AN ABSTRACT OF THE THESIS OF

Mary E. O'Dea for the degree of Master of Science in Forest Science presented on July 27, 1992.
Title: The Clonal Development of Vine Maple During Douglas-fir Stand Development in the Coast Range of Oregon.
Abstract approved: _______________________________________________________________________

John C. Tappeiner

Natural Douglas-fir stand development is the result of many types of disturbance, both natural and management induced. The magnitude and timing of these disturbances have profound effects on the structure and composition of both the overstory and understory plant communities. Vine maple responds to disturbance by basal sprouting, layering, producing seed and establishing seedlings. By means of clonal regeneration and seedling establishment, vine maple is able to maintain its presence from one stand to the next over a wide range of sites. Previous studies on vine maple have not quantified its growth in relation to the structural changes which occur during stand development and secondary succession in Douglas-fir forests. A knowledge of vine maple clone development is needed to understand the processes of understory development in secondary succession, and to predict the results of thinning and other silvicultural practices in these forests.

The objective of this study was to quantify changes in vine maple development in relation to Douglas-fir stand age and density. Also investigated were the effects of layering on clone development in Douglas-fir stands of different ages...
and under different management regimes. The second segment of this study was to examine layering more closely, in regards to the rate and pattern of root initiations, and the capability of severed stems to root. The clonal development of vine maple was found to be strongly related to stand age, with most developmental changes occurring during the first 50 years of stand development. Basal sprouting and layering are present throughout stand development, with basal sprouting present primarily in early stand development and layering in the later stages. Seed production and seedling establishment are present in all stages of stand development, except during the years immediately following crown closure.

Clone regeneration was found to be strongly influenced by cultural practices common to forest management, such as commercial thinning and prescribed fire. These management treatments affect clone regeneration by controlling clone size and forest debris. These treatments also affect the timing of seedling presence and the abundance of seedlings in stands.

In order to understand natural forest succession, and to predict the effect of management practices on stand development, it is important to understand how clonal understory plants, such as vine maple, reproduce and grow during different stages of stand development.
The Clonal Development of Vine Maple During Douglas-fir Stand Development in the Coast Range of Oregon

by

Mary E. O'Dea

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APPROVED:

Signature redacted for privacy.

Professor of Forest Science in charge of major

Signature redacted for privacy.

Head of Department of Forest Science

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Dean of Graduate School

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Typed by researcher for  Mary O'Dea
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THE CLONAL DEVELOPMENT OF VINE MAPLE DURING DOUGLAS-FIR STAND DEVELOPMENT IN THE COAST RANGE OF OREGON

INTRODUCTION

Vine maple (*Acer circinatum* Pursh.) is a common understory shrub in the Douglas-fir (*Pseudotsuga menziesii*) forests of the Pacific Northwest. It belongs to the *Acer* series *Palmatum* which includes eight other species which are native only to Japan (Vertrees, 1979). Its association with many of the plant communities of Oregon and Washington has been well documented (Anderson, 1967; Bailey, 1966; Franklin et al., 1973; Hemstrom et al., 1986; Russel, 1974; Schoonmaker and McKee, 1988; Yerkes, 1958). Vine maple is most common on upland sites, but also occurs on a variety of sites, including alluvial substrates above the flood plain in riparian zones (Gilkey and Dennis, 1975; Sudsworth, 1908; Zasada et al., 1992).

Natural Douglas-fir stand development is initiated by many types of disturbance including the effects of pathogens and insects, fire and windthrow. In managed forests, cultural practices such as commercial thinning, change overstory species composition and density, and thereby further influence stand development. The magnitude and timing of these disturbances have profound effects on the structure and composition of both the overstory and understory plant communities. Vine maple responds to both natural and management induced disturbances by basal sprouting, layering, seed production and seedling
establishment. With clonal regeneration and seedling establishment, vine maple is able to maintain its presence from one stand to the next over a wide range of sites. In order to understand natural forest succession, and to predict the effect of management practices on stand development, it is important to understand how clonal understory plants, such as vine maple, reproduce and grow during different stages of stand development.

LITERATURE REVIEW

Past research on vine maple

There are two published phytosociological studies on vine maple communities in the Coastal and Cascade Ranges of Oregon. Anderson (1967) studied vine maple communities in the Marys Peak Watershed in the Coast Range. The objectives of his study were the classification of the major plant communities on Marys Peak which included vine maple, and the description of the ecological features of vine maple that explain its presence in those communities. Anderson reported six plant community types on the watershed which include vine maple, and his study sites were chosen on the basis of these types. In each stand, the species abundance of all plants was classified into the herbaceous, shrub and overstory components of the stand.
In addition he studied vine maple development in these communities. Within each community type, the largest three or four stems, with ages ranging from 70 to 142 years, were measured for average stem diameter and height. Average stem diameters ranged from 1 to 8.2 inches and clone heights ranged from 15 to 28 feet. It should be noted that height does not represent stem length, but the height of the clone. Anderson also measured the average crown spread of the clumps, which ranged from 14.6 to 40 feet. It is important to note that he did not work with individual clones, but instead with clumps of clones. Therefore, one cannot infer how clones develop from his data.

Anderson describes four characteristics of vine maple which he feels account for its distribution in the plant communities: its convex growth form; its methods of reproduction; its relationship to the overstory; and vine maple's influence on the stand's shrub and herbaceous components. He reported that vegetative reproduction occurs by three methods: coppice shoots which arise from adventitious buds developing at the base of stems following above-ground stem removal; "rooting", which he reports is different from root suckering and is the ability for shallow roots to produce shoots; and layering, which occurs when adventitious roots and new shoots form on stems which come in contact with the forest floor. Anderson is the only investigator to report rooting. With respect to sexual
reproduction, Anderson noted few clumps producing seed and observed few seedlings. However, his observations on seed production and seedling establishment were not quantified. Anderson also reported a positive correlation between the average number of vine maple stems per clump and stand basal area for his six community types. But as he did not distinguish clumps from clone number, this relationship is difficult to understand.

A second phytosociological study was performed by Roach (1952) in the Nash Crater lava flows of the Oregon Cascade Range. In contrast to the study on Marys Peak, Roach observed that vine maple was primarily of seed origin, and he found no layering or basal sprouting.

In a third study in the Cascade Range of Oregon, Russel (1974) studied: vine maple's contribution to nutrient cycling; b) its biomass production within the plant communities; and c) its abundance in relation to environmental factors and a successional time frame. Following clearcutting in stands 7- to 22-years-old, Russel (1974) observed that basal sprouting was the predominant method of vine maple regeneration, with layering having only a minor role. Like Anderson, Russel did not discriminate individual clones from the clumps of vine maple stems. Russel noted some seed production in these stands, but observed no seedlings.

Russel found that in these young stands stem biomass
averaged from 1191 to 6260 grams, with the 13-year-old stand producing more stem biomass than the older 22-year-old stand. In these young stands, the average number of stems per clump ranged from 26 to 41 stems, with an average diameter of 1.7 cm and an average length of 195 cm. In what he classified as late successional climax stands (450-years-old), Russel observed that vine maple clumps are uneven-aged, have fewer stems (1 to 15) and demonstrate a decrease in stem growth and biomass accretion. Russel used the biomass equations that he derived from the young stands to estimate biomass accumulation in the older stand, but did not verify his results due to an inability to do destructive sampling. He found layering to be the primary mode of regeneration, but he did not quantify the amount of layering. He also observed no seedlings in this older stand.

