AN ABSTRACT OF THE THESIS OF

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David E. Hibbs

The processes that lead to stable, low-growing plant communities and the characteristics of the species that form them are of great interest to rights-of-way (ROW) managers and others wishing to better understand plant community resistance to tree invasion on managed landscapes. The use of stable, low-growing plant communities as a mechanism to control tree invasion on ROWs has been widely acknowledged, but little is known about what plant characteristics lead to stable communities or how different treatment methods affect low-growing communities in the Pacific Northwest.

The goal of this study was to assess the resistance of stable, low-growing communities to tree invasion on ROW in the Pacific Northwest and to identify common characteristics among the species in these communities that contributed to the formation of stable communities. To address this goal, we investigated 1) the abilities of different species within the low-growing component of the ROW communities to resist invasion by trees and to fill newly created gaps caused by disturbance, 2) the growth patterns and potential for vegetative reproduction of trailing blackberry (*Rubus ursinus* Cham. and Schlecht) and creeping snowberry (*Symphoricarpos mollis* Nutt.) to understand how different clonal propagation patterns affect spread into unoccupied space and infilling of currently colonized areas, and 3) the effectiveness of several common vegetation control methods for reducing the density of undesirable species and promoting the development of low-growing plant communities on ROW. These factors are important processes that determine the stability of a low-growing plant community.

This project was conducted at three sites in the western foothills of the Cascade Mountains of Oregon and Washington. Species composition and abundance was measured in roughly 330 2x2 m plots at each site prior to the application of three different treatments aimed at removing tall-growing target species. The plots were measured again two years later to assess changes in species cover. The growth pattern and architecture of trailing blackberry and creeping snowberry was also investigated through the careful excavation of both individual plants and 1x1 m plots centered in dense thickets of each species.

The various treatments used in this study resulted in an average increase in nontarget cover of 65% from 2000 to 2002 while reducing tall target cover by an average of 53%. No difference was found in the change in average nontarget cover or tall target cover among treatments. The effectiveness of the various treatments in reducing target cover varied significantly based on the type of target species being treated.

There were no strong differences in resistance among the common low-growing species to invasion by tall target species. The range in increase in tall target cover in plots dominated by low-growing species was highly skewed, as tall target cover increased very little in many plots and by as much as 28% in a very few.

In the first two years following disturbance, shrubs capable of rapid horizontal expansion through vegetative reproduction, such as trailing blackberry and bracken fern (*Pteridium aquilinum*), were most successful filling gaps. Their ability to expand rapidly led to their high abundance following disturbance.

The successful colonization of gaps by trailing blackberry was a result of its growth pattern, which focused on rapid spread as this species produced new canes annually that grew up to 1.9 m during their first year. This may allow it to be a successful colonizer of gaps. It was also capable of forming dense thickets and averaged 113 stems/m^2. The growth pattern of creeping snowberry, which focused more on infilling, may allow it to maintain areas of dense, persistent cover, as it averaged 237 stems/m^2 in dense thickets. It was also capable of horizontal spread through the initiation of new ramets along creeping stems. These stems averaged 0.6 m during their first year of growth. Both strategies of growth and spread allowed these shrubs to form thickets of dense vegetation.

The use of stable low-growing plant communities as a management tool to reduce tree seedling establishment and growth can have many benefits including reduced costs due to lower tree density and longer periods of time between

treatments, increased wildlife habitat, and aesthetic appeal. However, for this management approach to be most successful, one must have an understanding of the plant community where it is being applied, the plant characteristics that will lead to the formation of stable, low-growing communities, and how the different available treatment options will affect the resulting plant community. This study addressed many of these topics to produce a more comprehensive understanding of how stable, low-growing plant communities can be used as a management tool for reducing tree invasion in the Pacific Northwest. The two-year duration of this study, while allowing for many new insights, limited the scope of some of our conclusions. Continued monitoring of these research sites, as has been done in several locations in the northeast United States, would greatly increase the strength of our conclusions.

Stable, Low-growing Plant Communities in the Western Cascade Mountains: Species Processes and Their Implications for Rights-of-way Management

by
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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Jonathan C. B. Nesmith, Author

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CONTRIBUTION OF AUTHORS

Jeff Shatford assisted with data collection and interpretation, as well as writing of the second and fourth chapters of this thesis. David Hibbs provided detailed critics and edits for each of the four chapters.

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Stable, Low-growing Plant Communities in the Western Cascade Mountains: Species Processes and Their Implications for Rights-of-way Management

CHAPTER 1. INTRODUCTION

A project designed to evaluate the role that stable, low-growing plant communities could play in reducing management costs on electric utility rights-of-way (ROW) in the Pacific Northwest was initiated in 1999. This project aimed at addressing several questions including: 1) whether creation of stable, low-growing plant communities was a feasible method of controlling tree establishment on ROWs, 2) what species were most capable of forming stable, low-growing communities, and 3) what treatment methods were most successful at promoting the formation of stable, low-growing plant communities. To address these questions, one must have an understanding of several topics in community ecology, including what is community stability, what community or species properties contribute to stability, and how can these properties be manipulated by managers to produce the desired community functions.

Many studies have shown that stable, low-growing plant communities can effectively inhibit tree establishment (Bramble et al., 1990; Niering and Goodwin, 1974; Hill et al., 1995). Yet among studies, the type of species that were capable of forming stable communities varied widely, ranging from woody shrubs to grasses and forbs (Meilleur et al., 1994; Bramble et al., 1990; Bramble et al., 1996). This chapter will review the factors that influence the stability of a plant community to better evaluate what plant properties may facilitate the formation of stable communities.

One important component of community stability is resistance. Resistance is a measure of the change in composition or function of a community in response to disturbance (Westman, 1978; Sutherland, 1981; Connell and Sousa, 1983). A disturbance can be a change in the physical environment, such as a drought or fire, or it can be biotic in nature, such as the introduction of an invasive species (White, 1979). In the context of this study, both phenomena are of interest, though we will focus primarily on tree invasion as our measure of community resistance.

The resistance of a plant community to invasion by foreign species, referred to as its invasibility, is determined by many factors. These factors include properties of the species that compose the plant community, such as competitive ability, properties of the invading species, such as seed size and propagule pressure, and indirect processes that are affected by properties of both the host species and invading species, such as seed predation.

Competitive exclusion of invading species is the main mechanism through which the invasibility of a plant community is determined (Burke and Grime, 1996). Competition among individuals determines which, and how many species can coexist (Begon et al., 1996). The higher the intensity of competition among the species within an established community, the lower that community's invasibility will be (Crawley, 1986).

There has been a continuing debate about what types of plants, if any, are associated with increased competitive ability (Grime, 1977; Tilman, 1987; Grace, 1990). However, there has been some agreement that certain properties often lead to competitive superiority. They include density of plant cover and height of vegetation (Hill et al., 1995; Crawley, 1986; Kurmis and Sucoff, 1989).

The cover of a plant community controls the intensity of competition for both aboveground and belowground resources an invading plant will face. Many studies have demonstrated that areas dominated by dense thickets of vegetation inhibit the establishment and growth of tree seedlings (Berkowitz et al., 1995; Mercier et al., 2001; Meilleur et al., 1994; Bramble et al., 1990). Whether high plant density leads to competition for aboveground or belowground resources being more intense depends on what resource is most limiting (Putz and Canham, 1992; Wilson, 1988).

The height of a plant community controls the duration that an invading plant will be exposed to competition for aboveground resources (Berkowitz et al., 1995; Putz and Canham, 1992). While the duration of competition does not necessarily affect the growth rate of the invading plant, it does affect its likelihood of survival because the invader is exposed to more intense competition for a longer period of time (Hill et al., 1995). The effects of overtopping vegetation are not always negative, however, as shading has been shown to increase tree seedling survival in some cases where soil moisture is the limiting resource (Jones, 1995; Strothman, 1972).

Along with the properties of the species that comprise a plant community, properties of the invading species also dictate the likelihood that a community will be invaded. Higher propagule pressure leads to a greater likelihood that the invading species will be successful (Brown and Peet, 2003; Lonsdale, 1999). Therefore, an invading species that is able to inundate a community with many potential new plants has a greater chance that at least some individuals will become established. Other physical properties of the invading species such as seed size can also influence whether a plant community is invaded (Burke and Grime, 1996). Invading species that produce large seeds often have a greater chance of success than invaders that produce small seeds because they have more stored resources that allow them to be less sensitive initially to strong competition from neighboring plants.

Other factors that are indirectly associated with the properties of the plant community or invading species can affect its invasibility. The properties of a plant community such as the type of cover and food sources it produces influence the small mammal diversity and density as well as seed predation rates (Bramble et al., 1992; De Steven, 1991). Seed predation has been found to be the most important factor limiting Douglas-fir establishment in some shrub communities (Caccia and Ballare, 1998). Just as the type of cover can affect seed predation rates, the identity of the invading species can also be important, as some seeds are favored over others by different seed predators.

If a community is unable to recover quickly following a gap-creating disturbance, gaps can be filled by foreign species and the invasibility of the community becomes irrelevant. Therefore, for a community to be stable, it must not only be resistant to invasion, but also be able to recover following disturbance.

The resilience of a community is a measure of how quickly the community returns to its original composition following a disturbance (Westman, 1978). Resilience is influenced by the size, frequency, and intensity of the disturbance, as well as by the characteristics of the species that make up the community (Allison, 2004; Diaz-Delgodo et al., 2002). Community resilience is particularly sensitive to the method of reproduction and spread of the aggregate species within the community (Allison, 2004; Sousa, 1984). In general, communities composed of plants capable of rapid growth and spread are more able to fill gaps quickly following disturbance and return to their original state, thus making them more resilient (MacGillivray et al., 1995).

The plant properties associated with rapid recovery following a disturbance vary based on the size and intensity of the disturbance. Vegetative reproduction is one property that can be associated with high resilience to small scale disturbance as plants capable of vegetative reproduction can quickly spread horizontally over short distances through runners, rhizomes, or root suckers to re-colonize disturbed areas (Halpern, 1988). In large gaps, the ability to produce large amounts of seed or the production of a seed bank can greatly accelerate colonization (Canham and Marks, 1985; Armstrong, 1988).

There are many examples of stable communities representing a wide variety of species growth forms, ranging from grasses to shrubs to trees (Niering et al., 1986; Sutherland, 1981; Tilman and Downing, 1994; Niering and Goodwin, 1974; Collins, 2000). Within these communities, the properties that lead to their stability are often the same and promote a strong resistance to invasion and a rapid response to disturbance.

The following three chapters will investigate different aspects of the ROW plant communities to better understand how different plant properties contribute to community stability and what role stable, low-growing communities can play as a management tool on ROWs in the Pacific Northwest. Chapter 2 will investigate the species composition and abundance of ROWs in the foothills of the western Cascade Mountains of Oregon and Washington and look at the resistance to invasion and response to disturbance of the different low-growing species within these communities. Chapter 3 will look at how the growth forms of two common shrubs affect their potential to create resistant communities and spread into new space. Chapter 4 will investigate whether different treatment methods lead to communities with different species assemblages that result in differences in their stability. The questions addressed in each chapter require a clear understanding of community stability and how it is controlled. Therefore, the processes that have been discussed in this chapter will serve as important background for the questions that are addressed in this thesis.

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CHAPTER 2. STABLE, LOW-GROWING PLANT COMMUNITIES ON RIGHTS-OF-WAY IN THE PACIFIC NORTHWEST: ANALYSIS OF PLANT PROPERTIES

Abstract

We assessed the ability of different types of low-growing plant species to contribute to stable communities on utility rights-of-way (ROW) in the foothills of the Cascade Mountains in Oregon and Washington. Plant cover was measured prior to and two years after the selective removal of target species on three electric utility rights-of-way. Target species included trees, tall shrubs (e.g., hazel (*Corylus cornuta*)), and the exotic shrub scotch broom (*Cytisus scoparius*).

We investigated the abilities of different species within the low-growing component (shrubs, ferns, grasses, and forbs) of these ROW communities to 1) resist invasion by trees, and 2) fill newly created gaps caused by disturbance, two essential properties of stable communities.

Clonal shrubs were more abundant on the ROWs than other nontarget low-growing vegetation types but did not display a higher resistance to tree invasion than the other species. No common low-growing species was more often associated with high tall-growing species cover than another, and there were no strong differences in resistance to invasion by tall-growing species among any of the plots dominated by the common low-growing species.

