering.—In our artificial layering study, 57 of the 60 stems (95%) attached to a clone and pinned to the forest floor rooted within 1 yr. The remaining three stems died; what caused their mortality is unknown. All 24 stems that were severed from clones before pinning died without producing roots.

On the artificially pinned stems that survived, root initiation began in June 1991, after leaves had expanded. After 7 mo, average root density for covered stems ranged from 25 to 30 roots/m. On two sites, average root densities for uncovered stems were 20–25 stems/m and were not significantly different from the averages for covered stems. On the third site, however, uncovered stems had an average root density of 11 roots/m, significantly ($P < 0.02$) less than the average for covered stems on the site. Roots were evenly distributed along stems; 70% of the roots emerged from internodal regions of the stem. There was no significant relationship between stem diameter and root density on artificially layered stems; rooting occurred at stem diameters ≤ 5.5 cm but was most common on second- and third-order branches < 1.0 cm in diameter. (We observed rooting on naturally layered stems ≤ 9.0 cm in diameter in class 4 stands.) Among the three sites used in the artificial layering study, the maximum length of roots initiated from the pinned stems was 45 cm; average root length ranged from 2.9 to 6.0 cm. No new shoots were produced the 1st yr, and no mortality of second- or higher-order branches on surviving pinned stems was noted. From June through August 1991, there were no significant differences in soil moisture among the three sites or between bare soil and soil covered by litter, and thus substrate moisture does not seem to have been a determining factor for rooting.

Effects of silvicultural practices on vegetative reproduction

Burning.—Burning following clear-cutting had a major effect on clone structure in class 1 stands. Where-

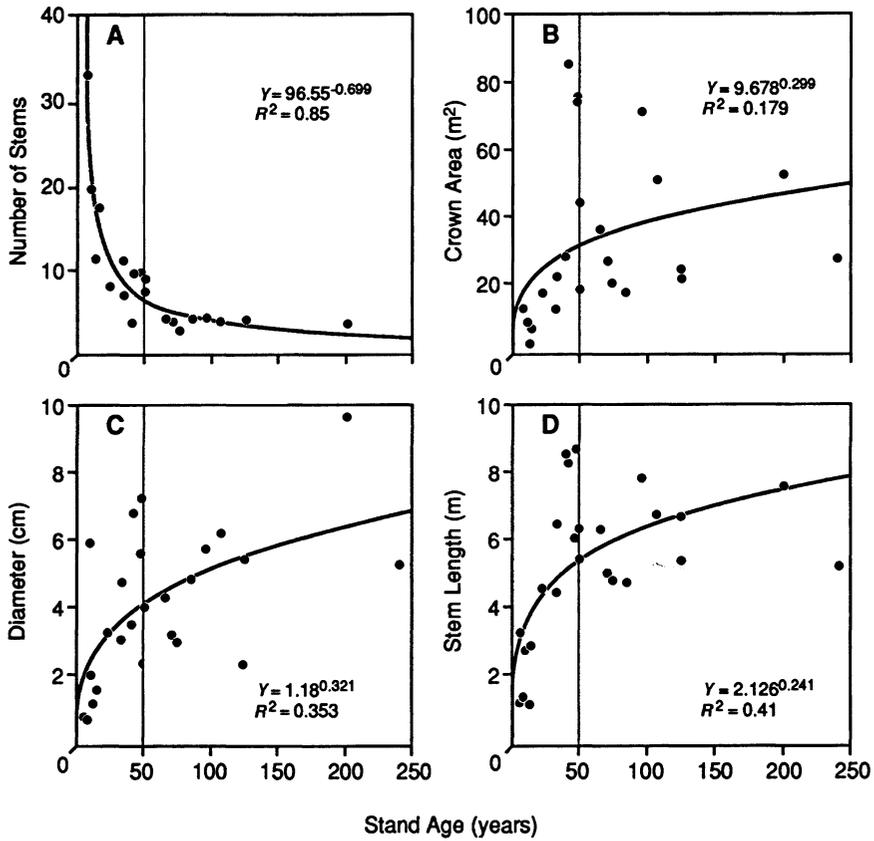


FIG. 4. Vine maple clone characteristics in the 25 Douglas-fir stands studied vs. age of the stand. Data points represent the mean value for each stand. All regression equations are significant ($P \leq 0.01$). The y values are the predicted averages of number of stems, crown area, stem diameter, and stem length per clone by stand age for equations A, B, C, and D.