Vegetative reproduction

Vine maple reproduces vegetatively by basal sprouting and layering. Basal sprouting has been observed in other understory Acer species, such as striped maple (Acer pensylvanicum) and mountain maple (Acer spicatum). Basal sprouting is the process of either dormant or adventitious
buds sprouting after the above-ground stems are removed or killed (Rinne et al., 1987). Vincent (1965) observed many dormant buds on the lower stem of mountain maple plants, particularly around the root crown. He also noted basal sprouting in mountain maple to be most prolific on moribund stems and that wounding did not appear to stimulate adventitious bud formation (Vincent, 1965). Yet for other species, such as Betula, wounding near the cambial region does promote the callus tissue formation required for the formation of adventitious buds and sprouts (Rinne et al., 1987). Kauppi et al. (1987) thoroughly describe the initiation, structure and sprouting of dormant basal buds in Betula pubescens, in both seedlings and mature plants, but there is no similar information for Acer spp. Other understory Acer species which have the ability to layer include mountain maple and striped maple. As with vine maple, layering is more important for mountain maple population maintenance than seedlings (Post, 1969 and Vincent, 1965). Whereas with striped maple, layering plays an insignificant role in population dynamics with only 3% of the individuals observed to originate from layering (Hibbs and Fischer, 1979).

Vegetative reproduction appears to be very important in the maintenance of vine maple populations since it does not appear to regenerate readily from seed in the understory of Douglas-fir stands. Neither Anderson (1967) nor Russel
(1974) observed any seed originated individuals in their studies, even though seed was often observed on plants (Anderson, 1967).

Low numbers of established seedlings appear to be the function of many factors which include: poor light in the understory of Douglas-fir forests, rodent predation, erratic seed germination, and stratification requirements (Anderson, 1967; Corns, 1957; Vettees, 1975; Zasada, 1992 pers. comm.). In recent germination trials under various stand conditions with a known quantity of seed, germination was found to be similar in thinned and unthinned stands, but was much less in clearcuts. However, the survival of the seedlings was found to be best in the thinned stands. In addition, germination occurred over a three year period with 5-10% of the seeds germinating the first year after sowing, 70-78% the second year, and the remainder the third year (Zasada, 1992, per. comm.). On the other hand, under open stand conditions other than clearcuts, vine maple reproduction also appears to be quite successful. On old lava flows at Nash Crater in the Cascades, Roach (1952) found only seedlings and a lack of layering substrate in the pumice rock.

Vine maple is often observed to produce seed, yet few if any seedlings have been observed in previous studies (Anderson, 1967). The results of these studies indicate that the ability of vine maple to regenerate vegetatively,
primarily through basal sprouting, enables it to maintain itself following major disturbances in Douglas-fir stands. The ability to layer appears to have a significant role in vine maple's survival and spread in undisturbed stands or in stands following minor disturbances, such as disease pathogens or windthrow which cause small openings in the overstory canopy (Spies and Franklin, 1989).

Unlike many clonal species, vegetative buds on vine maple are maintained above-ground on residual stem material rather than below-ground on rhizomes, such as with salmonberry (*Rubus spectabilis*) (Tappeiner et al., 1991) or salal (*Gaultheria shallon*) (Huffman, 1992, per. comm.; Smith, 1991), or quaking aspen (*Populus tremuloides* Michx.) which suckers from shallow roots (Peralta, 1990). However, previous studies on vine maple have not quantified its clonal structure or growth in relation to the structural changes which occur during stand development and secondary succession in Douglas-fir forests. A knowledge of vine maple clone development is needed to understand the processes of understory development in secondary succession, and to predict the results of thinning and other silvicultural practices in these forests.
STUDY OBJECTIVES

Study of clone development and spread

The primary objectives of studying vine maple clone development were to: a) quantify changes in clonal development in relation to Douglas-fir stand age and density and, b) to assess the effects of layering on clone development and spread in Douglas-fir stands of varying ages, and with the different cultural treatments of stand thinning and prescribed fire. A secondary objective was to determine if seedling reproduction was related to stand age, stand density or management practices.

Layering Study

The objectives of this segment of the study were to determine: a) how quickly rooting occurred when stems came into contact with the forest floor; b) if rooting is limited by stem size or age; c) if rooting is limited to a region of the stem (internode or node); d) if rooting is affected by organic layers of the forest floor; and e) if stems severed from the clone are able to root on the forest floor.
METHODS

Site selection

A total of twenty-five Douglas-fir stands, ranging from 5 to 240 years in age and containing a substantial component of vine maple were selected in the Coast Range from as far south as Mapleton and north to Mist, Oregon. Stand selection was based on the examination of stand inventories where stand age, management history and vine maple presence were documented. Stands were also selected on the basis that the majority of the stand's basal area was composed of Douglas-fir, and not other conifers or hardwoods. Since the primary objective of this study was to examine clonal populations under different stages of stand development, the stands were arbitrarily grouped into: a) age classes and b) stages of stand development which generally correspond to Oliver and Larson's (1990) description of stand succession. Stands were therefore grouped and labeled: 5- to 15-years-old (stem initiation), 23- to 70-years-old (stem exclusion), 71- to 120-years-old (understory reinitiation), and greater than 120 years of age (old growth) (Table 1).

In order to determine the effects of commercial thinning on clone development, I studied eight 33- to 87-year-old stands that had been commercially thinned within the past ten years. To evaluate the effects of prescribed fire on
clone development, I selected six plantations from ages 5- to 15- years-old: three were burned at the time of stand establishment and three were not. These stands were also selected in the manner described above (Table 1).

<table>
<thead>
<tr>
<th>Stand type</th>
<th>Number of stands</th>
<th>Basal area (m²/ha)</th>
<th>Trees (no./ha)</th>
<th>Total no. of clones sampled</th>
<th>Vine maple clones (no./ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clearcuts (5-15 yr) (burned)</td>
<td>3</td>
<td>-</td>
<td>-</td>
<td>203</td>
<td>73</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(25.9-168.4)</td>
</tr>
<tr>
<td>Clearcuts (5-15 yr) (unburned)</td>
<td>3</td>
<td>-</td>
<td>-</td>
<td>142</td>
<td>51.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(16.2-220.2)</td>
</tr>
<tr>
<td>Unthinned stands (23-70 yr)</td>
<td>5</td>
<td>50.1</td>
<td>471</td>
<td>191</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(20.7-56.0)</td>
<td>(237-628)</td>
<td></td>
<td>(13.0-51.8)</td>
</tr>
<tr>
<td>Thinned stands (23-70 yr)</td>
<td>5</td>
<td>30.0</td>
<td>248</td>
<td>168</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(31.4-42.3)</td>
<td>(133-319)</td>
<td></td>
<td>(6.5-68.0)</td>
</tr>
<tr>
<td>Unthinned stands (71-120 yr)</td>
<td>3</td>
<td>40.8</td>
<td>131</td>
<td>120</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(30.6-53.6)</td>
<td>(121-141)</td>
<td></td>
<td>(19.4-142.5)</td>
</tr>
<tr>
<td>Thinned stands (71-120 yr)</td>
<td>3</td>
<td>44.37</td>
<td>171</td>
<td>107</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(38.2-50.45)</td>
<td>(148-213)</td>
<td></td>
<td>(32.4-55.0)</td>
</tr>
<tr>
<td>Unthinned stands (120+ yr)</td>
<td>3</td>
<td>31.1</td>
<td>30</td>
<td>152</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(30.5-32.1)</td>
<td>(20-49)</td>
<td></td>
<td>(32.4-93.9)</td>
</tr>
</tbody>
</table>

Table 1. Average stand characteristics (range of averages).
Clone description and measurement

Within every stand, I located three 1/20 ha plots which contained a minimum of 10 clones and were located under a Douglas-fir overstory, and not under other species or within gaps. A total of 1083 clones were sampled in all the stands. Each clone was excavated and measured for: a) stem ages (counting annual rings or discs taken at a height of 0.5 meters from the clone's base) of the largest and smallest stems; b) the number, diameter (0.1 cm), length (0.1 m) of all stems; c) 5-year shoot growth rates (cm/5 years); and d) crown area (m²) and extent (0.1 m). Crown extent is the longest extension of a branch or portion of the crown from clone center. The crown area was determined from two measurements taken a right angles through the center of the clone. Although the age of the clone could not be determined, the average age of the largest stems was used to approximate clone age in relation to current stand development.