In the first two years following treatment, trailing blackberry (*Rubus ursinus*) and bracken fern (*Pteridium aquilinum*) were the most successful low-

growing species at colonizing new gaps. The high abundance of these species following disturbance makes them potential candidates for contributing to the formation of stable communities on ROW as the abundance of low-growing cover is often associated with high resistance to tree invasion. Continued sampling of these ROWs over the coming years will provide a better picture of what types of species are most capable of resisting tree invasion and invading gaps, allowing them to form stable, low-growing communities on ROW.

Introduction

The control of tree regeneration and growth is a major objective in utility rights-of-way (ROW) management. The creation of stable, low-growing plant communities on ROWs is one strategy that has been widely discussed to meet this goal (Egler, 1958; Niering, 1958; Bramble and Byrnes, 1983).

Many different management strategies have been used to maintain utility ROW over the years. The preferred strategy has shifted over time, especially on public lands. Historically, the primary treatments used were hand-cutting, broadcast herbicide applications, and mowing (Egler, 1958; Niering and Goodwin, 1974; Luken et al., 1991). More recently, as restrictions on herbicide use became more prevalent treatments shifted to a more selective use of herbicides and increased use of hand-cutting and mowing. However, some of these methods have not been successful at creating stable, low-growing plant communities on ROW. Broadcast application of herbicides tends to reduce species diversity and open the site to tree invasion (Niering and Goodwin, 1974). This treatment approach also does little to increase the competitive effect of other vegetation that might retard the establishment and growth of trees. Manual cutting has proven to be ineffective at reducing the density of trees or rotation time between treatments because many tree species regenerate through stump or root sprouting (Luken et al., 1991). This can result in increased stem density, which often leads to an increased cost of future treatments.

More selective management approaches that target specific ecological processes began to gain popularity in northeastern North America in the mid 1960's (Niering and Goodwin, 1974). Such approaches promote or impede ecological processes such as competition or germination to obtain the desired management objective. These strategies have gained in popularity by showing that managing for a specific type of plant community or characteristic reduces the frequency and intensity of management that is required (Niering, 1958). This also often leads to higher quality wildlife habitat, a more aesthetically appealing appearance, and reduces soil compaction and erosion (Egler, 1958; Niering, 1958; Geier et al., 1992).

The most common method used to implement a more ecologically based management approach is the creation of low-growing plant communities that are resistant to tree invasion (Egler, 1958; Brown, 1995; Hill et al., 1995; Shatford et al., 2003). This is usually accomplished through the selective removal of target species. Target species are those that have the potential to grow into the zone below the electric lines. Historically, all woody vegetation was targeted for treatment. However, as more selective management approaches have been adopted, only tall-growing species were considered targets and the low-growing species were often encouraged to try to create a more stable, low-growing community. For this approach to be successful, a clear understanding of what plant properties and assemblages of species facilitate the creation of stable plant communities is essential for the successful implementation of this approach.

For a low-growing plant community to be stable, it must be resistant to invasion (Connell and Slayter, 1977; Tappeiner et al., 1991; Foster et al., 2002) and be able to recover quickly after a disturbance (Westman, 1978; Halpern, 1988; De Grandpre and Bergeron, 1997), filling gaps with low-growing vegetation before tree seedlings can become established. These two properties of a plant community are determined by the characteristics of the species found within that community and by the characteristics of the disturbance that is being applied. Identifying what plant properties contribute to resistance to invasion and to a rapid post-disturbance response is a necessity for understanding what types of plants can contribute to stable, low-growing plant communities.

Because the creation of stable, low-growing communities has become such an important strategy for ROW managers, several studies like the one to be described here have been done (Bramble and Byrnes, 1983; Dreyer and Niering, 1986; Brown, 1994; Mercier et al., 2001). These have been long term studies that span over several decades in some cases and have provided a wealth of information regarding the issues of ROW management. However, very few studies like these have taken place in the Pacific Northwest environment of dry summers and wet winters. The highly productive coniferous forests of the Pacific Northwest offers a very different ecological setting than that of the Northeast to observe the processes that control the creation of stable, low-growing plant communities. This study, conducted in the western hemlock ecological zone of Western Oregon and

Washington (Franklin and Dyrness, 1973), offers the opportunity to test previous conclusions in a fundamentally different ecosystem.

OBJECTIVES

This study is part of a larger project aimed at developing an ecosystem management approach for creating stable, low-growing plant communities in rights-of-way within the western hemlock ecological zone of the Pacific Northwest. The goals of this study were to develop a comprehensive understanding of current plant communities within ROWs in this area and to evaluate whether the potential of the different species within these communities differed in their ability to contribute to stable, low-growing plant communities. Stability in this context is a function of resistance to invasion by new plants and recovery (gap filling) after disturbance. Therefore, our objectives were to: 1) describe the types of plant communities present on the ROW, 2) evaluate what species were most effectively retarding the establishment of tall-growing vegetation, and 3) determine what species were capable to rapid colonization of newly created gaps.

Methods

SITE DESCRIPTION

Three sites under 500 Kvolt power-lines were selected from the western foothills of the Cascade Mountains in Oregon and Washington (Figure 2.1). The sites were selected to be within the western hemlock ecological zone, a dominant community type in the Pacific Northwest, (Franklin and Dyrness, 1973) to minimize the differences in climate and species composition among them. Similar sites were selected to allow for comparisons in species composition and abundance over time. The western foothills of the Cascades in Oregon and Washington are characterized by coniferous forest with high stand productivity and biomass accumulation (Franklin and Dyrness, 1973). High total annual precipitation with dry summers and mild winters and periodic fires (Agee, 1988) are the driving forces that have led to the vegetation characteristic of this region. Soil profiles, although originating from a host of various parent material, are generally moderately deep and of medium acidity (Franklin and Dyrness, 1973).

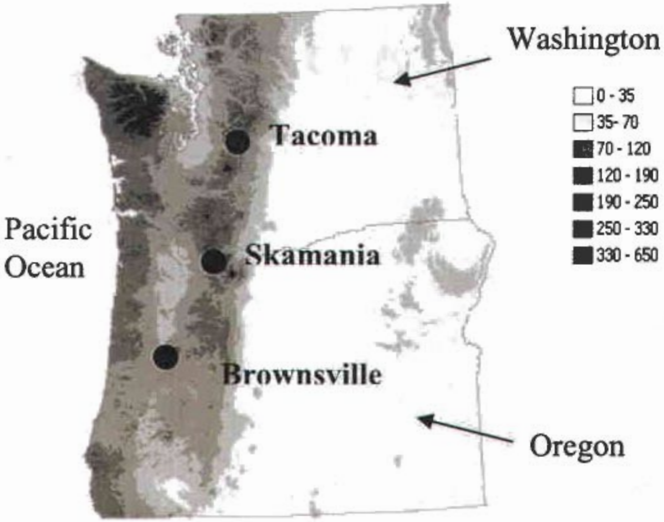

Figure 2.1. Location of the sites in Oregon and Washington. Legend indicates average annual precipitation in cm. Figure created from data described in Thornton et al., 1997.

Each site was surrounded by forest dominated by Douglas-fir (*Pseudotsuga menziesii*), the dominant tree species in the western hemlock zone, especially in early- to mid-successional stages (Franklin and Dyrness, 1973). The Brownsville, Skamania, and Tacoma sites had been in use by the electric utility since 1965, 1938, and 1972, respectively. The vegetation on these areas had not been treated to remove unwanted species for at least three years prior to the start of the study. The past management history on the sites had likely involved many different treatment methods with the most recent treatment cycles using manual cutting of target individuals with no herbicides as the main treatment method.

The Brownsville site was located on the eastern border of the Willamette Valley southeast of Corvallis, Oregon at an elevation of 315 m (1040 ft.) (Figure 2.1). It was the driest site, averaging 154 cm of precipitation/year (12 cm during Jun-Aug.). The soil at Brownsville was a Bellpine or Jory silty clay loam classified as clayey, mixed, xeric Haplohumults (Natural Resources Conservation Service, 2002a). The Skamania site was located in Washington, just north of the Columbia River near Multnomah Falls, Oregon at an elevation of 100 m (330 ft.). It averages 221 cm (17 cm during Jun-Aug) of annual precipitation. Skamania was characterized by shallow soils and dimpled terrain, forming wet depressions on some areas of the site. The soils were Steever stony clay loam, classified as loamy-skeletal, mixed, mesic Typic Haplumbrepts (Natural Resources Conservation Service, 2002b). The Tacoma site was located in Eagle Gorge, Washington at an elevation of 450 m (1475 ft.). Tacoma averages 208 cm/year of rain (23 cm during

Jun-Aug). Average annual rainfall was derived from models described in Thornton et al. (1997). The soil at Tacoma ranged from deep to shallow and was formed from glacial outwash. The soils were Pitcher sandy loam and Sulsavar loam, classified as loamy-skeletal, mixed, frigid Typic Haplorthods and coarse-loamy, mixed, mesic Typic Haplorthods, respectively (Goldin, 1992). As at Skamania, rocky outcrops were scattered across the site.

STUDY AREA DESIGN AND TREATMENTS

Each site was approximately five hectares (12.5 acres) in size, though the length and width of each area varied. The ROW was 80-100 m wide at Brownsville and Skamania and 160 m wide at Tacoma. These sites had been set up as part of a long-term project with multiple objectives. One of the project objectives that was not the focus of this study was to investigate how various treatment methods affected the plant communities present on the ROWs over time. Therefore, each site contained three blocks that spanned the width of the ROW in which different treatment methods were applied during July of 2000. The aerial extent of a treatment was approximately 1.25 hectares (3.2 acres).

In this study, we utilized portions of these treated areas to address our questions. Each treatment was designed to reduce target species occurrence and abundance. Target species were defined prior to treatment application as any species that the ROW managers were trying to eliminate. These included both tall-growing trees and shrubs that could interfere with the lines, as well as scotch broom

(*Cytisus scoparius*), an invasive species that had established on the ROW. Throughout this paper, "target species" will refer to the tall-growing species plus broom and "tall-growing species" will refer only to the tall-growing trees and shrubs. Nontarget species were defined as all other species that had not been specifically targeted for treatment. The treatments were:

1) Manual Cut, in which target species were cut six to twelve cm from the ground using a chain saw so that no live stems were left attached to the stump.

2) Foliar Herbicide application with follow-up basal stem herbicide application in the summer of 2001.

3) Cut and Spray, in which target species were manually cut and the stumps were treated with an herbicide.

For the objectives of this study, the type of selective treatment that was applied was not considered. The only property of a selective treatment that was important was whether or not it removed target cover for the duration of the study and created a gap into which other species could invade.

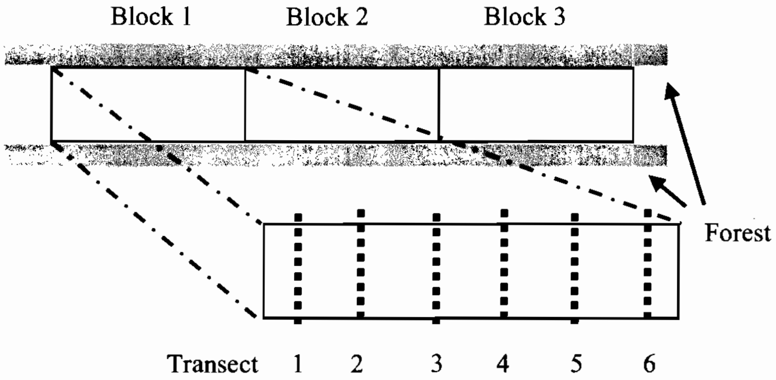

Figure 2.2. Sampling design for permanent vegetation transects across utility rights-of-way near Brownsville, Oregon and Skamania, Washington, established in 2000. Each block was approx. 90 x 130 yards. At the Tacoma, Washington site, treatment blocks were 140 x 90 yards and 3 transects instead of 6 were installed per block.

SAMPLING DESIGN

Permanent transects running across the ROW from forest edge to forest edge were installed in 2000 in each block prior to the treatment applications. Each transect started and ended at the forest edge drip line, defined as the vertical boundary where the overhanging forest braches stop. The first transect was placed at an arbitrary location within the first 25 meters of a given block, and subsequent transects were then placed every 50 meters across the block (Figure 2.2). The total transect length at each site was similar. Transects at Brownsville ran across the ROW from east to west and from north to south at the other two sites.

Two different types of sample plots were used in this study: transect and gap plots. The purpose of the transect plots was to measure change in species abundance and composition over time. The transect plots were 2x2 meters in size and located every four meters along each permanent transect (Figure 2.2). Between 470 and 511 plots were sampled at each site, representing roughly 3-5% of the total area of a site. For each species of woody plant in a plot, percent cover was visually estimated. Grass cover and forb cover were recorded as plant types rather than as individual species. Certain woody species such as willows (*Salix spp.*) were also grouped together to simplify identification and sampled at the genus rather than species level. The plots were measured prior to treatment application in mid-April through mid-June in 2000 and then again in July-August, 2002.