FIG. 5. Photograph of layered aerial stem in a vine maple clone showing the thickened portion distal to the point of layering and the thinner portion proximal to the point of layering. Aerial stems decay at the thinner part of the stem, thereby creating independent ramets.



FIG. 6. Photograph of mat formation caused by the layering of multiple stems of a vine maple clone in an 8-yr-old unburned plantation. The resulting aerial stems are 2–3 m in height.

as unburned clones often had large (5–10 m long) aerial stems remaining from the previous stand as well as many new stems sprouting from the basal bud bank, clones that developed in burned clearcuts were compact clumps of new sprouts. In unburned class 1 stands, average crown areas ranged from 6.3 to 12.7 m², significantly ($P \leq 0.05$) greater than the averages of crown areas in burned class 1 stands, which ranged from 2.2 to 7.5 m². Also, unburned class 1 stands had an average of 2.4 independent ramets per clone and 0.7 layers per clone that had not yet become independent ramets. Both these values were significantly ($P \leq 0.05$) greater than those for clones in burned stands (0.7 independent ramets per clone and 0.03 layers per clone). The mean number and area of mats (layered vine maple stems and crowns) were, respectively, 70 mats/ha and 1293 m²/ha in unburned stands, significantly ($P \leq 0.05$) more than in burned stands, which had an average of 30 mats/ha with mean area 525 m²/ha (Fig. 7). The largest mat of rooted branches on our study sites (175 m² in area) was found in an 11-yr-old stand that had not been burned after clear-cutting.

Thinning.—Clone expansion and vegetative reproduction were generally higher in thinned class 2 and 3

stands than in unthinned class 2 and 3 stands. Thinned stands had 4.0 layered branches per clone and 1.6 independent ramets per clone, significantly ($P \leq 0.003$) more than unthinned stands, which had 1.2 layers per clone and 1.1 independent ramets per clone. The most conspicuous difference between clones in thinned and unthinned stands was the number and extent of rooted vine maple stems or entire crowns (i.e., amount of mat formation) in class 3 stands. In thinned class 2 stands, mat density was not significantly different, averaging 31 mats/ha compared to 26 mats/ha in unthinned stands; mat area in thinned stands was greater than in unthinned stands (409 vs. 182 m²/ha, respectively; Fig. 7). In thinned class 3 stands, both mat density (74 mats/ha) and mat area (1285 m²/ha) were significantly ($P \leq 0.05$) greater than in unthinned class 3 stands, which had 16 mats/ha and a mat area of 244 m²/ha. In addition, overall average shoot growth in class 2 and 3 thinned stands (11.0–15.3 cm/yr) were significantly ($P = 0.04$) greater than average shoot growth in unthinned stands (9.0–10.0 cm/yr).