All stems were examined for layering, with a total of 1,911 points of layering examined. I measured: a) layering distance from clone center (0.1 m), b) stem diameter at the point of layering (0.1 cm), c) 5-year shoot growth rates of layered stems, d) the cause of layering (pinning from branches, trees or other forest debris), and e) whether ramets formed by layering were independent from the
progenitor (i.e. a rotted stem was present between the ramet and the progenitor).

**Conifer stand measurements**

Within the 1/20 ha plot, the Douglas-fir stand was characterized by: stand basal area (m²/ha), Curtis' relative density index (Curtis et al., 1981), stocking (stems/ha) and stand age. Stand age was determined from increment cores at a height of 1.4 m from 2 to 3 dominant trees at each plot.

I searched for vine maple seedlings on all plots. The number, age, height, and 5-year stem growth of all seedlings were recorded. The ages of seedlings were determined by counting bud scars.

**Layering study**

Three of the twenty-five stands were selected to study branch layering. These stands ranged from 35- to 70-years-old with 148 to 628 trees per hectare and basal areas of 44.39 to 84.19 m²/ha. Within each stand, twenty pairs of stems of 1.76 to 2.41 cm in basal diameter and 2.3 to 3.89 m long were selected from a minimum of five clones in each stand. There was no significant differences in the stem diameters or lengths between the pinned stems at each site (Table 3).
Beginning in the early fall of 1990, 120 stems were pinned so that between 2.5 to 3 meters of each stem were in contact with the forest floor. Metal staples or wooden stakes held the distal portion of the stem in contact with the forest floor while the proximal portion remained attached to the clone. This technique resembles the French or continual layering method described by McMillan (1969). Prior to pinning, the forest floor was removed to expose mineral soil for a standard rooting medium and to permit maximum contact of the stem with mineral soil. For each pair, one stem was covered with forest floor litter and unincorporated organic layers while the other stem was left uncovered. An additional 6 to 8 stems per site were also pinned and examined at 14 to 21 day intervals to note the beginning of root initiation.

In the fall of 1991, I carefully removed the stems from the forest floor and noted: a) the number and location (node or internode) of roots; b) whether pin locations had associated with root or shoot growth; c) shoot development above points where roots had initiated; d) the age at the largest pinned diameter; and e) stem length. Half of the pinned sets were randomly selected for measurement of stem diameter at the point of root initiation and the lengths of initiated roots.

In order to determine if severed stems could root, I pinned three pairs of severed stems to the ground in each
stand in the fall of 1990 and the same number the following spring, prior to bud break. Half of the stems were covered with forest floor and the other left uncovered in the same manner as the attached stems. Overall there were 60 covered and 60 uncovered pinned stems that remained attached to the clone, 18 covered and 18 uncovered severed stems, and between 6 to 8 demonstration stems at each site.

In July, August, and September of 1991, I determined the percent soil moisture for each study site. At each site, two samples were taken below the forest floor and three samples were taken from exposed soil. The samples were taken from the top 5 cm of soil, weighed, dried at 90°C for 24 hours, and then reweighed. The drying continued until there was no significant change in the sample's weight.

Data Analysis

Clone development and measurement

I used linear and nonlinear regression to examine the relationships of number of stems per clone, crown area, stem diameter and length, the frequency of layering, and stem growth in relation to stand age, stocking level, basal area and Curtis' relative density measure (SAS statistical software, SAS Institute, Inc., 1987).

Two-way analysis of variance (ANOVA) was used to
compare average stem diameter and length, number of stems per clone, crown area and extent, and 5 year stem growth in relation to different stand age classes (Statgraphics ver. 5.0, 1991). Because of unequal variance, differences in mat number and area, and seedling number among stand age classes were evaluated in relation to stand age classes using the Wilcoxon-Mann-Whitney Two-Sample test (Steel and Torrie, 1980).

**Thinning and site preparation effects**

I tested the hypothesis that there was no difference in clonal development and layering in thinned and natural stands using two-way ANOVA (Statgraphics version 5.0, 1991). Comparison of means between treatments was performed on clone stem number, crown area and extent, and stem length and diameter. In the comparison of the effect of prescribed fire, differences in clone stem number, diameter and length, and the incidence of layering were also evaluated with two-way ANOVA. The Wilcoxon-Mann-Whitney Two-Sample Test was used to test the hypotheses that there were no differences in average mat area and size in commercially thinned stands or in plantations without prescribed burning, and that seedling number are greater in stands which have not had
site preparation or have been commercially thinned (Steel and Torrie, 1980).

**Layering study**

A randomized complete block design with the three sites as blocks was used for this study (Steel and Torrie, 1980). ANOVA was used to test the differences in root numbers in covered and uncovered stems among sites (Statgraphics ver. 5.0, 1991). Linear regression was used to determine if there was a significant relationship between stem diameter and number of roots using the data from all the sites.

**RESULTS AND DISCUSSION**

Study 1.

Clone Development in Unmanaged Stands

Clone development in different stand age classes

The morphological characteristics of vine maple change notably throughout stand development, with clone growth and development strongly related to stand age. During the early stages of conifer stand development, clones are not directly
Table 2. Average clone characteristics (range of averages).

<table>
<thead>
<tr>
<th>Stand type</th>
<th>Crown area (m²)</th>
<th>Stem diameter (cm)</th>
<th>Stem length (m)</th>
<th>Number of stems</th>
<th>5 yr. stem growth (cm)</th>
<th>5 yr. layered stem growth (cm)</th>
<th>Mat¹/² number per clone (no./ha)</th>
<th>Mat¹/² areas (m²/ha)</th>
<th>Layers per clone (no./ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Clearcuts (5-15 yr)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(burned)</td>
<td>4.6</td>
<td>.92</td>
<td>1.4</td>
<td>39</td>
<td>90.5</td>
<td>-</td>
<td>29.7</td>
<td>525.3</td>
<td>.03</td>
</tr>
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¹Mat refers to an entire crown or branch that is layered.
influenced by a conifer overstory. They became re-established in the new stand with stem sprouts originating from adventitious or dormant buds at the base of stems killed by fire or cutting.

From 5 to 15 years following overstory removal, clone clumps consisted of between 11 to 72 upright stems 1.3 to 1.5 m in height, and had crown areas of 2.0 to 7.5 m² (Table 2) (Figures 1A and 2a). If stems were not killed during logging, they persisted as upright or layered stems. Layered stems often formed dense a mat of new upright stems (Figures 1A and 2b).

Figure 1 (page 20). A general life history of the vine maple clone in Douglas-fir stands.

(A) Vine maple sprouts after its stems have been removed due to fire or logging. It grows at rates comparable to the Douglas-fir seedlings. Often, if live stems remain following the disturbance, they can become pinned to the forest floor and form a matted area of rooted clone stems (upper left corner).

(B) The vine maple stems continue to grow and become overtopped by the Douglas-fir. Its stems are often intertwined in the conifer branches. By this time, the vine maple stems significantly decrease in elongation and in number of stems (1). Vine maple stems are supported vertically in the dead branches of the conifers. 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 it, the clone's stems resemble the characteristic "convex" shape. During this phase of development, clones often layer and form mats as debris from the overstory, such as limbs or trees, fall and pin stems to the ground (2).