The gap plots were installed in the spring of 2001 to monitor which species were filling gaps created by the treatments. These plots were centered on stumps or standing dead target species. Each plot was at least five meters away from the permanent transects. We installed a total of 121 gap plots at the three sites (Table 2.1).

Table 2.1. Distribution by site of the 1004 2x2 m transect plots measured in 2000 and 2002 and 121 1x1 meter gap plots measured in 2001 and 2002 used in the analysis.

Site	Transect Plots	Gap Plots
Brownsville	352	40
Skamania	325	45
Tacoma	327	36

DATA ANALYSIS

Data were analyzed using the statistical packages PC-ORD, Version 4.2 (McCune and Mefford, 1999) and S-Plus version 6.1 (Insightful Corp., 2002). Plots that occurred on roads, or had been managed in a manner that was inconsistent with the treatments at some time during the study, were excluded from the analysis. Before any data were analyzed, rare species, defined as those species whose summed cover was <0.0001% of the total summed cover of all data (Total # of plots each measured twice), or who occurred in <0.01% of the plots (measured twice) were eliminated. This reduced the number of species used in the analysis from 53 to 32. Plots in which the cover of these rare species was ≥25% of the total cover within a plot were then dropped from the dataset. This eliminated only 7 of the 1011 plots leaving a sample size of 1004 (Table 2.1). Rare species were dropped from the analysis because they had no influence on the results and dropping them simplified the analysis and presentation of results.

Objective 1: Plant Communities

Species richness, total average plant cover, and average species cover was calculated for each site. Differences among sites in initial species composition and abundance in 2000 were tested statistically using Multi-Response Permutation Procedures (MRPP) (Mielke, 1984). MRPP is a nonparametric procedure for testing the hypothesis of no difference between two or more groups (McCune and Grace, 2002). Sorensen’s distance was used to measure distance in species space between the 1004 plots grouped by site.

Objective 2: Low-growing species resistance to invasion

To determine the association between tall-growing species cover and different nontarget species, cluster analysis was used to group all 1004 plots into different groups based on the composition and abundance of nontarget species in 2000. We chose to split the plots into nine groups because this grouping level clearly separated the plots based on the abundance of 9 common species (Table 2.2). These plot groupings will be called "species groups" and identified by their characteristic species. The species groups were "Black", dominated by blackberry, "GaSh", dominated by salal, "Grass", dominated by grass, "PoMu, dominated by sword fern, "PoMu/HoDi", dominated by sword fern and oceanspray, "PtAq", dominated by bracken fern, "RuPa", dominated by thimbleberry, "RuUr", dominated by trailing blackberry, and "Sysp", dominated by snowberry. A full table of species average cover by site for all species groups is given in Appendix 1.

Table 2.2. Average cover of the characteristic species within the 9 cluster groups within each group. Not all groups occurred at each site. "+"= 0< value <0.05. Each of the 9 groups was named based on its dominant species. "Black"=blackberry, "GaSh"=salal, "Grass"=grass, "PoMu"=sword fern, "PoMu/HoDi"=sword fern and oceanspray, "PtAq"=bracken fern, "RuPa"=thimbleberry, "RuUr"=trailing blackberry, and "Sysp"=snowberry.

Brownsville	**Cover of species (%)**								
Type	**Black**	**GaSh**	**Grass**	**HoDi**	**PoMu**	**PtAq**	**RuPa**	**RuUr**	**Sysp**
Black	**19.1**	0.5	0.7	0	1.5	2.6	1.8	5.3	3.9
GaSh	1.4	**24.5**	0.1	0	1.5	3.8	6.7	1.9	1.5
Grass	1.7	0.5	**6.9**	0	0.7	2.4	0.6	2.9	3.2
PoMu	4.4	0.6	0.5	0	**27.5**	2.5	2.8	2.4	2.0
PoMu/HoDi	3.5	3.4	0.4	**6.3**	**8.9**	1.9	0.4	3.3	0.7
PtAq	1.3	0.5	0.7	0	0.5	**17.9**	4.2	3.5	2.2
RuPa	5.6	1.7	0.2	+	1.5	2.9	**25.3**	2.1	1.6
RuUr	1.5	1.8	2.4	0	1.2	2.5	0.1	**12.5**	1.9
Sysp	1.8	1.6	0.9	0	0.9	3.8	0.8	2.3	**34.5**
Skamania									
Black	-	-	-	-	-	-	-	-	-
GaSh	+	**24.1**	0.8	0.2	4.3	5.6	1.5	1.2	3.5
Grass	0.1	2.2	**6.4**	0.4	1.9	2.6	1.3	1.6	5.8
PoMu	0	2.0	1.6	0.5	**37.9**	2.3	2.4	1.4	3.4
PoMu/HoDi	0.2	8.9	0.9	**2.6**	**7.6**	3.6	0.6	1.0	4.8
PtAq	0	6.0	1.7	+	1.6	**15.5**	1.9	1.6	2.0
RuPa	0	3.0	1.1	0	1.6	6.9	**32.5**	1.3	7.0
RuUr	0	5.3	2.3	0.1	2.7	3.2	1.6	**4.4**	3.4
Sysp	0	13.6	1.1	0.1	3.0	4.3	3.3	1.6	**29.5**
Tacoma									
Black	-	-	-	-	-	-	-	-	-
GaSh	0.1	**24.3**	1.3	0.1	2.0	4.7	4.8	5.1	0
Grass	0	0.3	**12.1**	0	0.5	3.4	5.1	2.1	+
PoMu	0	2.5	0.3	+	**26.7**	1.4	16.2	4.3	0
PoMu/HoDi	0	8.0	1.3	**15.8**	**4.3**	3.8	4.0	1.8	0
PtAq	0	1.3	2.7	0	1.2	**13.2**	10.0	6.4	0
RuPa	+	0.7	0.9	0	3.8	1.8	**26.9**	9.1	0
RuUr	0	1.7	1.0	0	2.6	4.3	2.3	**20.0**	0
Sysp	-	-	-	-	-	-	-	-	-

Within each species group, average tall-growing species cover was calculated. The proportion of plots within each species group that contained <5% tall-growing species cover was also determined and used to rank the different groups from 1 to 9, with 1 representing the species group least associated with tall-growing species cover. Differences in the proportion of plots containing <5% tall-growing species cover among species groups were evaluated by comparing 95% confidence intervals constructed assuming a normal distribution after adjusting for multiple comparisons with Bonferroni's procedure (Ramsey and Schafer, 1997).

The resistance to invasion by tall-growing species was assessed for each species group by determining the average change in tall-growing species cover from 2000 to 2002 in plots that had <5% target cover in 2000 for each species group by site. Thus, this analysis utilized plots that did not contain target plants and were not treated in 2000. This reduced the sample size from 1004 to 328, with almost 2/3 of the plots occurring in Tacoma. Each species group was then ranked based on the proportion of plots that did not increase in tall-growing species cover from 2000 to 2002 from 1-9 with 1 representing the species group with the highest proportion of plots that did not increase in tall-growing species cover. The proportion of plots that did not increase in tall-growing species cover was also used to determine if there were differences among species groups based on 95% confidence intervals constructed using a normal distribution multiplier that had been adjusted for multiple comparisons with Bonferroni's procedure.

Objective 3: Nontarget species response to gap creation

To assess how different nontarget species responded to new gaps, we examined cover changes in transect plots from which target species had been removed and cover changes in gap plots where target cover remained low (<5%) in 2002. Transect plots utilized in this analysis were plots where target species had been initially abundant (>25% total cover in 2000) and then reduced to only trace amounts (<5% total cover). This illustrated how the importance of the different nontarget species changed over time in areas without target cover. There were 42, 42, and 51 transect plots that met these criteria at Brownsville, Skamania, and Tacoma respectively.

Along with examining nontarget species change in cover in the treated transect plots, change in each nontarget species' relative cover was determined. Change in relative cover was calculated as the average change in the proportion of a plot covered by each nontarget species in 2000 and 2002. Change in relative cover can be thought of as a measure of how the dominance of a nontarget species changed relative to the other nontarget species.

The gap plot analysis was parallel to that done using the treated transect plots. Only the 52 gap plots where target species had not re-sprouted (<5% tall target cover in 2002) were used. These plots were unevenly distributed among sites. Change in nontarget species cover and relative cover were calculated to determine which species were filling in the gaps.

Results

SPECIES DISTRIBUTION

All sites consisted of a mix of many different types of plants with few homogenous patches of a single species. Species richness, as well as species composition, was similar among sites. Sites contained between 24 and 29 species, and 28 of the 32 species observed were found in more than one site (Table 2.3). Fourteen of the sixteen shrub and fern species could reproduce vegetatively. Many of the tall-growing species, including vine maple, cherry, and hazel, could also reproduce vegetatively.

While species composition was similar among sites, the average cover of many of the species differed dramatically. This variation in species abundance resulted in a significant difference in the type of plant community that was present at each site (MRPP A=0.088, $p<0.001$). Brownsville was characterized by a higher abundance of exotic species (blackberry and broom) and less vegetation overall (Table 2.3). The main tall-growing species was hazel. Skamania was characterized by high total cover, especially of vine maple and salal. Skamania had a fairly equal mix of tall- and low-growing plant species. Tacoma differed from the other sites in that it contained a high cover of thimbleberry. The most abundant tall-growing species was alder.

Table 2.3. Pre-treatment (2000) common species composition, cover (%), and richness at three study sites (Brownsville (BR), Skamania (SK), and Tacoma (TA)). + indicates 0.0 < cover < 0.05. The target species that were treated included all tall-growing species as well as Broom.

Species	Sp. Code	% Cover		
Low-growing Plants		BR	SK	TA
Grass spp.	Grass	2.3	2.1	2.2
Forb Spp.	Forb	1.1	1.8	1.9
Oregon Grape (*Berberis nervosa*)	BeNe	+	3.6	+
Salal (*Galtheria shallon*)	GaSh	3.5	10.5	5.9
Thimbleberry (*Rubus parviflorus*)	RuPa	2.6	2.1	15.7
Salmonberry (*Rubus spectabilis*)	RuSp	-	-	2.0
Wild Rose (*Rosa spp.*)	Rose	0.1	0.3	-
Red Huckleberry (*Vaccinium parvifolium*)	VaPa	+	0.2	0.3
Snowberry (*Symphoricarpos albus and S. mollis*)	SySp	7.4	8.6	+
Oceanspray (*Holodiscus discolor*)	HoDi	0.1	0.7	0.2
Trailing Blackberry (*Rubus ursinus*)	RuUr	5.8	1.5	7.5
Honeysuckle (*Lonicera ciliosa and L. hispidula*)	LoSp	0.1	0.1	-
Bracken Fern (*Pteridium aquilinum*)	PtAq	3.8	4.8	3.8
Lady Fern (*Athyrium filix-femina*)	AtFi	-	0.1	0.1
Sword Fern (*Polystichum munitum*)	PoMu	2.1	6.8	5.0
Deer Fern (*Blechnum spicant*)	BlSp	-	+	0.1
Blackberry (*Rubus discolor and R. laciniatus*)	Black	3.7	0.1	+
Broom (*Cytisus scoparius*)	CySc	8.9	1.6	-
	Cover	**41.5**	**44.8**	**44.7**
Tall-growing Plants				
Saskatoon (*Amelanchier alnifilia*)	AmAl	0.2	0.3	-
Indian Plum (*Oemleria cerasiformis*)	OeCe	+	-	0.1
Hazel (*Corylus cornuta*)	CoCo	5.4	7.5	-
Vine Maple (*Acer circinatum*)	AcCi	0.5	12.0	5.6
Willow (*Salix spp.*)	SaSp	0.6	0.5	-
Apple (*Pyrus/Malus spp.*)	Fruit	0.2	0.1	-
Oregon White Oak (*Quercus garryana*)	QuGa	0.1	+	-
Cascara (*Rhamnus purshiana*)	RhPu	2.2	3.7	0.1
Bitter cherry (*Prunus emerginata*)	PrEm	1.9	0.3	0.1
Big-leaf maple (*Acer macrophyllum*)	AcMa	0.1	1.5	+
Red alder (*Alnus rubra*)	AlRu	-	0.1	5.7
Douglas-fir (*Pseudotsuga menziesii*)	PsMe	1.8	0.9	1.8
Western red cedar (*Thuga plicata*)	ThPl	-	+	0.8
Western hemlock (*Tsuga heterophylla*)	TsHe	-	-	0.4
	Cover	**13.1**	**26.9**	**14.6**
# of Nontarget Species		14	16	15
# of Target Species		12	13	9
Total Species Richness		26	29	24

SPECIES GROUP RESISTANCE TO TALL-GROWING SPECIES INVASION

To assess the resistance of the different species groups within the ROW communities to tall-growing species invasion, it must first be established that nontarget and tall-growing species can co-occur. The 2000 transect plot data revealed the strength of these associations.