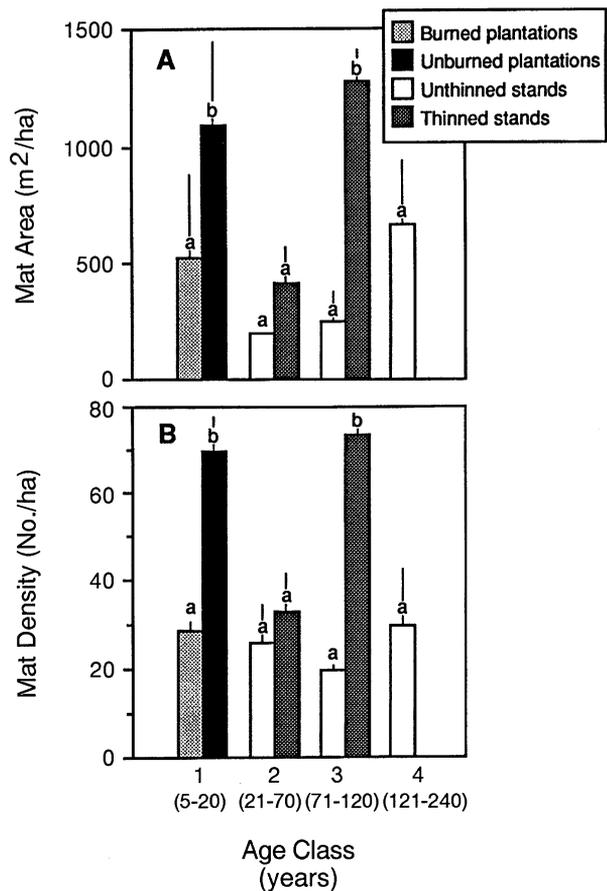


FIG. 7. (A) Mat area and (B) number of mats/ha of vine maple clones in Douglas-fir stands vs. age class. Means accompanied by the same letter are not significantly ($P \geq 0.05$) different using Tukey's mean comparison test. Vertical bars represent 1 SE.

Clone seed production and seedling density

Clone seed production and number of seedlings present in stands were related to stand age and treatment. Significantly ($P < 0.01$) more clones produced seed in class 1 stands, in which the vine maple was not overtopped by conifers, than in the other age classes. In class 1 stands that had been burned, 19% of the clones produced seed compared to 30% in unburned class 1 stands, in which clones retained large stems from the previous stands. No seed was found in unthinned class 2 stands, while 10% of clones in thinned class 2 stands produced seed. In unthinned class 3 stands, 7.5% of clones produced seed, compared to 5% of clones in thinned class 3 stands. In class 4 stands (all unthinned), 7.9% of clones produced seed.

The highest average for seedling stocking (143 seedlings/ha) occurred in unburned class 1 stands; this average was significantly ($P \leq 0.01$) higher than that for burned class 1 stands (19 seedlings/ha) as well as those for the other age classes (Fig. 8). Seedlings in young unburned stands dated back to the time of disturbance; they were not established prior to clear-cutting. We found no seedlings in unthinned class 2 stands and only ≈ 20 seedlings/ha in unthinned class 3 and 4 stands. Thinned class 2 and 3 stands had averages of ≈ 90 and 49 seedlings/ha, respectively; these averages were significantly ($P \leq 0.001$) greater than those for unthinned stands in these age classes.

Seedling growth in burned and unburned class 1 stands (7.9–8.2 cm/yr) was significantly ($P \leq 0.001$) greater than in thinned and unthinned class 2–4 stands (3.2–4.0 cm/yr); the older stands did not differ significantly from one another in average seedling growth (Fig. 8).

DISCUSSION

Vine maple growth, vegetative reproduction, and seedling establishment are closely related to stand development but can be altered by silvicultural treatments. Following a stand disturbance that removes most aboveground vegetation, and prior to overtopping by conifers, clones are aggregations of upright stems resulting from activation of the buds at the base of the stems. For clones growing close to the Douglas-fir trees, many stems become intertwined in the Douglas-fir crowns. After natural stem thinning occurs in the conifer canopy, vine maple stems are no longer passively supported upright. Once released, these stems droop to the forest floor and take on their characteristic convex shape. As mortality from self-thinning, root disease, or windthrow occurs, falling trees and limbs are apt to pin the flexible vine maple stems to the forest floor, layering occurs, and ramets with new aerial stems are produced that may also layer (Figs. 1, 6, and 7). After multiple layering events, clones in stands over ≈ 100 yr of age often “ramble” over considerable areas. The layered stems may connect ramets of upright