(D) In stands greater than 120-years-old, the clones are usually decumbent or prostrate in form. Secondary or tertiary layering may have occurred, frequently occurring in dead logs or stumps, as well as the soil. New individual ramets are also prevalent in these stands as the connections between the layered stem and the progenitor are severed (3).
Following crown closure, clones undergo changes in development that allow them to persist in understory stand conditions. In stands 23 to 70 years of age, the average number of stems per clone had decreased to 4 to 10 stems, stem diameters averaged 3.1 to 6.8 cm and stem lengths averaged 4.6 to 8.4 m. The average crown area ranged from 12.34 to 85.3 m², with larger crown areas in the older stands (Figures 1B, 3, 4). 5-year stem growth averaged 44.9 cm/year for unlayered and 29.4 cm/year for layered stems (Table 2).

While growing in close proximity to conifer seedlings, the vine maple stems become entangled in the branches of the Douglas-fir and continue growing intertwined with the conifer. Immediately following crown closure in stands 20- to 30-years-old, clone stems are often observed still being supported by the conifer branches in the overstory canopy, giving the clone a "viney" appearance (Figure 3). In one stand, I observed a vine maple stem rooted in the dead branch of a Douglas-fir tree approximately 3 m off the ground. Eventually, the conifer branches will be shed and the unsupported vine maple stems "droop" to the ground and take on the characteristic "convex" form (Figure 1B).

My data suggests that the majority of vine maple's extension and crown development occurs during the first 50 years of stand development (Figure 5). Stem lengths ranged from 4.6 to 8.8 m in stands less than 50-years-old, and from
Figure 2. Vine maple clumps during stand reestablishment. a) a clone consisting of basal sprouts 2 years after clearcutting, b) a clone consisting of basal sprouts and residual stems approximately 2 years following harvesting.
Figure 3. a) A typical clone in a 25-year-old stand representing the "viney" stage of clone development. b) Vine maple stems are intertwined among and are supported by conifer branches.
Figure 4. Typical clone in a 65-year-old stand with the convex stem shape which is characteristic of many understory vine maple clones.
4.9 to 7.8 m in stands 71- to 120-years-old. Similarly, crown areas ranged from 3.51 to 71.87 m$^2$ in the younger stands, and from 17.1 to 70.6 m$^2$ in the older ones. During the first 50 years of stand development, there is also a significant ($p=.0005$) increase in stem diameters, with averages ranging from 0.83 to 7.7 cm. There was also a significant ($p=.006$) decrease in the number of stems per clone (Figure 5). The number of stems ranged from an average of 7.4 to 49.2 stems (Table 2).

Even though maximum growth appears to occur before the stand reaches approximately 50 years of age, there are significant increases in crown area and stem length in older stands. There was a significant linear relationship of stem length ($p=.02$) and crown area ($p=.05$) to age in stands greater than 50 years. However, there was no significant relationship between stem diameter and stem number in stands older than 50 years of age.

It also appears that clone development may be related to site productivity, although my sampling was not designed to address the questions of the influence of site productivity, stand density or the continual effect of stand thinning on clone growth. However, the greatest average crown areas (74.2 to 85.3 m$^2$) and stem lengths (8.6 to 8.8 m) were found in two highly productive sites, 45 and 47 years of age and in two other stands, 35 and 45 years of
Figure 5. Average characteristics of vine maple clones in Douglas-fir stands of various ages. N=natural stands; T=thinned stands; U=unburned stands. All regression equations are significant (p< 0.01).
age, which were extraordinary from other sites for these particular measurements (Figure 5).

In stands 71- to 120-years-old, clones had average crown areas of 48.5 m$^2$, average stem diameters and lengths of 5.0 cm and 4.8 m, respectively, and an average of 3.9 stems per clone (Figures 1C and 6). The average 5-year stem growth for upright, unlayered stems was 50.0 cm, whereas layered stems had an average of 43.5 cm (Table 2). Note
this stem growth (measured on second and third order branches) does not result in extensive stem elongation, rather it appears to be important in maintaining crown area.

Clone structures in stands greater than 120 years were quite different than those in younger stands. These clones ranged in form from tree-like (Figure 7) to decumbent and rambling, no longer having the characteristic single clump form of younger clones (Figure 1D). In stands greater than 120 years, number of stems averaged 4.5 stems per clone with average crown areas of 21.1 to 52.9 m², stem diameters from 2.4 to 9.0 cm, and average stems lengths ranging from 5.3 to 7.7 m. The 5-year stem growth of unlayered stems averaged

Figure 7. Clones in a 240 year old stand illustrating the upright stems from typical clones growing in open stands.
Figure 8. Measurements of a typical clone in a stand between 120 to 130-years-old, in the late successional stage of stand development.
In these older stands, I measured layered stems which had produced upright stems with maximum diameters of 7.4 cm and lengths of 10.4 m, and decumbent stems up to 15 m in length and 15.9 cm in diameter. In a stand greater than 120-years-old, I measured a clone approximately 10 m across which had 40 upright stems, many stem sprouts, and was presently layered at 15 points (Figure 8). The clone was characterized by several 1- to 5-year-old sprouts and larger stems which ranged in age from 18 to 125 years. Another clone was approximately 20 m across with crown areas up to 33.8 m², and had layered at 8 points. It had 19 upright stems up to 10.8 m long, many of which were leaning and capable of layering.

Layering

The layering of vine maple is associated with mortality in the Douglas-fir overstory, from self-thinning, root pathogens and windthrow. As dead limbs and trees fall, they pin vine maple stems to the forest floor, and layering occurs. Layering can induce root production in intact plants even if potential primordia initials are not present before the treatment (Davis, 1982; Jackson, 1986). The
physiological process of layering is discussed by Haissig (1974). I commonly observed roots not only on the main stems up to 4.0 cm in diameter, but also on smaller second and third order branches less than 1.0 cm in diameter.

Layering in stands 5- to 15-years-old was very rare (an average of 0.3 layers/clone) and limited to stems surviving from the previous stands. On the other hand, layering was common in older stands. In stands 23- to 120-years-old, clones averaged 1.2 layers per clone, with a range of 0 to 2.7 layers per clone. In the stands greater than 120 years, clones averaged 2.2 layers per clone with a range of 0 to 5.22, significantly (p=0.1) more than in younger stands (Table 2).

I found layering to be strongly dependent on falling debris such as limbs and trees. Of the 1,911 points of layering that I examined, only two stems (approximately 0.1%) were not pinned by debris. The probability of a stem layering appears to be related to its diameter, and to the quantity and likelihood of debris pinning the stem to the forest floor. Large upright stems are not easily bent and pushed to the forest floor by small quantities of debris such as tree limbs. In one stand with Phellinus spp. root disease, there was extensive layering which occurred as a consequence of large amounts of fallen trees, branches and other litter falling throughout the entire stand (1.79 layers/clone). On the other hand, in a fairly open
healthy stand of similar age, layering was less frequent (0.91 layers/clone).

It is common for several large stems or entire crown areas to be pinned to the forest floor and layer. When this occurs, a rooted "mat" composed dense upright stems spaced at .13 to 1 m forms, many of which become independent ramets. In this study, mats were formed from the layering of 1 to 13 stems and from 1 to 3 clones contributing to a typical mat's formation. The largest mat occurred in a stand approximately 120-years-old and measured 293.74 m² (Figure 9).

Figure 9. A natural mat forming in a 120 year old stand. The mat has been formed by a bigleaf maple (A. macrophyllum) falling on at least one vine maple clone.
In unmanaged stands, the average number of mats ranged from 16.2 to 29.7 mats/hectare, with no significant difference among the stand age classes. The average area of mats ranged from 181.8 to 669.3 m²/hectare, with the largest mats found in plantations and stands greater than 120-years-old (Table 2). There was a large variance in the mat areas of unmanaged stands. Therefore, there were no significant differences found among the mat areas of the stand age classes (Figure 10).