Within the plant community at each site, tall-growing species could be found in high abundance in at least some of the plots in each species group (Figure 2.3). While tall-growing species cover in many plots was 0, it was commonly found reaching cover amounts of >25%, and could reach values of >75% in most species groups (Figure 2.3). Therefore, no species group was consistently associated with high or low tall-growing species cover.

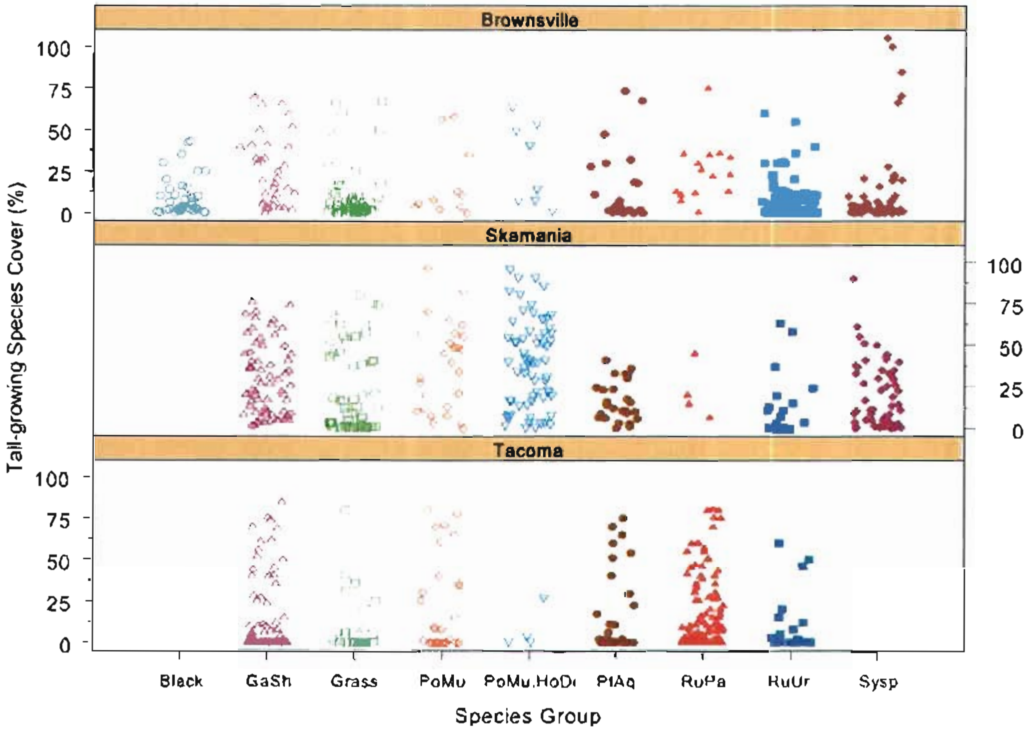

Figure 2.3. Tall target cover in each transect plot in 2000 (n=1004). Plots separated by species group derived from cluster analysis and site. Y-axis is tall target cover (%), x-axis is species group.

We assessed differences in the strength of the association among the species groups and tall-growing species cover by evaluating the proportion of plots in a species group that contained <5% cover of tall-growing species. As would be expected from examining Figure 2.3, we found few significant differences among species groups (Table 2.4). There were some general trends in the rankings of the species groups based on these proportions, however. PoMu, RuPa, and GaSh plots always had a lower proportion of plots with <5% tall target cover than Grass, Sysp, and RuUr plots.

Table 2.4. Average cover of tall-growing species in plots assigned to different species groups by site. “N” is the number of plots at each site categorized by species group. “Tall” is average tall-growing species cover in 2000. “Prop” is the proportion of plots within a species group that had <5% tall-growing species cover. “Rank” is the ranking of each species group within a site based on the proportion of plots that contained <5% tall-growing species cover from 1=low association with tall-growing species cover to 9= high association with tall-growing species cover. “-” denotes species groups that were absent from a particular site. The proportion of plots with <5% tall-growing species cover among species groups with the same letter were not significantly different based on 95% confidence intervals adjusted for multiple comparisons using bonferroni’s procedure.

Site	Brownsville				Skamania				Tacoma			
Type	N	Tall	Prop	Rank	N	Tall	Prop	Rank	N	Tall	Prop	Rank
Black	36	9.9	0.52 a	4	-	-	-	-	-	-	-	-
GaSh	34	25.5	0.21 a,b	7	67	29.1	0.15 a,b	5	67	16.8	0.52 a	6
Grass	68	11.1	0.56 a	2	60	21.5	0.45 a	1	33	8.1	0.64 a	2
PoMu	11	17.9	0.36 a,b	6	27	37.5	0.11 a,b	6	31	20.4	0.52 a	7
Pomu/HoDi	8	29.1	0.13 a,b	8	67	38.7	0.10 b	7	4	7.3	0.75 a	1
PtAq	22	16.0	0.55 a,b	3	26	16.3	0.15 a,b	4	30	17.3	0.57 a	5
RuPa	15	24.9	0.07 b	9	4	21.5	0 a,b	8	141	14.0	0.56 a	4
RuUr	103	7.6	0.52 a	5	18	14.8	0.44 a,b	2	21	10.6	0.62 a	3
Sysp	55	12.8	0.58 a	1	56	20.1	0.29 a,b	3	-	-	-	-

We assessed resistance to invasion of the species groups by assessing the average increase in tall-growing cover from 2000 to 2002 in the 328 transect plots that did not contain target cover (<5%) in 2000. The increase, or in some cases, decrease in tall-growing species cover varied widely ranging from –4.5% to 28.5% (Figure 2.4). The values of tall target cover change in most species groups were highly skewed, as there were many plots that increased very little from 2000 to 2002 and a few that increased a lot. Several of the species groups did not contain any plots where target cover had been <5% in 2000 (Figure 2.4).

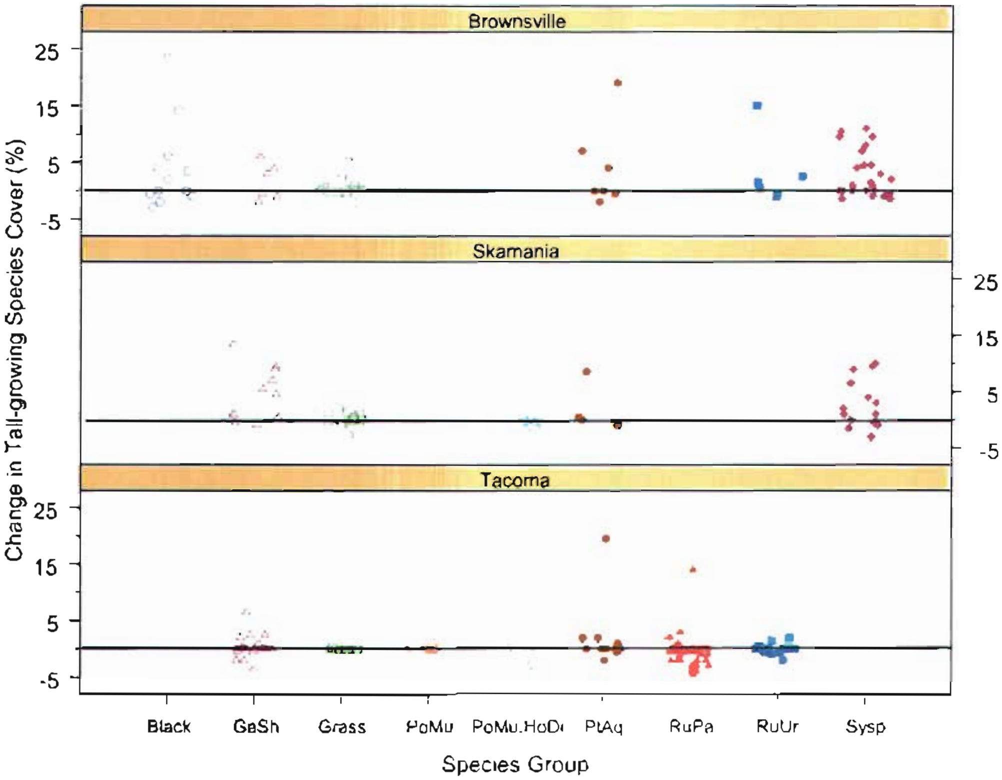

Figure 2.4. Tall-growing species cover in each transect plot that contained <5% target cover in 2000 (n=328). Plots separated by species group derived from cluster analysis and site.

During the two years of this study, there was no statistical difference among species groups in the proportion of plots that increased in tall-growing species cover among plots that had been free of tall-growing species cover in 2000 at any of the three sites (Comparison of 95% confidence intervals adjusted by Bonferroni's procedure of species groups within a site). Despite the similar proportion of plots within each species group that increased in tall-growing species cover, some trends were apparent based on the group rankings that may result in significant differences in the future. PoMu, Grass, and PtAq plots were often associated with smaller proportions of plots that increased in tall-growing species cover than the other species groups. RuUr and Sysp were often associated with larger proportions (Table 2.5).

Table 2.5. Change in average cover of tall target species in plots characterized by different species by site. "Change" is the difference in average tall target cover from 2000 to 2002. "Prop" is the proportion of plots within a species group that did not increase in tall target cover. "Rank" is the ranking of each species group within a site based on the average change in tall-growing species cover from 2000 to 2002 in a species group from 1=low increase in tall target cover to 9= large increase in tall target cover. Ties were broken based on average cover. "-" denotes species groups that were absent from a particular site. "+" denotes species groups where 0<cover change<0.05. The proportion of plots that increased in tall target cover among species groups with the same letter were not significantly different.

	Brownsville				Skamania				Tacoma			
Type	N	Change (%)	Prop	Rank	N	Change (%)	Prop	Rank	N	Change (%)	Prop	Rank
Black	12	3.9	0.50 a	5	-	-	-	-	-	-	-	-
GaSh	6	1.6	0.50 a	3	10	4.9	0.20 a	6	35	0.2	0.83 a	3
Grass	24	1.8	0.50 a	4	24	0.6	0.62 a	3	21	+	0.95 a	1
PoMu	3	-1.0	0.66 a	1	2	-1.5	1.00 a	1	16	2.4	0.63 a	7
Pomu/HoDi	1	1.0	0 a	8	7	0.1	0.86 a	2	3	-0.8	0.67 a	6
PtAq	7	3.9	0.57 a	2	4	2.0	0.50 a	4	17	1.3	0.76 a	5
RuPa	-	-	-	-	-	-	-	-	79	0.1	0.91 a	2
RuUr	5	3.7	0.20 a	7	-	-	-	-	13	0	0.77 a	4
Sysp	25	2.8	0.44 a	6	14	2.9	0.36 a	5	-	-	-	-

NONTARGET SPECIES RESPONSE TO GAPS

We assessed the ability of different nontarget species to fill gaps created by the removal of target species by evaluating the change in nontarget species cover in transect and gap plots where target species had been removed. This allowed us to determine which species were most successful at quickly filling gaps.

In the treated transect plots, the cover of almost all nontarget species increased from 2000 to 2002 (Table 2.6a). In general, plant community composition shifted from high cover of target species towards higher cover of woody shrubs and ferns, especially trailing blackberry and bracken fern. Some nontarget species that had been abundant prior to treatment in 2000, like sword fern at Skamania and thimbleberry at Tacoma, remained so in 2002. The total cover decreased sharply, however, in the two years following treatment, indicating that the gaps created by the removal of the target species were not completely filled. These results are not surprising, given the short time since the treatments were applied.

Similar nontarget species responses were observed in the non-sprouting gap plots (Table 2.6b). Bracken fern, salal, and thimbleberry were the most abundant species in these plots in 2002 at Brownsville, Skamania, and Tacoma respectively.

Table 2.6a. Average cover of nontarget species in transect plots that had >25% target cover in 2000 and <5% target cover in 2002 by site and year.