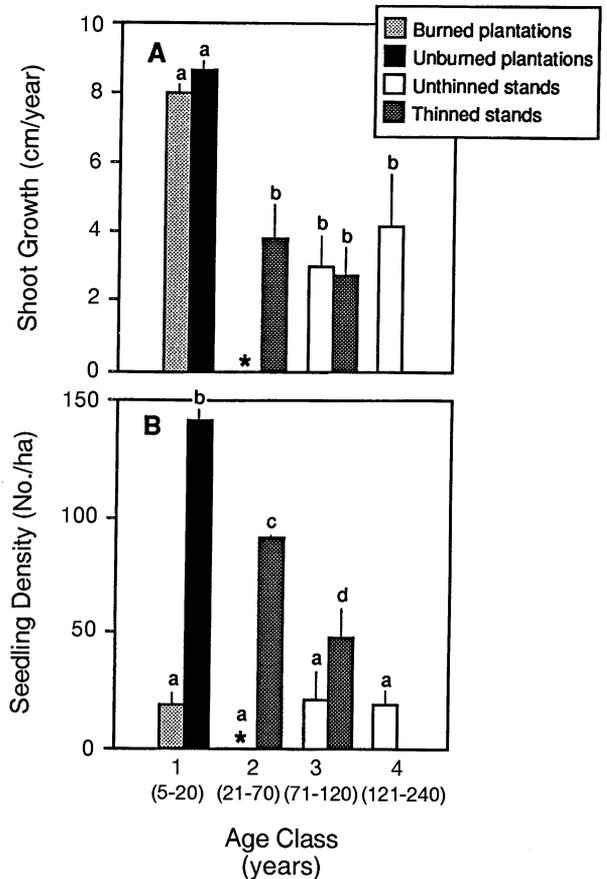


FIG. 8. (A) Seedling shoot growth and (B) number of vine maple seedlings/ha in Douglas-fir stands vs. the age of the stand. Means accompanied by the same letter are not significantly ($P \geq 0.05$) different using Tukey's mean comparison test. Asterisks (*) indicate that there were no seedlings in unthinned class 2 stands. Vertical bars represent 1 SE.

stems to one another (Fig. 2), or the layered stems may decompose, creating independent ramets. We observed layering up to 20 m from the clone center, indicating the potential of clone expansion and invasion by layering. In class 4 stands, we observed second and third generations of layering.

Vine maple clone development appeared to follow a fairly predictable pattern for the first 50–60 yr following disturbance and stand regeneration. Starting with sprout clumps in 5–15 yr old stands, stem growth and reductions in stem numbers were reasonably predictable until stands reached 50–60 yr (Figs. 1 and 3). In stands >60 yr old, clone development is much less predictable because it is influenced largely by fallen debris, and clone form is therefore much more variable. Also, the effects of site productivity and overstory density on vine maple clone development (not quantified in this study) may have a strong influence on clone development. For example, in several 40–45 yr old stands, stem length on highly productive sites averaged

8–9 m and crown area averaged 75–85 m², compared to average stem length of 5–6 m and crown area of 25–30 m² for clones on less productive sites.

Clonal expansion appears to rely largely on events beyond genetic control or physiological processes within the clone, since 99% of the layered stems we observed had been pinned by fallen trees or branches. Anderson (1967) suggested that layering is more common on steep slopes than on gentle ones, but we could not confirm this observation. Anderson (1967) also reported that vine maple reproduces from roots. We found no evidence of root suckering, however, and surmise that what may have been noted was actually layering of buried stems or entire crowns.

Vine maple clones that develop as a result of layering can be simple structures composed of variable numbers of basal sprouts, or, when entire stems or crowns are pinned to the forest floor, the resulting structure can be quite complex, resembling that of clones produced from rhizomes or roots such as salmonberry (*Rubus spectabilis* Pursh.; Tappeiner et al. 1991). Layered stems produce numerous roots, and a dense stand of shoots develops from buds present aboveground on second- to sixth-order branches of these stems. In turn, these new shoots are then able to layer and contribute to clonal expansion. There are two general strategies for the clonal expansion of woody species: (1) ramets remain connected and function as extensions of the clone progenitor, or (2) as with vine maple, each ramet becomes independent as the stem connections decompose (Reinhartz and Popp 1990). However, unlike salmonberry clones and various other clonal shrubs and trees (Cook 1985), layered aerial stems do not expand belowground, and further clonal expansion depends on the growth of new aerial stems and ramets followed by layering.