The eventual outcome of layering is the production of individual ramets. Layering stems produce upright shoots or branches, which thicken in diameter as a root system become established, often producing a tap root (Figure 11). Eventually the proximal end of the layered stem decomposes and an independent ramet is produced. In stands less than 120-years-old, the maximum number of newly formed individual ramets observed was 80 individuals/ha, with a range of between 0 and 80 individuals/ha. However, in the stands greater than 120-years-old the number of newly formed individuals ranged from 40 to 99 individuals/ha (Table 2).

I did not observe any shoot production arising from shallow roots to support Anderson's (1967) finding of rooting in vine maple. I believe that he may have been describing the mat phenomenon as root suckering, not realizing that the source of dense upright shoots was from layered stems.
Figure 10. Mat area and number of mats per hectare of vine maple clones in Douglas-fir stands by age class. Both mat area and number are significantly greater ($p< 0.05$) in managed stands than in natural stands. See text for the definition of a mat.
Figure 11. A small diameter stem has layered (1), established a new root system and the distal end of the stem is thickening (2), and a new ramet is slowly severing its connection to the progenitor.

The relationship of stem age to stand age

There is a highly significant (p< 0.0001) relationship between the oldest stem age of a clone and stand age (Figure 12). This relationship is 1:1 for approximately the first 40 to 50 years of stand development, when new stem sprouts and natural stem mortality result in the average stem age being less than that of the stand. And it suggests that the clones sprouted at nearly the same time that the Douglas-fir seedlings became established following the removal of the
Figure 12. The relationship of largest clone stems to stand age. Each point represents the average age of the six largest stems of the clones sampled in each stand.

Previous stand, either by fire or logging. Also these results indicated that the clones that I measured developed with the present stand, with the exception any residual stems that survived the disturbance. Actual clone age could not be determined by my methods, and may represent a genet which became established hundreds of years before.

Clone development was also found to be related to the age of the oldest stems on the clone. The number of stems...
decreased significantly during the first 40 years of clone growth (p=.03) and crown area, stem diameter and length also significantly increased during this time (p<.001). These characteristics were also found to be strongly related to increases in clone basal area (p<.001).

Clone stem age distributions in different stand age classes

In stands 23- to 70-years-old, the age distribution of the vine maple stems show that the majority of the clone's stems continue to age with the stand. However, many of the stems which originated during stand establishment are no longer present in stands greater than 40-years-old (Figure 13A). Also evident is the introduction of new stem sprouts through continual basal sprouting. For example, in a 25-year-old stand, the largest vine maple stem was estimated to be 22-years-old, probably the same age as the overstory trees. However, the other stems ranged in age from 10- to 16-years-old. There was also a considerable range of stem ages in clones in stands 71- to 120-years-old. In these stands there are few stems present whose estimated ages correspond to the average stand age. The majority of stems present appear to have originated after the stand was established, and probably after understory light conditions became favorable for basal sprouting (Figure 13B).

The oldest stem found in this study was 125-years-old
and in a stand of approximately 120 to 130 years of age. The range of stem ages for this age class shows great variance, with ages of 20 years to greater than 80 years of age (Figure 13C). Few recent stem sprouts were observed in these older clones, and new stems occur mainly through layering. Younger clones however, are capable of producing new stems by layering and basal sprouting.

Effect of stand density on clone development

In addition to stand age, the 5-year stem growth of vine maple stems was found to be negatively associated with stand basal area (p=.02, R^2=.26). However, because of significant correlations between stand age, basal area and stocking (P< .05) and sampling methods, no independent relationships between clone characteristics and stand density could be derived from this study. Observations on my study sites indicate that in stands with a high proportion of vine maple, stem densities may be too dense for extensive clone growth. In stands 50 to 60 years of age, dead stems 5 to 6m long were often present. Their presence indicates that they had grown well at younger ages, but could not continue to survive in the understory of the older stand.
Figure 13. A composite of age distributions of vine maple stems in a) stands 23- to 70-years-old, b) stands 71- to 120-years-old, and c) stands greater than 120-years-old. Indicate that stands with a high proportion of vine maple...
Height to diameter ratios and clone development

In the understory of conifer stands greater than 20 years of age, vine maple stems are generally not upright, but lean or are decumbent on the ground. I compared the ratio of stem length (cm) to stem diameter (cm) to determine if lower ratios corresponded to more upright stems. There were no significant differences in height to diameter ratios between the different stand age classes. Values ranged from 156.8 to 190.5. These results did not correspond to those of Anderson (1967). He reported clone height, not stem length, to diameter ratio differences between young and mature stands, but presented no data to support this hypothesis.

Height to diameter ratios for conifers indicate the stability of a tree in a stand. For many years, it has been accepted that conifer ratios less than 100 indicate stability, whereas ratios greater than 100 indicate instability (Zasada, 1992, pers. comm.). Therefore, although no relationship was found between height to diameter ratios and stand conditions, vine maple has height to diameter ratios which would suggest that the stems are not stable and easily bend. But it should be noted that this ratio has been traditionally used to describe a conifer overstory and may not be appropriate for understory plant communities.
Changes in clone form during development

During the early phases of clone development, the clone grows as each stem sprout develops by the vegetative extension of one apical meristem forming a single shoot unit with monopodial stem structure (Bell, 1991). After crown closure though, the clone adapts its branching pattern to correspond to changes in resource availability in the understory. It is during this time that the mode of vine maple stem extension appears to change from monopodial to sympodial. With a sympodial branch structure, each new shoot develops from an axillary bud on the previous unit (Bell, 1991).

Vine maple, like other Japanese maples in the *Palmatum* series, is most likely a species characterized by determinate shoot growth (Sakai, 1990). In late successional Japanese maples, the sympodial branching pattern with determinate growth was commonly found in light limited environments because short duration leaf emergence allows for a longer period of photosynthesis and growth (Sakai, 1987, 1990). In older stands, vine maple appears to have a sympodial structure with shoots and leaves oriented in a cantilevered or inclined orientation. The cantilevered orientation in clonal plants appears to be an environmental adaptation, which exploits a single plane without allowing the overlapping of leaves, and thereby decreasing the energy
investment in structural tissue (Pickett and Kempf, 1980). According to Canham (1988) the ability of a plant to take advantage of openings in the canopy is a function of the magnitude of the increase in resource availability, and the ability of the plant to modify physiological and morphological traits that enable it to take advantage of the increase.

Another aspect to vine maple clone development is its ability to survive under very limiting understory light conditions. I hypothesize that the green stems are an important factor in energy capture and clone maintenance during the crown closure phase of stand development.

Just after crown closure when light levels are low, vine maple stems are green and may be able to photosynthesize. Photosynthesis in stems and twigs has been observed in many plants. In temperate forests, chlorophyllous twigs have corticular photosynthesis in which its primary function is to reduce the respired carbon by nonphotosynthetic tissue (Nilsen and Bao, 1990). The ability to photosynthesize in the understory where light is limited during most of the growing season, may provide an important source of carbohydrates for deciduous trees. Also, active photosynthesis during a leafless period may be a mechanism for shade tolerance. In a study comparing corticular photosynthetic rate and respiration of five deciduous trees, dogwood (*Corylus florida*), quaking aspen
(Populas tremuloides), red maple (Acer rubrum), white oak (Quercus alba) and yellow poplar (Liriodendron tulipifera), had between 19.1% and 78.8% compensation for carbon lost during respiration. (Coe and McLaughlin, 1980).