Site	**Brownsville**		**Skamania**		**Tacoma**	
N	**42**		**42**		**51**	
Year	**2000**	**2002**	**2000**	**2002**	**2000**	**2002**
Oregon Grape	0	0	3.8	5.0	0	0
Blackberry	2.5	2.8	0	0.1	0	0
Deer Fern	0	0	0	0	+	+
Forb	0.8	2.9	1.5	6.3	1.0	5.0
Salal	0.9	1.4	6.3	7.5	4.4	7.8
Grass	1.6	6.2	0.8	4.6	1.1	3.2
Oceanspray	0	0	2.9	0.5	0	0
Honeysuckle	+	0.1	+	0.2	0	0
Lady Fern	0	0	0	0	0.3	0.5
Sword Fern	2.1	1.7	12.6	12.9	4.5	5.9
Bracken Fern	2.4	9.3	2.9	8.8	2.4	5.1
Rose	0.2	+	0.1	0.2	0	0
Thimbleberry	0.2	0.6	1.5	3.3	13.7	15.1
Salmonberry	0	0	0	+	2.6	3.1
Trailing Blackberry	11.9	14.1	2.0	6.5	9.3	21.3
Snowberry	6.2	7.6	7.2	7.4	0	0
Red Huckleberry	0	0	0.7	0.1	0.2	0.3
All Nontarget spp.	28.9	46.8	42.4	63.5	39.4	67.3
All spp.	78.1	48.4	96.7	65.3	91.0	67.9

Table 2.6b. Average cover of nontarget species in non-sprouting (<5% target cover in 2002) gap plots by site and year.

Site	**Brownsville**		**Skamania**		**Tacoma**	
N	**5**		**21**		**26**	
Year	**2001**	**2002**	**2001**	**2002**	**2001**	**2002**
Oregon Grape	0	0	2.4	3.5	0	0
Deer Fern	0	0	0	0	0.2	0.3
Forb	2	3	0.1	5.2	0.4	4.6
Salal	0	0	9.6	8.6	8.7	4.0
Grass	1	5.3	0.4	2.0	1.3	3.8
Lady Fern	0	0	0	0	0.0	0.4
Sword Fern	0	0	6.3	4.8	2.7	3.9
Bracken Fern	12.4	25.8	2.0	7.3	1.9	3.5
Thimbleberry	0	0	0.5	2.1	4.5	17.2
Salmonberry	0	0	0	0	0.2	1.3
Trailing Blackberry	7.4	9.8	0.4	5.6	1.5	10.8
Snowberry	8.6	3.8	3.5	4.8	0	0
Red Huckleberry	0	0	0	0	0.3	0.1

The change in relative cover of the nontarget species allowed us to assess which species were most capable of filling gaps. Trailing Blackberry and bracken fern were the most successful nontarget species at filling gaps in the treated transect plots (Figure 2.5a). The relative cover of these two species increased more from 2000 to 2002 than most other nontarget species at all three sites. Bracken fern, trailing blackberry, and thimbleberry showed the largest increase in relative cover from 2001 to 2002 in the non-sprouting gap plots (Figure 2.5b). Grass and Forbs also showed a consistent, but smaller increase in relative cover in both the treated transect and gap plots.

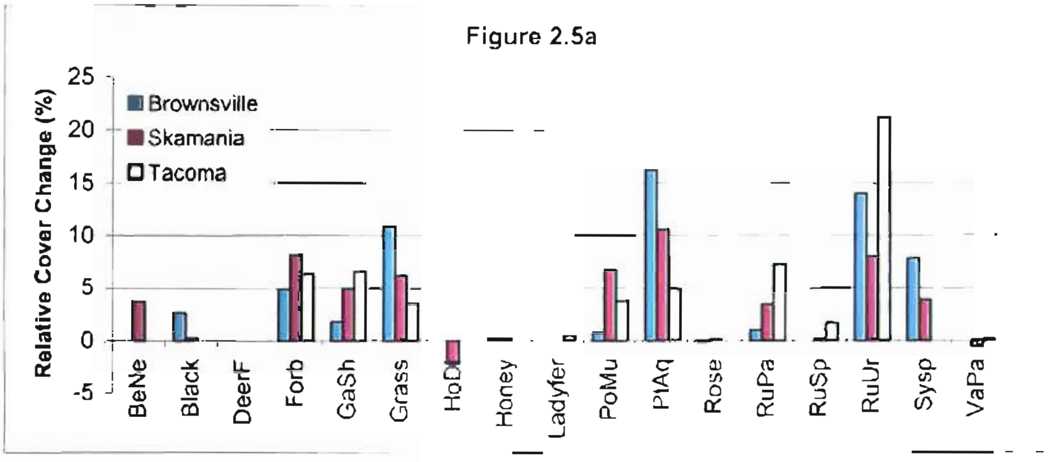

Figure 2.5a

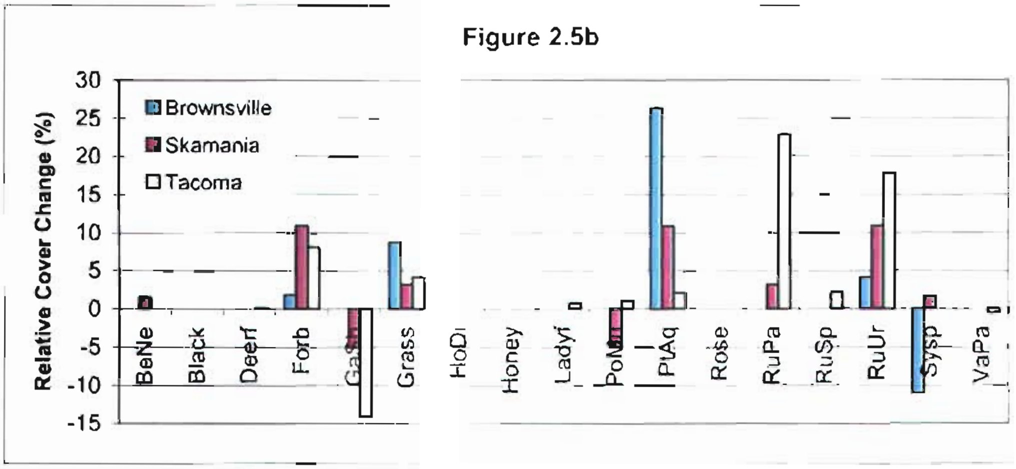

Figure 2.5b

Figure 2.5. Change in relative cover from 2000 (2001 in non-sprouting gap plot data) to 2002 for each nontarget species by site. "Relative Change" is the average change in relative cover from 2000 or 2001 to 2002 ((2002 species cover/2002 total cover – 2000 or 2001 species cover/2000 or 2001 total cover)*100). Figure 5a is from treated transect plot data and Figure 5b is from non-sprouting gap plot data.

Discussion

We evaluated community stability by assessing the invasibility of several common low-growing species to tall-growing species invasion and by assessing the ability of low-growing species to colonize gaps created by treatments applied to the

ROW. Both resistance to invasion and rapid recovery following disturbance are important factors for the creation of stable, low-growing plant communities.

There were no strong differences in the association between tall-growing species cover and the various species groups in 2000. Tall-growing species occurred in all groups and ranged in cover from 0 to 100% in the transect plots (Figure 2.3). Though differences among species groups were small, there were some trends based on the proportion of plots within each species group that contained <5% tall-growing species cover. A consistently smaller proportion of the plots in the PoMu, RuPa, and GaSh species groups contained <5% tall-growing species cover than in the Grass, Sysp, and RuUr species groups (Table 2.4). This means that PoMu, RuPa, and GaSh tended to be associated with high tall-growing species cover more often than Grass, Sysp, and RuUr. This may be due to environmental differences in habitat as the latter species are generally associated with more open canopies and therefore drier soil conditions than the former species groups.

There were no strong differences in species group invasibility, measured as change in tall-growing species cover from 2000 to 2002 in plots where target cover had been <5% in 2000. Many plots remained free of tall-growing species cover in 2002, but several plots increased dramatically, some by as much as 25% (Figure 2.4). A few trends were apparent based on the proportion of plots within each species group that increased in tall-growing species cover. The proportion of plots that increased in the Grass and PoMu species groups tended to be lower than the proportion of plots in the RuUr and Sysp species groups (Table 2.5). This means that plots dominated by grass and sword fern tended to be more resistant to tall-growing species invasion than plots dominated by trailing blackberry and snowberry.

There are several factors that could contribute to the apparent higher resistance of the Grass and PoMu species groups to invasion by tall-growing species. Resistance of the Grass plots may be due in part to a difference in the type of environments favored by grass species vs. the common tall-growing species measured in this study. A difference in favorable environmental conditions may be the reason why the Grass species group was slightly less associated with tall-growing species cover than some of the other species groups (Table 2.4). Another possible factor that may contribute to resistance of grass-dominated communities is strong competition for resources, especially water, grass can impose on invading tree seedlings (Kolb and Steiner, 1990; Newton and Preest, 1988; Monleon et al., 1999). A final factor that may contribute to the Grass species group's resistance to tree seedling invasion is a high level of seed predation from rodents within this community type (Bramble et al., 1996; Yahner, 2004). Seed predation can be the most important factor regulating Douglas-fir seedling survival in areas with active rodent populations (Caccia and Ballare, 1998).

The increased resistance of the PoMu species group may be due to the high levels of competition encountered by invading tree seedlings resulting from the high cover produced by the dense growth form of this species (Hauessler et al., 1990). A strong competitive ability is a commonly cited plant characteristic in determining community invasibility. Many studies have shown that woody shrubs, which often form dense thickets, can be strong competitors with surrounding vegetation (Minore and Weatherly, 1994; Haeussler and Coates, 1986; Tesch and Hobbs, 1989) and in some instances form persistent communities (Henderson, 1978; Kurmis and Sucoff, 1989; Niering et al., 1986; Young et al., 1995).

The possible increased resistance of the PoMu species group may also be due to the large amount of litter produced by the death of the large fern fronds. This may reduce the invasibility of this species group because large litter layers can lead to reduced tree seedling establishment (Caccia and Ballere, 1998; Facelli and Pickett, 1991).

The duration of this study allowed for only two growing seasons in which tall-growing species could invade. To more clearly detect any differences among species groups in their invasibility, a longer time period is needed. Therefore, the similarity in invasibility among the different species groups may be due to an insufficient time period to observe tall-growing species invasion rather than to no difference in invasibility among species groups.

Along with resisting invasion, the ability of low-growing plant species to colonize gaps quickly, reducing the amount of open space available for tree seedling establishment, is an important property of stable, low-growing plant communities. Trailing blackberry and bracken fern were the most successful nontarget species at filling gaps (Figure 2.5). The relative cover of these two species increased more than any other nontarget species, an indication of their ability to spread rapidly into gaps and increase quickly in cover (Table 2.6). The small but consistent increase in relative cover of Grass and Forbs may be due to the germination of individuals from an existing seed bank (Pakeman et al., 1998; Egley and Chandler, 1983).

Both trailing blackberry and bracken fern are capable of rapid horizontal expansion through vegetative reproduction. Trailing blackberry produces long, creeping canes that can tip-root to form new clones (Chapter 3). Bracken fern produces long rhizomes that allow it to quickly capture new space (Daniels, 1985; Hauessler at al., 1990). The growth pattern of these species makes them well suited for spreading quickly over small areas. Conversely, clonal species that are incapable of rapid horizontal spread through vegetative reproduction, such as sword fern, Oregon grape, and red huckleberry, increased very little in relative cover, or not at all (Figure 2.5). Therefore, the ability of low-growing species to spread through the production of organs capable of rapid expansion (e.g. stolons, rhizomes), leads to the successful colonization of small gaps.

Conclusions

All nontarget species displayed at least some properties that contribute to stable, low-growing plant communities on ROWs. The plant properties that were associated with resistance to tree seedling invasion were more varied and quite different from those associated with rapid colonization of gaps. The plant characteristics associated with species resistance to invasion included a strong competitive ability, often resulting from the formation of dense thickets of vegetation, high litter production, and a positive association with seed predators. The capacity for rapid horizontal expansion through vegetative reproduction was the plant characteristic most strongly associated with successful gap colonization. Therefore, communities that contain a mix of species with these different characteristics may be most capable at forming stable, low-growing plant communities.

One characteristic shared among most of the low-growing species was a strong potential for vegetative reproduction. Vegetative reproduction can facilitate the formation of stable communities by providing a mechanism through which plants can quickly spread into new areas and fill gaps created by a disturbance (Maxwell et al., 1993; Tappeiner and Zasada, 1993). Vegetative reproduction also allows a plant to maintain a dense, persistent cover by continually replacing dead or injured stems with new growth (Tappeiner et al., 1991; Boeken and Canham, 1995). These dense thickets are often associated with high resistance to invasion because of the high competition imposed on invading plants (Berkowitz et al., 1995; Putz and Canham, 1992). Thus, while many different plant characteristics seem to contribute to community stability, vegetative reproduction may provide a mechanism that can lead to both low invasibility and rapid gap-filling.