It appears that vine maple is well adapted to layering and survival in the understory of Douglas-fir stands. The long stems are very flexible and often grow at angles >60° from vertical. Height-to-diameter ratios of well over 150 suggest a very unstable stem structure. (In conifers, height-to-diameter ratios of >80–100 indicate unstable stand conditions, and those >150 would be considered extremely unstable.) In open-stand conditions, stems may be more upright and layering less frequent (Roach 1952). Consequently, at least the distal part of the stems can easily contact the forest floor when even small tree branches fall on them. Vine maple clones are shade-tolerant and many are able to survive stem exclusion in young Douglas-fir stands. Part of their shade tolerance may be related to the fact that vine maple stems contain chlorophyll and may have the capacity for corticular photosynthesis (Coe and McLaughlin 1980). Similarly to tanoak (*Lithocarpus densiflorus* (Hook and Arn) Rhed), a multistemmed understory hardwood in Douglas-fir forests, vine maple initiates new aerial stems from basal sprouts even though the existing aerial stems are not damaged (Rus-

sel 1974). And like tanoak, vine maple aerial stem ages may vary by >50–100 yr (Tappeiner and McDonald 1984). Thus, it appears that vine maple clones can maintain themselves after the death of the original ramets.

As with clone development and vegetative regeneration, seedling establishment is also related to stand development and may be dependent on overstory thinning. In our study, we observed no seed production and found no vine maple seedlings in unthinned class 2 stands. Anderson (1967) and Russel (1974) also reported a lack of seedlings in the understory of unthinned Douglas-fir stands. However, the open environments created by clear-cutting and the moderate canopies created by thinning, both of which provide suitable seedbeds, apparently stimulate seed production and seedling establishment (Fig. 8). Similarly, Tappeiner and Zasada (1993) found lower rates of vine maple seedling establishment in unthinned stands of this age and higher rates in thinned stands. As with other clonal species, seedling growth is slow relative to vegetative expansion (Cook 1985). For vine maple, vegetative expansion appears to be more important than seedling establishment and growth in rapid establishment of a dense understory.

MANAGEMENT IMPLICATIONS

Results of this study suggest ways to manage the regeneration and density of vine maple in forest stands. While the species provides structure, cover, some mast, and fall color, dense vine maple cover may prevent establishment of herbs, conifers, and other shrubs, both in openings and in understories. Because vine maple cover decreases light levels and may have allelopathic effects (Del Moral and Cates 1971), it undoubtedly plays an important role in regulating the microenvironment for regeneration and growth of tree, shrub, and herb species in the understory of Douglas-fir stands. Both thinning and regeneration harvest of Douglas-fir can potentially increase vine maple density, mainly by increasing layering, mat formation, and stem growth of the species, and secondarily by increasing vine maple by seedling establishment. Any pinning of live stems by tree felling, slash-pile placement, or tractor skidding promotes layering. Burning, cutting, or treating stems with a light application of herbicide reduces layering and seed production. Cutting, however, will not remove vine maple from stands; instead, basal sprouting produces a new cohort of aerial stems.

These suggestions are supported by the results of an unpublished exploratory study that we conducted. In that study, vine maple clones were mapped before clear-cutting on two 10–20 ha sites and were then re-examined after logging. On one site, vine maple stems were cut at the time the trees were felled. On this site, only 6% of the clones layered and basal sprouting was profuse, as with clones in the burned stands of this study. On the other site, stems were not cut at the time

of tree felling, and the effect was dramatic: 54% of the clones layered, 90% of the pinned stems layered, and several clones were in the early stages of mat formation.

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