In addition, since the stems are supported by the conifer branches and stem growth may be limited by physiological maintenance costs, I hypothesize that the clone does not form enough structural wood to support upright stems, which results in the convex, "floppy" appearance of the mature clone.

Vine Maple Regeneration From Seed in Unmanaged Stands

Seeds and seedlings were found in all stages of stand development, except in stands 23- to 70-years-old. Seed production appears to be greatest in stands 5- to 15-years-old, where vine maple is above the conifer canopy. Under these conditions, 19.4% of the clones produced seed, significantly (p < .01) more than clones in the understory of 71- to 120-years-old stands (7.5%) and stands greater than 120 years in age (7.9%). In stands 23- to 70-years-old, there were no clones with seeds present (Figure 14).

Seedling density averaged 20 seedlings per hectare for all the stands, except the 23- to 70-years-old stands where no seedlings were found (Figure 15). The greatest range in number of seedlings was in the 71- to 120-years-old stand
Figure 14. The percentage of clones with seed present at different age classes, and within thinned and unthinned stands.

where density ranged from 5 to 40 seedlings per hectare. When present, seedlings were commonly found in areas with exposed mineral soil such as around windthrown trees, for example.
Figure 15. Number of vine maple seedlings per hectare and seedling shoot growth by age classes of Douglas-fir stands. Differences in seedling numbers between burned and unburned plantations, and thinned and unthinned stands are significantly (p < 0.05). Seedling growth in the 5- to 15-year age class is significantly greater (p < 0.01) than in the older age classes.
Effects of Stand Management on Vine Maple

Vegetative regeneration

Stand disturbance, such as thinning, generally affect vine maple clones in three ways: a) by promoting basal sprouting; b) causing mechanical damage; and c) by increasing the frequency of layering. Thinning of the overstory in 23- to 120-year-old stands produced a significantly (p= .003) greater number of layers per clone than occurred in natural, unthinned stands of the same age. The number and size of mats was significantly (p=0.1) greater in the thinned stands than in natural stands (Table 2). In thinned 23- to 70-year-old stands, there were an average of 30.9 mats/ha with average areas of 409 m²/ha, compared to 26.4 mats/ha with areas of 181.8 m²/ha in natural stands. In 71- to 120-year-old thinned stands, there were an average of 74.1 mats/ha with average crown areas of 1285.4 m²/ha, compared to 16.2 mats/ha with areas of 243.7 m²/ha in natural stands (Table 2). In 71- to 120-years-old thinned stands, both mat area and number were significantly (p<.05) greater than in unthinned stands (Figure 10). The size and number of mats appears to be related to the quantity of debris that falls on clones during thinning (Figure 16).

Clones sprout vigorously when stems are cut or broken.
Therefore there is an increase in basal sprouting and number of small stems following thinning. Consequently stem length and diameter are significantly less (p ≤ .03) in the thinned stands than in unthinned stands. Thinning was also found to increase stem growth significantly (p=.04), both for layered and unlayered material, in older thinned stands (Table 2).

The use of fire or other site preparation techniques appears to have a major effect on the abundance or density in stands 5- to 15-years-old. If vine maple stems are cut or burned, clones sprout from the base. If residual stems remain, they are often pinned to the ground by logging residue and nearly all clones on a site form mats.

The most prominent difference between treatments in the plantations is in the presence of mats, both in number and in the area that they occupy. The unburned stands had a significantly greater number of mats (p=.004) and surface area covered by mats (p=.028) (Figure 17). In the unburned stands, there was an average of .77 layers/clone, and 70 mats/ha with average areas of 1,293.4 m²/ha. In comparison there were .03 layers/clone, and 29.7 mats/ha with average areas of 525.3 m²/ha in the burned stands (Table 2). Only one of the three burned plantations sampled had mats present, whereas all of the unburned plantations had mats in every plot. This situation was not unexpected since prescribed fire usually kills the stems that could layer,
Figure 16. The increase in stand debris during thinning pins a greater number of vine maple stems to the forest floor.
Figure 17. Mat formation in unburned plantations.
and reduces the quantity of slash present which keeps the stems pinned to the ground long enough to layer.

The largest mat I measured was 174.6 m² in an 11 year old unburned plantation. My data indicates the clones in unburned stands had a greater number of stems, and were significantly (p<.01) larger than their counterparts in the burned stands, due to layering and basal sprouting after the stems were killed (Table 2). In a 15-year-old stand not included in my study, I observed a contiguous understory cover of vine maple greater than 2 ha, the result of all clones on the site layering as a result of logging and site preparation.

There were also more individual ramets in the thinned stands and unburned stands. In thinned stands the number of individual ramets ranged from 10 to 119/ha compared to 0 to 80/ha ramets in the natural, unmanaged stands. In unburned plantations there were 40 to 277 individual ramets/ha observed compared to 0 to 80 ramets/ha in the burned plantations.

Seedling regeneration

There was a measurably greater number of clones with seed present in the 23- to 70-years-old thinned stands, as compared to natural stands of the same age. In these stands approximately 10.1% of the clones produced seed
compared to no production in natural stands. This result suggests that thinning stimulates seed production earlier in the clone's life in the understory. In the older stands there was a decrease in seed production possibly as a result of physical damage to the clone during thinning (Figure 14).

In 5- to 15-year-old plantations, which had not been burned prior to establishment, 30% of the clones produced seed, whereas only 19.8% of the clones in the burned plantation had seed (Figure 14). The older stems of the unburned clones may produce stress crops of seed in response to any harvesting damage or there may be greater seed production due to plant maturity.

I found a significantly (p = .003) greater seedling density in thinned stands (96.7/ha) than in natural stands (18.12/ha) (Figure 15). The most significant (p = .003) increase in seedlings occurred in thinned stands, age 23- to 70-years-old, in which there were 76 seedlings/ha compared to none in the unthinned stands. In thinned stands, the majority of seedlings were found on skid trails and their age generally corresponded directly to the time of thinning. In natural stands, seedlings were usually in canopy gap openings.

Seedling growth was significantly (p < .001) greater in 5- to 15-years-old stands (7.9-8.2 cm/yr) than in other age classes (3.2 to 4.0 cm /yr). There were no significant
differences in seedling growth between thinned and unthinned stands of the same age, or between burned and unburned plantations.

Study 2.

Layering of Artificially Pinned Stems

Fifty-seven of the sixty pairs of pinned stems survived and produced roots the first growing season. Three pairs died as a result of mechanical injury due to deer browsing and pinning. Rooting was found to occur along the entire length of the pinned stem, on all branch orders (1-4). The first adventitious roots were initiated in June after leaf development ceased and about seven months after the stems were pinned to the ground. Root initiation and growth continued into September when the stems were lifted. Of the stems pinned in this study, 97% formed at least one root.

The average number of roots initiated per stem or per meter of stem was not significantly different between the Woods Creek and the Bummer Creek sites, but over all the treatments both of these sites had significantly (p < .02) lower average numbers of roots per stem than the Blodgett site (Table 3).

In the first growing season after being pinned, minimum root lengths ranged from less than 1 mm to 448 mm (Table 4).
In general, I believe that because of the soil characteristics at the Bummer Creek and Woods Creek sites, there was an impediment to root elongation. The soil at the Blodgett site had substantial components of organic matter and rock, whereas the soil at the other two sites had considerable clay content. The clay soil at the Bummer Creek and Blodgett sites did not allow for the easy removal of the roots. The root lengths should therefore be considered as minimum growth for these roots.