In the western hemlock ecological zone of the Pacific Northwest, as in the deciduous forests of the northeastern United States, woody shrubs were well suited for forming stable, low-growing plant communities resistant to tree invasion (Bramble et al., 1990; Niering and Goodwin, 1974; Dreyer and Niering, 1986; Meilleur et al., 1994). In our study, the strong competitive ability of these species under open conditions and their potential for rapid vegetative reproduction allowed them to quickly invade gaps and resist invasion. These same properties have led to similar types of species creating stable, low-growing communities in the temperate deciduous forests of the Northeast (Meilleur et al., 1994; Hill et al., 1995; Putz and Canham, 1992). Therefore, while many of the species encountered in this study differ from those that have been cited in most ROW literature, the same generalities of the types of plants that can successfully form stable, low-growing plant communities on ROW apply.

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CHAPTER 3. CLONAL GROWTH PATTERNS OF TRAILING BLACKBERRY (*RUBUS URSINUS*) AND CREEPING SNOWBERRY (*SYMPHORICARPOS MOLLIS*)

Abstract

Trailing blackberry (*Rubus ursinus* Cham. and Schlecht) and creeping snowberry (*Symphoricarpos mollis* Nutt.) are two common Pacific Northwest shrubs capable of vegetative reproduction. These shrubs display markedly different patterns of clonal propagation, yet both species are able to form dense thickets of vegetation under open conditions. We studied growth and vegetative reproduction of these two species to understand how different clonal propagation patterns contribute both to spread into unoccupied space and to infilling of currently colonized areas.

Trailing blackberry thickets were composed of many disconnected ramets ($67/m^2$). Each ramet generally produced one biennial cane annually that grew up to 1.9 m long its first year (avg.=0.9 m). A cane could tip-root to form a new ramet. In thickets, cane density averaged 113 canes/m^2 producing over 54 m of total cane length/m^2.

Creeping snowberry thickets were composed of many connected, multi-aged ramets ($155/m^2$). Ramets produce perennial stems that could be long-lived; stems ranged from 1- to 15-years-old. Annual increment of a creeping snowberry stem averaged 0.6 m, but ranged from 0.2 m to 1.3 m. New ramets were produced by the formation of adventitious roots from nodes along a stem. We found an average of

2.7 ramets/m of stem and an average stem density of 237 stems/m^2 in dense thickets that resulted in over 81 meters of total stem length/m^2.

The strategy of infilling and spread employed by each species differed. Trailing blackberry exclusively produced long canes that spread away from the parent ramet and were capable of rooting at the tips, allowing plants to spread quickly. This growth pattern required trailing blackberry to rely on immigration of new canes from remote ramets to infill existing areas. Creeping snowberry produced both long, creeping and short, upright stems. The creeping stems could produce new ramets in close proximity to the parent ramet, filling in the existing area, or they could produce new ramets at the distal ends of the stems away from the parent ramet, giving it the potential to spread into new areas. Both strategies of growth and spread allowed these shrubs to form thickets of dense vegetation. However, the more spreading growth strategy employed by trailing blackberry focused on rapid spread may allow it to be a better colonizer, while the more dense, branching growth strategy employed by creeping snowberry, focused more on infilling may allow it to better maintain areas of dense, persistent cover.

Introduction

Clonal growth is a common reproductive process in plants, especially among woody shrubs (Salisbury, 1942; van Groenendael et al., 1997). Plants have developed many different methods of vegetative reproduction including the production of rhizomes, stolons, and adventitious roots (Walters and Keil, 1996). Whatever method is employed, clonal growth allows plants to maintain cover in areas where they are established and to spread into new areas. Maintaining cover is obviously important for local persistence. High local cover may also play a role in hindering the establishment of other species that can ultimately out-compete the clonal species (Niering and Goodwin, 1974; Berkowitz et al., 1995). Long-term persistence may also require that a clone explore space to find a more favorable environment (Salsman, 1985; van Kleunen and Fisher, 2001; Bazzaz, 1991). The ability to spread into new space allows the clone to increase in abundance and adapt to fluctuating resource levels on a local scale (Cook, 1983).

In general, plants capable of vegetative reproduction are able to form areas of dense cover because vegetative reproduction leads to the production of new ramets close to the parent (Silvertown and Charlesworth, 2001). Thicket density is maintained through infilling, which can occur in two ways. New ramets can be initiated from either existing plants, or they can enter into the area from an external source. Either strategy allows clonal plant populations to maintain areas of dense, persistent cover.

Some methods of vegetative reproduction can be a mechanism for medium-distance dispersal, and so function to colonize new space (Angevine and Handel, 1986; Handel, 1981; Luken, 1990; van der Valk, 1992). Plants that reproduce using organs capable of horizontal growth, such as rhizomes or stolons, have the potential for vegetative spread, while plants that reproduce through basal buds or burls do not (Luken, 1990).

The distance that a parent plant can extend its reproductive organs strongly influences its potential rate of horizontal expansion. Lovett Doust (1981) described two patterns of growth found in plants capable of horizontal expansion through vegetative reproduction and termed these strategies as “phalanx” and “guerilla” patterns. The phalanx strategy involves the production of many ramets that are congregated into a dense network due to short internode lengths and frequent branching of the reproductive organs (e.g., rhizomes). This growth strategy leads to a slow rate of spread, but produces many ramets. The guerilla strategy of clonal growth involves the production of few, widely-spaced ramets from long, seldom-branching reproductive organs. This strategy leads to rapid spread, but at the expense of ramet production. Most clonal plants exhibit aspects of both strategies of spread and can be categorized as somewhere along the continuum between these two extremes (Bell and Tomlinson, 1980).

Trailing blackberry (*Rubus ursinus* Cham. and Schlecht) and creeping snowberry (*Symphoricarpos mollis* Nutt.) are two common shrubs in western Oregon that are capable of vegetative reproduction and exhibit two very different life histories. They can comprise a sizable portion of the vegetation in some open-grown, shrub-dominated communities, forming dense thickets of relatively stable vegetation (Chapter 2).

Trailing blackberry is an evergreen shrub that produces biennial canes from basal buds (Halverson, 1986) (Figure 3.1). It produces both flowers and leaves from lateral branches that grow from canes produced the previous year. It can reproduce both sexually and asexually (Morgan et al., 1988; Stewart, 1978). The long, flexible canes are incapable of much upright growth so they tend to trail along the ground or drape over other vegetation. The stems produced by trailing blackberry are exclusively long, biennial canes that can tip-root to form new ramets (Great Plains Flora Association, 1986). Over time, this leads to the formation of many disconnected ramets.

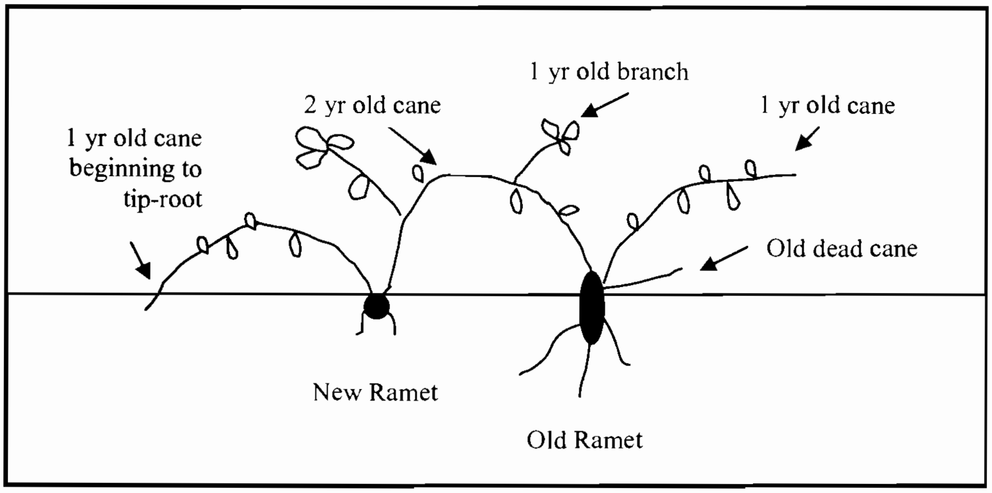

Figure 3.1. Morphology of trailing blackberry (*Rubus ursinus*). An "Old Ramet" produces biennial canes. During the second growing season of a cane, it can produce short lateral branches that produce leaves and flowers. Canes can tip root and create new rooted independent plants (New Ramet).

Creeping snowberry is a perennial deciduous shrub with long-lived stems. It can reproduce both sexually and asexually by rooting at nodes located along the length of a stem (Pojar and Mackinnon, 1994). Once rooted, these nodes are considered ramets and are capable of independent existence. Ramets can produce new stems annually (Figure 3.2).

Creeping snowberry produces both upright, short stems, which generate a majority of the leaves and flowers, and long, creeping stems, which may root and produce new ramets along their length. New stems are initiated from the location of lateral buds, making identification and aging of annual increment relatively simple. Plants form large networks of interconnected ramets that can occupy large areas.

While this shrub has been cited as rhizomatous (Snyder, 1991), no rhizomes were found during this study. Creeping snowberry co-occurs frequently with common snowberry (*S. albus* (L.) Blake), a more upright, rhizomatous species (Haeussler et al., 1990). It is possible that Snyder's (1991) assertion may have represented a confusion of the two species in past work.

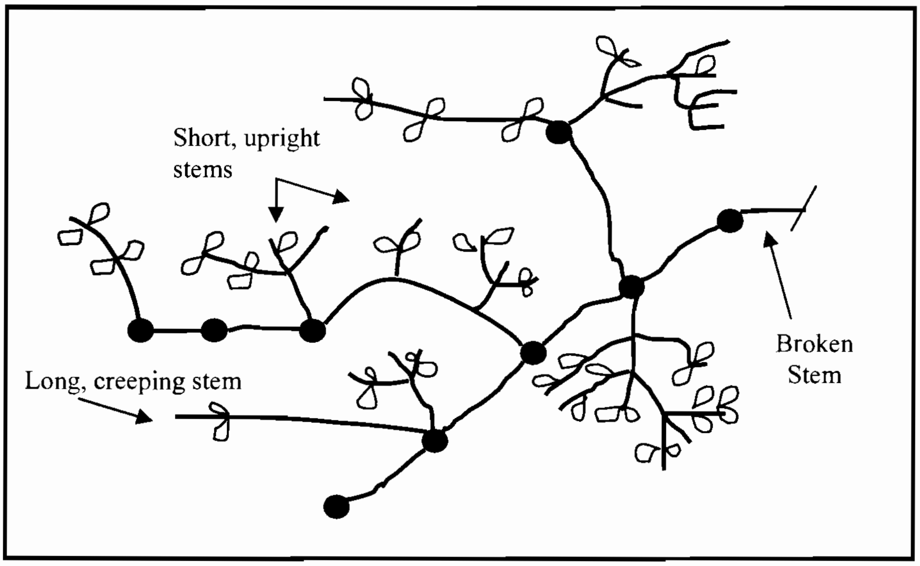

Figure 3.2. Morphology of creeping snowberry (*Symphoricarpos mollis*). Each filled circle represents a ramet (= rooted node).

OBJECTIVES

The goal of this study was to assess whether different strategies of horizontal clonal growth result in different capacities for infilling and spread and thus the formation of dense thickets. Trailing blackberry and creeping snowberry were chosen for this study because of their dissimilar life histories and growth patterns. We investigated the physical structure, growth rate, and spatial pattern of growth of creeping snowberry and trailing blackberry by 1) determining the average density of stems and ramets each species produced in dense, established thickets and comparing them to several other common shrub species, 2) evaluating the ability of trailing blackberry and creeping snowberry to maintain a persistent cover through in-filling, and 3) predicting the potential rate of lateral vegetative spread of these two shrub species.

Methods

SITE DESCRIPTION

This study was conducted on an electric utility right-of-way (ROW) near Brownsville, OR. The site is located on the eastern border of the Willamette Valley southeast of Corvallis, Oregon at an elevation of 315 m (1040 ft.). The soil was deep, fine and relatively uniform across the site. The soils are a Bellpine or Jory silty clay loam, classified as clayey, mixed, xeric Haplohumults (Natural Resources Conservation Service, 2002). The average annual rainfall is 154 cm/year (12 cm during June through August) (derived from models described in Thornton et al., 1997).

In 2002, woody shrubs and ferns dominated the site. Some of the more abundant species were trailing blackberry, creeping snowberry, and bracken fern (*Pteridium aquilinum*). The site covered an area of approximately five hectares (12.5 acres) and had been in use by the power utility since 1965. The vegetation had last been selectively treated to remove tall-growing vegetation using a combination of manual cutting and herbicide spray techniques in the fall of 2000. Prior to that treatment, the site had been treated regularly every 4-5 years to remove large shrubs and trees. The ROW was 80-100 m wide and both sides were bordered by Douglas-fir (*Pseudotsuga menziesii*) forest.

FIELD SAMPLING

The data were collected during the winter of 2002/03. All sampling was done away from locations where tall target species had been removed in 2000. Two field studies were conducted to 1) measure stem density and length on an area basis (1x1 m plots) in dense thickets of a species and 2) describe age, size, and growth patterns of individual plants.

Thicket Density Characterization

To establish the maximum density of stems and ramets that trailing blackberry and creeping snowberry are capable of producing, all of the areas of high cover of each shrub within the site were first identified. To be considered an established thicket, cover of creeping snowberry or trailing blackberry had to be >50% on an area of at least 9 m^2. A total of 47 blackberry thickets and 21 snowberry thickets were found at the site. A sub-sample of five thickets was randomly selected for each species and 1x1 m plots were established in the area of highest cover within each thicket. All of the stems were cut at the plot boundary and the length of each stem in the plot was measured. Whether the stem originated from within the plot or outside of it was also noted. As the stems were cut and removed, the number of stems that originated from each ramet, as well as the number of ramets within the plot was counted. A ramet was defined as the location along a stem that had become rooted in the ground.

Individual Plants

Ten individual plants of each species were selected using random coordinates. Once the coordinate was located, the first plant encountered along a random azimuth at least two meters from the original coordinate was selected. Each individual plant was carefully excavated using hand trowels so as not to break any connections between ramets. As each new ramet was encountered, the minimum age and stem length between ramets as well as the length of stems originating from that ramet that were not rooted were recorded. For unrooted stems, both the total length and its initial annual growth increment were recorded (Figure 3.3).

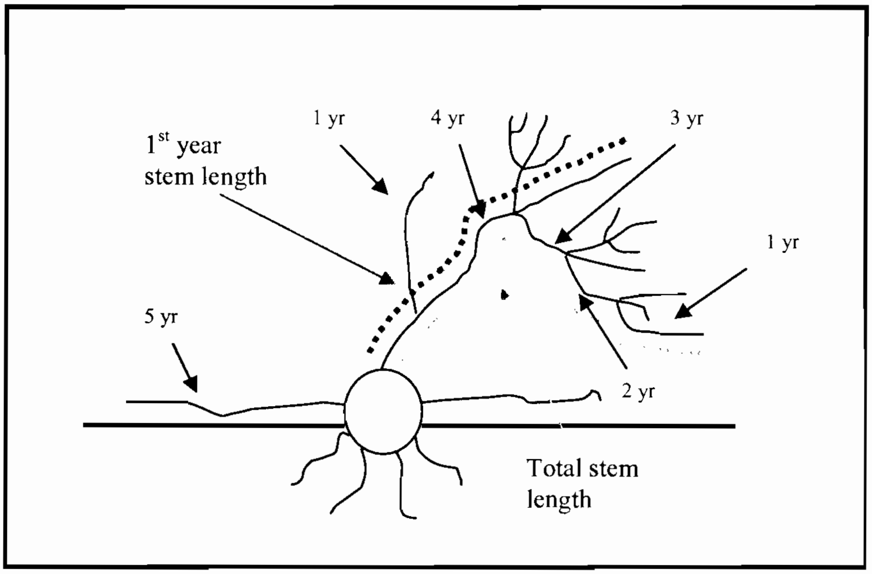

Figure 3.3. Determination of age and length of creeping snowberry stems. "Total stem length" is total stem length from a ramet to its most distant end without another intervening ramet. "1st year stem length" is length of the stem following its first year of growth from a ramet.

The dramatically different growth pattern of the two shrubs necessitated different methods for determining plant age. The age of trailing blackberry ramets was unknown because canes die after two years, leaving little evidence of their existence once they are gone. Therefore, only the age of the existing canes was recorded as 1 or 2 years old based on whether or not they had produced secondary branches (Figure 3.1).

Minimum age of creeping snowberry stems and ramets was determined by examining the branching pattern and bud scale scars of a plant and counting backwards from the most recent growth (Figure 3.3). The ramet from which a stem originated was always at least one year older than the oldest stem it had produced. It should be noted that a plant could have been much older than our estimates because we assumed that the oldest stem produced by a ramet was one year younger than its parent ramet, when it may have actually been several years younger.

Total plant length for trailing blackberry was determined by summing the length of all live canes growing from an individual plant. In most cases, this consisted of one two-year-old cane and one one-year-old cane, although multiple canes were sometimes produced during the same year.

Total plant length for creeping snowberry was determined by adding the length of all stems for each plant. This included the summed length of stems that had produced ramets and now functioned as connectors between ramets as well as the summed length of all the unrooted stems. The network of stems and ramets that comprised a plant were then drawn to record the connections between stems and ramets, but the exact spatial relationships among them were not recorded.

DATA ANALYSIS

In each 1x1 m thicket plot, the average number of stems, total length of stems, number of ramets, and stems per ramet were calculated for both trailing blackberry and creeping snowberry. Each stem was classified into one of two groups depending on whether a stem was rooted inside or outside of the plot.

Total plant length, average stem length, and number of stems per ramet were averaged for the ten individual trailing blackberry plants. Average length of a stem produced in one growing season was calculated using only one-year-old stems since there was a greater chance of stem breakage and mortality of older stems. The number of live, one- and two-year-old stems per ramet was also counted and averaged separately among the ten individuals.

For individual creeping snowberry plants, the rate of increase in total plant length over time was determined. This was accomplished by estimating the total plant length for every year of a plant's life. Total plant length per year was calculated by first summing the length of all the rooted stems functioning as the interconnections between nodes that originated during the same year. For stems that had not rooted, the first year's growth was subtracted from the total growth and assigned to the year that the stem had originated. The remaining length was divided up equally between the remaining years that the stem had been alive. For example, if a stem was four-years-old and was a total of 40 cm long, and had a first year stem length of 31 cm, then the remaining 9 cm were distributed evenly among the following three years so that the stem was assumed to have grown 3 cm in each of the following three years after initially growing 31 cm.

Average annual increment for individual stems was calculated for creeping snowberry using one-year-old stems. The length of these stems was averaged first within a plant to calculate each plant's average annual increment and then among plants. One plant did not produce any one-year-old stems and was excluded from the analysis. The number of one-year-old stems found on the remaining plants ranged from 1 to 46 stems. Snowberry stems from earlier years were not used to calculate average annual increment because of the increasing likelihood of stem breakage and dieback.

The age of the ramet from which each one-year-old stem originated was used to determine whether creeping snowberry produced new stems from young or old ramets. New ramets were defined as ramets that were ≤ three-years-old and old ramets were ≥ four-years-old. The number of one-year-old stems in each age class was then tallied so that the proportion of the stems originating from each age class of ramets could be determined.

A length of 50 cm was used as the delineation between short, upright and long, creeping stems because it was the average canopy height of creeping snowberry at the study site in 2002. Thus, each stem on a plant was defined as either short (<50 cm growth in first year) or long (>50 cm growth in first year) to determine the number, total length, and proportion of short and long stems produced by creeping snowberry. Only one- and two-year-old stems were used for this analysis to minimize misclassification of stems because of breakage or dieback.

The association between the number of ramets per plant and total plant length, the association between proportion of the total annual increment devoted to the production of long stems and total plant length, and the association between plant age and total plant length were assessed using r^2 values derived from linear regression. Total plant length was the independent variable in all three comparisons. Scatter plots of the independent vs. dependent variable for each dataset were inspected for outliers and skewness before the regressions were preformed.

Results

TRAILING BLACKBERRY

Trailing blackberry was capable of forming dense thickets (Table 3.1). Sixty percent of the total stem length within the 1x1 m thicket plots originated from ramets growing outside of the plots. Therefore, the majority of the vegetation within a plot did not originate there, but had spread into it from outside.

The total length of trailing blackberry plants was relatively small compared to creeping snowberry (Table 3.1). In most cases, there was one two-year-old cane and one one-year-old cane, although one ramet had produced two one-year-old canes and four two-year-old canes. In the 1x1 m thicket plots, many of the plants that had only one stem were very small with no large roots and appeared to be newly germinated seedlings. One-year-old canes produced by trailing blackberry in 2002 averaged 0.9 m in length. Evidence of older canes produced by ramets was commonly encountered in the form of dead, broken stems.

Table 3.1. Summary statistics for trailing blackberry and creeping snowberry. Means and ranges are given for both 1x1m plots (n=5) and individual plants (n=10).

Plot Type	**Trailing Blackberry**		**Creeping Snowberry**	
1 x 1 Meter Plots	**Mean**	**Range**	**Mean**	**Range**
Total # of stems	113.0	82-207	237.0	178-309
Total # of ramets	67.0	33-122	154.8	99-218
Total stem length (m)	54.2	46.7-59.7	81.4	64.3-94.7
Individual Plants				
Total length (m)	1.3	0.3-3.1	33.1	2.3-100.6
1-year-old stem length (m)	0.9	0.2-1.9	0.6	0.2-1.3
Stems/Plant	2.6	2-6	72.2	5-209
1 yr old stems/plant	1.1	1-2	NA	NA
2 yr old stems/plant	1.5	1-4	NA	NA
Stems/Ramet	NA	NA	1.2	0.5-2.5
Ramets/Plant	NA	NA	58.9	3-203
Ramets/Meter of stem	NA	NA	2.7	1.0-9.7
Average Plant Age (yrs)	NA	NA	10.1	6-15

CREEPING SNOWBERRY

Creeping snowberry formed very dense thickets (Table 3.1). Eighty percent of the total stem length found within the plot was rooted there, indicating the frequent occurrence of ramets along creeping snowberry stems.

Creeping snowberry plants were large and consisted of many connected stems and ramets (Table 3.1). Plant age ranged from 6- to 15-years-old. The average annual increment of a new stem produced by creeping snowberry in 2002 was 0.6 m (Table 3.1).

An average of one in four ramets produced a new stem in 2002. Of the new, one-year-old stems produced by creeping snowberry plants, 44% originated from ramets that were young (2 or 3 years old) and 56% from older ramets (Figure 3.4). Only an average of 10% of the ramets of a plant were young, however, so young ramets produced new stems more often than older ramets relative to their frequency.

The basic structural characteristics of creeping snowberry that are quantified in Table 3.2 are illustrated in Figure 3.4 for one of the sampled plants. This figure shows how a single plant is made up of a complex association of many interconnected ramets and stems. It illustrates how the spacing of ramets along a stem can vary greatly, with some ramets occurring right next to each other while others are separated by much greater distances. It also depicts how some ramets produce many new stems, while others produce none at all.