Furthermore, I often observed that rooting was enhanced by the presence of organic matter, such as decomposing cones, branches and logs. At these microsites there were

Table 3. The average number of roots initiated per stem and per meter of stem sizes by treatment. (Standard errors).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>n</th>
<th>Stem Diameter (cm)</th>
<th>Stem Length (meters)</th>
<th>Roots/stem</th>
<th>Roots/meter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bummer Creek</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>covered</td>
<td>20</td>
<td>1.8</td>
<td>2.4</td>
<td>46</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.1)</td>
<td>(0.2)</td>
<td>(0.1)</td>
<td>(0.2)</td>
</tr>
<tr>
<td>uncovered</td>
<td>20</td>
<td>1.9</td>
<td>2.5</td>
<td>55</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.1)</td>
<td>(0.2)</td>
<td>(0.1)</td>
<td>(0.2)</td>
</tr>
<tr>
<td>Blodgett</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>covered</td>
<td>19</td>
<td>2.0</td>
<td>2.6</td>
<td>73</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.1)</td>
<td>(0.2)</td>
<td>(0.1)</td>
<td>(0.2)</td>
</tr>
<tr>
<td>uncovered</td>
<td>19</td>
<td>1.9</td>
<td>2.7</td>
<td>61</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.1)</td>
<td>(0.3)</td>
<td>(0.1)</td>
<td>(0.3)</td>
</tr>
<tr>
<td>Woods Creek</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>covered</td>
<td>18</td>
<td>2.3</td>
<td>3.9</td>
<td>79</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.1)</td>
<td>(0.9)</td>
<td>(0.1)</td>
<td>(0.9)</td>
</tr>
<tr>
<td>uncovered</td>
<td>18</td>
<td>2.4</td>
<td>2.8</td>
<td>22</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.2)</td>
<td>(0.2)</td>
<td>(0.2)</td>
<td>(0.2)</td>
</tr>
</tbody>
</table>
often up to 15 roots initiated compared to single roots in mineral soil, with both deep tap roots and fibrous branching roots extending into the organic matter as well. Over seventy percent of the roots initiated were in the internodal region of the stem when compared to those being initiated in the nodal region. This significant (p< 0.001) distribution is most likely the result of there being more surface area in internodal areas.

Roots were more likely to be initiated individually rather than as multiple roots originating from the same point on the stem. There were exceptions, for example on sites with high organic matter multiple roots originating from the same point were common. More than 4 times as many roots were initiated as singular roots than as groups of two or more within the covered treatment, and almost three times as many were in the singular group with the uncovered treatment (Figure 18). The number of roots present is likely related to the period of layering. It is also likely that root initiation would continue, and if the stems remained pinned that multiple groups of roots would form at sites with singular roots. Examination of stems which had layered for several years indicated that groups of roots were common.
Table 4. Comparison of the average initiated root lengths and stem diameters within treatments. The maximum and minimum values are also shown to illustrate the range of values measured. (Standard errors).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Root lengths (mm)</th>
<th>Max/Min (mm)</th>
<th>Diameter at rooting (mm)</th>
<th>Max/Min (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Woods Creek</td>
<td>covered</td>
<td>29.6 (1.3)</td>
<td>182/1</td>
<td>5.9 (0.2)</td>
</tr>
<tr>
<td></td>
<td>uncovered</td>
<td>42.1 (2.5)</td>
<td>280/1</td>
<td>9.0 (0.5)</td>
</tr>
<tr>
<td>Blodgett</td>
<td>covered</td>
<td>60.0 (1.3)</td>
<td>190/1</td>
<td>8.8 (0.1)</td>
</tr>
<tr>
<td></td>
<td>uncovered</td>
<td>50.6 (1.8)</td>
<td>190/0</td>
<td>8.7 (0.4)</td>
</tr>
<tr>
<td>Bummer Creek</td>
<td>covered</td>
<td>44.3 (1.8)</td>
<td>448/2</td>
<td>7.9 (0.2)</td>
</tr>
<tr>
<td></td>
<td>uncovered</td>
<td>32.3 (1.5)</td>
<td>240/0</td>
<td>8.3 (0.4)</td>
</tr>
</tbody>
</table>

Figure 18. The frequency and number of roots initiated at a given site on the stem, and the location on the stem of these sites.
Of the roots initiated, more than 76% were on stem diameters of less than 1 centimeter, with the remaining majority of roots on stems of 1 to 2 centimeters. Less than 3% of initiated roots were observed on stems of diameters greater than 2 centimeters, with 5.5 cm being the largest diameter on which roots were observed (Table 5). Two possibilities for this pattern of rooting are that the majority of the stem that was pinned was less than 1 cm in diameter and that the smaller diameter portions of the stems are more physiologically active than the larger diameter portions.

There was no indication that root initiation was greater at points where stems were pinned to the forest floor. Less than 1% of all roots occurred at points of pinning. There was also no indication of new shoot development on the layered stems in the first growing season. Root development seems to have priority over new shoot initiation, possibly because layered stems already have functional shoots.

Table 5. Distribution of newly initiated roots by stem diameter classes.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Stem Diameter Classes (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 - 1.0</td>
</tr>
<tr>
<td>Covered</td>
<td>945</td>
</tr>
<tr>
<td>Uncovered</td>
<td>508</td>
</tr>
<tr>
<td>Percent of roots initiated</td>
<td>76.1</td>
</tr>
</tbody>
</table>
Root production on covered and uncovered stems

Only at the Woods Creek site was there a significantly (p ≤ .001) greater number of roots initiated on covered stems (79) than on uncovered stems (21). On other sites, root numbers on covered stems averaged 55 to 73, and 45 to 61 on uncovered stems (Table 3). The significantly (p ≤ .001) fewer roots on the uncovered stems at Woods Creek could have resulted from almost complete stem defoliation by deer browsing. In general, there is no evidence to suggest that covering facilitated layering.

The lower number of roots produced at Woods Creek and Bummer Creek compared to Blodgett is not likely explained by differences in soil moisture since it was not significantly different among the sites on any sampling date. For example, in August it ranged from 16% at Woods Creek to 19.4% at Bummer Creek. However, there was significantly (p = .006) greater soil moisture at all of the sites in July than there was in August or September (Table 6).

There was also no significant difference found between samples from under the forest floor covering or in exposed soil. Under natural layering conditions, the forest floor was characterized by live mosses and other plants, as well as debris which created a relatively moist condition. The artificial covering in this study did not replicate natural conditions.
Table 6. Percent soil water at layering study sites throughout the growing season (Standard errors).

<table>
<thead>
<tr>
<th>PERCENT SOIL WATER</th>
<th>July 22</th>
<th>August 23</th>
<th>September 23</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bummer Creek</td>
<td>54.4*a</td>
<td>19.4*b</td>
<td>18.2*b</td>
</tr>
<tr>
<td></td>
<td>(3.1)</td>
<td>(1.7)</td>
<td>(2.8)</td>
</tr>
<tr>
<td>Blodgett</td>
<td>53.3*a</td>
<td>17.0*b</td>
<td>17.8*b</td>
</tr>
<tr>
<td></td>
<td>(4.4)</td>
<td>(1.0)</td>
<td>(2.7)</td>
</tr>
<tr>
<td>Woods Creek</td>
<td>52.9*a</td>
<td>16.7*b</td>
<td>14.5*b</td>
</tr>
<tr>
<td></td>
<td>(4.9)</td>
<td>(2.4)</td>
<td>(3.3)</td>
</tr>
</tbody>
</table>

( a,b indicate significant difference at p < .01 )

Effects of stem severing on root initiation

All 48 stems which were severed from the clone died. The stems at each site which were severed in the fall when leaves were present desiccated rapidly, and there was no possibility of root initiation. At each site, the three pairs severed in the early spring produced leaves. One covered stem produced two roots, but they dissappeared. The severed stems apparently desiccated rapidly and do not appear to function independently of the clone. These results are similar to those of Vertrees (1975), who reported that few if any cuttings out of several thousand rooted or survived. I conducted exploratory studies and did not observe any rooting on dormant cuttings collected in late spring and treated with various rooting hormones. However, approximately 50% untreated, semi-hardened cuttings collected in September rooted in a mist chamber, indicating
that there is high potential for rooting of stem pieces if properly cultured.

CONCLUSION

The ability to reproduce vegetatively has some distinct advantages for a plant. Once established on a site through seed reproduction, vegetative reproduction can enable a plant to expand and exploit its environment and resources (Haissig, 1974). Following a disturbance, vegetative reproduction provides the plant with the ability to rapidly reestablish itself, as well as allowing an individual genotype to maintain and expand its presence on a site.

Clonal growth is an important process for maintaining stable plant populations and conserving adapted genotypes. Reinhartz and Popp (1987) reported two general strategies of clonal expansion for woody species. With the first strategy, ramets remain connected and function as extensions of the clone progenitor. The physically attached ramets are not necessarily able to transfer assimilates, such as water and nutrients, to the older ramets. In most of the cases, the majority of assimilate transfer is from the older ramets to the younger, as with quaking and bigtooth aspen (Populus tremuloides and P. grandidentata Michx.) (De Byle, 1964). With the second strategy, the ramets become physically independent from the progenitor, such as with vine maple or
Clone morphology and development

Vine maple is a common understory plant in Douglas-fir forests of the Oregon Coast Range. It has the ability to persist throughout stand development because of its ability to alter its growth habit to suit current stand conditions and to regenerate vegetatively. The general stages of stand development correspond closely to the changing stages in clonal development. During the stem initiation phase of stand development, the vine maple clone is a mass of rapidly growing, even-aged basal stem sprouts with monopodial stem structure. As the clone continues to grow, a few shoots gain apical dominance and the number of stems decreases. Clone regeneration during this stage of development is primarily limited to sprouting from residual stem bases or buried stems, and to seedling establishment.

The second stage of stand development is referred to as the stem exclusion phase and is generally concurrent with the crown closure of the overstory. Clone growth is greatly reduced, which can probably be attributed to low light conditions under the closed portions of the conifer canopy, as well as other changes in resource availability. It is during this time that clones takes on a "viney"
appearance. Stems are generally entangled in the lower, dead limbs of the Douglas-fir, and crown area and stem number are greatly reduced. At this stage corticular photosynthesis may help to maintain vine maple at this phase of stand development. Some sprouting and layering occurs, but seed production and seedling establishment are not present.

The third phase of stand development is the understory reinitiation period, when herb and shrub layers are reestablished in the understory. During this phase, vine maple changes from a monopodial to a sympodial branching pattern to more efficiently utilize the limited light in the understory. The clone may take on either a "convex" shape in the understory or an erect tree-like shape growing in a gap. Crown area increases and becomes cantilevered in orientation, and the clone continues to increase slowly in both stem length and crown areas. Clone maintenance and expansion is primarily through layering, forming ramets both singularly and in multiples as mats form and disintegrate into individuals. Seed production and seedling establishment are also present during this developmental stage.

By the final old-growth stage, the clones have either taken on an erect tree-like growth habit or are multi-layered and "crawling" on the forest floor, the result of multiple layers caused by fallen trees and dead limbs.
Clone maintenance and expansion is primarily through layering, but basal sprouting is common. Seed production and seedling establishment are also common in old stands.

The effects of stand thinning and prescribed fire on clone development

Thinning overstory conifers affects the life history and the timing of different stages in clonal development. Thinning may also affect vine maple abundance and density in a stand, thereby affecting vine maple's role in the development of the understory plant community.

If a clone's stems are broken or severed, it will regenerate primarily by sprouting of the basal stem bud bank. The size of stems and size of the entire clone are significantly reduced, as is its ability to layer and to produce seed. In general, if the clones are sufficiently damaged during the removal of the overstory, the stature of vine maple in the stand is reduced.

On the other hand, if the vine maple clone remains intact, then significant increases in layering can occur in thinned stands, especially in the older stands. In these stands, clones are large and there is likely to be a considerable quantity of logging slash. Thus, layering and the formation of mats may be extensive. On the other hand, young stands were more likely to have clones with flexible
stems and little mechanical damage, and the harvested stand produced a smaller quantity of slash.

The thinned stand also provides the environment for increased seed production and the necessary seedbed for seedling establishment. The effect of thinning on sexual reproduction was most profound in the 23-to 70-years-old stands, where overstory removal allowed for crown development and seed production to occur much earlier in the clone's life history.

Prescribed fire or severe site preparation does not generally alter clone development in Douglas-fir plantations. The clones, which have been cut or broken during stand harvest and site preparation, sprout basally and continue developing as described above. However, where the clones remain partially or completely intact the composition and structure of the next stand may be substantially affected. Intact clones layer easily and form mats during logging, thereby allowing for the possibility of large areas of the stand to be dominated by vine maple to the exclusion of conifers, other shrubs and herbaceous plants.

An additional consideration is that vine maple may exclude plants from the understory by means other than occupying growing space. In a greenhouse study, Del Moral and Cates (1971) found that vine maple leaf litter contained at least two strongly inhibitory extracts to Douglas-fir and
other plants. Vincent (1965) also hypothesized that there may be allelopathic properties in striped maple leaf litter to which may retard conifer regeneration. Sugar maple (A. saccharum) has been shown to produce substances which inhibit the development of yellow birch seedlings (Betula alleghaniensis) (Tubbs, 1973). Another consideration is that there may also be a physical effect of the vine maple leaf litter on small seedlings beneath vine maple's crown.

Adventitious root production in artificially layered stems

The layering of vine maple stems is a mechanism for relatively rapid clonal expansion. Once pinned to the ground, whether naturally or during harvest operations, adventitious roots form and clonal expansion growth is rapid. Adventitious roots were initiated and root systems established during the first growing season after stems are pinned.

It appears that it is not the actual pressure of pinning or stem orientation but the close contact of soil and stem which stimulates layering. Roots are initiated and distributed over the entire stem as singular roots in both the internodal and nodal regions of the stem, not just at the points of pinning. Although roots were observed over a range of stem diameters (up to 5 cm), over 75% of roots were initiated at diameters of 1 cm or less. In general, there
was not a significant difference found between covered and uncovered pinned stems.

Vine maple provides both forage and cover to blacktail deer and other animals (Rhodes and Sharrow, 1990). It may also be a major impediment to conifer stand establishment. Therefore, the layering study also provides important insights into some forest management considerations for Douglas-fir stand establishment, management and wildlife habitat planning. Since severed stems died and eliminated the potential for layering, the practice of cutting stems during logging may locally decrease the spread of vine maple and aid in conifer establishment. Alternatively, by maintaining vine maple stems and allowing logging slash to pin them to the forest floor, stems are available for browsing and layering. By increasing vine maple abundance, there is a concurrent production of wildlife shelter and browse, but also an increase in vine maple spread throughout the stand.

Another management benefit of increasing vine maple abundance is the benefit to recreational planning and alternative forest products. Vine maple is aesthetically pleasing to look at in a forest landscape, as it adds fall color and layers to the forest structure. Vine maple is also used in many alternative forest products such furniture and basket making.

With the probable future increase in the intensity of
management on some forest timber lands, a rapid increase in
vine maple abundance on some lands will need to be
considered. With the inability to use many traditional
forestry tools, such as herbicides and prescribed fire, or
the possible inappropriateness of their use on some sites,
the ability to control a plant communities composition and
structure becomes more difficult and expensive. An
understanding of the plant's ecology and the effects of
disturbance on the plant's development that provides answers
to many forest management questions and provides insight
into an array of possible silvicultural strategies.


LIST OF PERSONAL COMMUNICATIONS