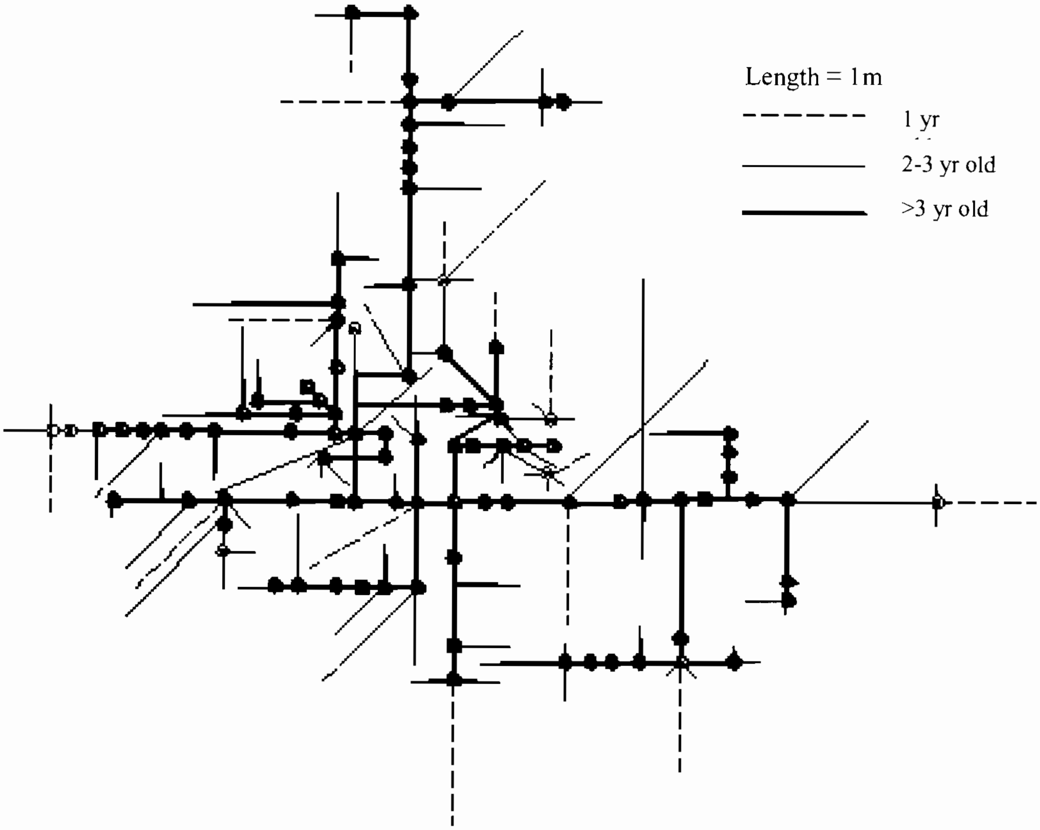

Figure 3.4. Diagram of a creeping snowberry plant. The total stem length of this plant was 66.7 m, and it contained 95 rooted nodes. The oldest stems were at least 12 years old. Each dot along a stem was a ramet. This map illustrates the growth pattern of this individual snowberry plant through time with line style representing stem age.

On average, long, creeping stems (>50 cm) were fewer in number than short, upright stems, but had a greater cumulative length (Table 3.2). However, the proportion of the total annual increment devoted to the production of long stems varied greatly among individual plants. This variation was not associated with total plant length ($r^2 = 0.07$).

Table 3.2. Average and range of the number of stems greater or less than 50 cm in length after their first growing season and cumulative length of those stems per creeping snowberry plant. Only 1 and 2 year old stems were evaluated to reduce the possibility of broken stems affecting the results. "Proportion of Length" is the proportion of total stem length within each size class. 50 cm was used as the delineation between short and long stems.

Initial Stem Length	# of stems	Total length (cm)	Proportion of Length
<50cm	21.1 (0-77)	4.2 (0.0-16.3)	0.29 (0.00-1.00)
>50cm	8.7 (0-24)	7.4 (0.0-20.1)	0.71 (0.00-1.00)

The rate of increase of total plant length for creeping snowberry varied over time as well as among plants. Some plants maintained a constant, slow increase in total length while the total length of others increased rapidly as the plant aged (Figure 3.5). This annual total increase in plant length indicates that every plant was adding more new stem length than it was losing. Because of the variable rate at which total plant length increased, it was not a dependable predictor of plant age ($r^2 = 0.14$). However, total plant length was highly associated with the number of ramets per plant ($r^2 = 0.85$). The number of ramets on a plant limits the potential number of stems that can be produced and thus its potential growth.

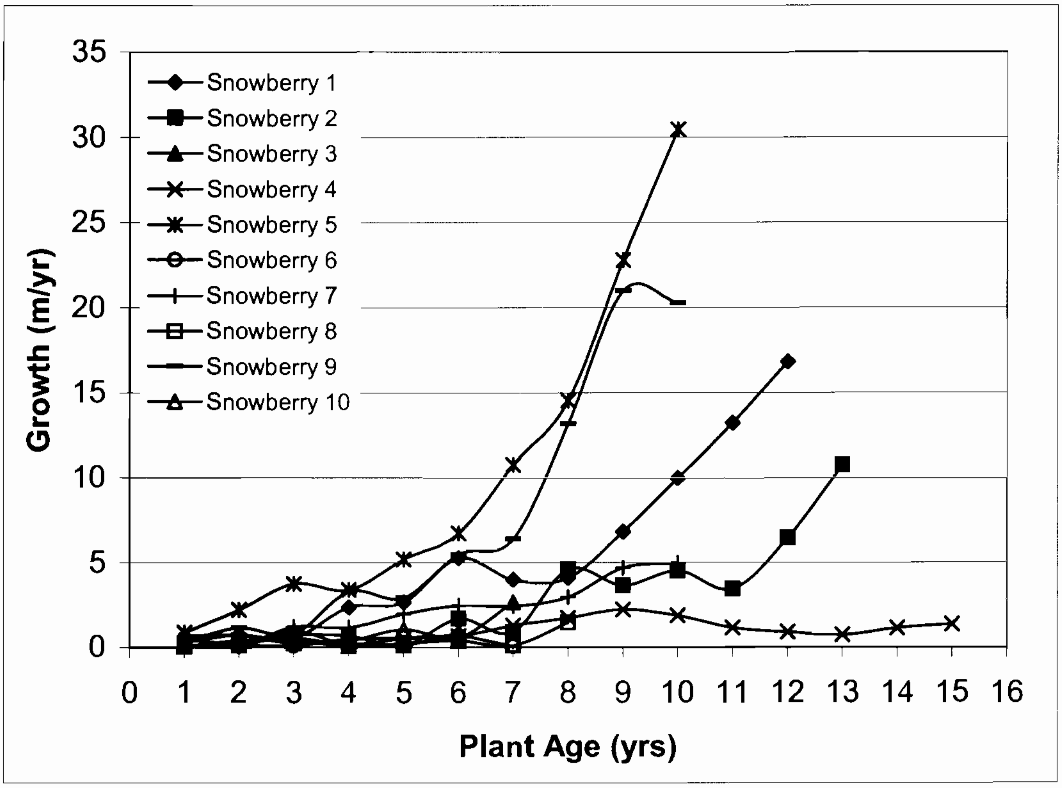

Figure 3.5. Increase in total plant length (Growth) vs. Plant age of ten individual creeping snowberry plants.

Discussion

The two species exhibited very different approaches to vegetative reproduction, which resulted in dissimilar physical and population structures. Trailing blackberry plants were relatively small, averaging only 1.3 m in total length and usually consisting of one ramet with two canes: a one-year-old cane and a two-year-old cane (Table 3.1). Trailing blackberry ramets appeared to be long-lived, though their canes were not. This species formed populations of many disconnected ramets, averaging 67 ramets/m^2 in dense thickets.

Creeping snowberry plants could be long lived, averaging over ten years in age (Table 3.1). They could also be very large, averaging over 33 m in total length and consisting of hundreds of interconnected stems and ramets (Table 3.1). The morphology of this species led to populations consisting of a few, large individuals that produced large networks of many interconnected ramets resulting in thicket densities of up to 218 ramets/m^2.

The ability to maintain stable populations through infilling is an important requirement for long-term survival of clonal populations. Both trailing blackberry and creeping snowberry displayed the potential to perform this function, though their methods for accomplishing it were different.

Trailing blackberry relied heavily on immigration of canes from other areas to maintain a dense cover. Sixty percent of the 54.2 m of canes within the 1x1 m thicket plots originated from ramets that were rooted outside of the plot. Even though trailing blackberry individuals do not seem well suited for infilling because they produce long canes only capable of tip-rooting, immigration of canes from other areas within the population allowed trailing blackberry to infill effectively.

The process of infilling by creeping snowberry occurred as existing stems rooted at new locations along the stem, producing new ramets. Thus, the number of interconnected ramets along a stem can increase over time. This led to over 80% of the total stem length within the 1x1 m thicket plots being rooted there. The ability to produce multiple ramets from existing stems allowed creeping snowberry to be quite successful at infilling.

The strategy of infilling used to produce new ramets by creeping snowberry is similar to that employed by several other woody shrubs commonly found in the forest understory and clearings (Table 3.3). The rhizomes of salmonberry (*Rubus spectabilis*) and salal (*Gaultheria shallon*) are similar to creeping snowberry stems in that a rhizome can produce multiple ramets (Tappeiner et al., 1991; Hufman et al, 1994). The potential production of many new ramets along a single stem or rhizome has proven to be an effective strategy for maintaining dense populations of ramets as these shrubs have been shown to produce, stable, persistent populations (Tappeiner et al., 1991).

Table 3.3. Average density reported as stems/m^2 for 4 common clonal shrubs. "Stem Density" refers to density of upright stems. "NA" indicates the production of no upright stems. "Stem/Rhizome Extension" refers to the reported average annual lateral stem or rhizome elongation. "Habitat" refers to the type of site where the study was performed. "ROW" = Electric utility Right-of-way.

Species	**Stem Density**	**Ramet Density**	**Potential for Lateral Vegetative Spread**	**Stem/Rhizome Extension**	**Life Cycle**	**Habitat**	**Source**
Trailing Blackberry	NA	67 Ramets/m^2	113 canes/m^2	Stems=0.9m	Perennial Deciduous	ROW	Table 1
Creeping Snowberry	156* stems/m^2	155 Ramets/m^2	58 m long stems/m^2**	Stems=0.6m	Perennial Deciduous	ROW	Table 2
Salmonberry	38 stems/m^2	11 ramets/m^2	11 m rhizome/m^2	Rhizomes=1.9m	Perennial Deciduous	Clearcut	Tappeiner et al., 1991
Salal	346 stems/m^2	Not Reported	135 m rhizome/m^2	Rhizomes= 0.1m-2.8m	Perennial Evergreen	Clearcut	Huffman et al., 1994

* Stem density = average stem density in a 1 x 1 m thicket plot multiplied by the proportion of all 1-year-old stems produced by individual creeping snowberry plants that were short, upright stems.

** Reproductive potential = average stem length/m2 multiplied by the proportion of total plant length composed of long stems

Infilling is an important function of clonal plants because it controls the future density of existing populations. Though ramets are often long-lived, stem production often declines with age (Bunnell, 1990). This was the case in our study as the younger ramets of creeping snowberry produced new stems more often than older ramets in 2002 (Figure 3.4). Therefore, the initiation of new ramets is essential for the maintenance of cover (Bunnell, 1990). The maintenance of a dense cover is an important characteristic of many clonal shrub populations and is key factor in their long-term survival because dense populations are often more resistant to invasion (Tappeiner et al., 2001; Huffman et al., 1994). The rate of infilling in many clonal plants has been found to be remarkable stable so that the ramet density of a population changes very little over time (Noble et al., 1979; Cook, 1983).

The ability of clonal plants to spread into new areas through vegetative reproduction is an important function that allows plants to adapt to a changing and patchy distribution of resources (Cook, 1983). Trailing blackberry spreads into new areas through the production of long canes. Canes produced in 2002 reached up to 1.9 m long (average= 0.9 m). Genets can hop across the landscape, relying on long canes to spread away from the parent ramet and form new ramets in a distinct and sometimes distant location from their parent. This method of spread is similar in function to the formation of new ramets by long, pinned vine maple (*Acer circinatum*) branches (O'Dea et al., 1995). Branches are often pinned well away from the parent and a new ramet is produced only at the point along the stem where it was pinned. Thus, as with trailing blackberry, vine maple spreads across the landscape in distinct hops.

Creeping snowberry spreads into new areas through the production of long stems. However, the potential rate of spread of creeping snowberry is slower than trailing blackberry, as new stems averaged only 0.6 m (maximum of 1.3 m). In general, plants produced fewer long stems than short stems (Table 3.2). The long stems of creeping snowberry are similar in function to rhizomes produced by other clonal shrub species like salmonberry and salal, and act as a mechanism for spread (Table 3.3). As they extend away from the parent ramet, they have the potential to produce many ramets along a stem/rhizome and thus produce new ramets anywhere in the newly occupied area.

There is some evidence that the growth pattern (phalanx vs. guerilla) employed by a clonal species leads to differences in competitive abilities under varying densities (Schmid and Harper, 1985). Schmid and Harper used two different clonal species to examine how their growth strategy influenced their competitive ability at variable densities. They found that *Bellis perennis*, which exhibits a phalanx growth strategy, displayed a higher competitive ability when it and its competitors were planted at high densities and *Prunella vulgaris*, which exhibits a guerilla growth strategy, was the competitive dominant when planted with its competitors at low initial densities. Therefore, in the context of our study, we would expect to see a rapid expansion of species that employ a guerilla growth strategy under the conditions of low plant density created by disturbance, such as the treatments applied to ROWs. Trailing blackberry, whose growth strategy is more similar to the guerilla growth strategy than that of creeping snowberry, is one of the more abundant species at our site and increases in cover quite rapidly following disturbance (Chapter 2). Several other studies support this conclusion and have found that trailing blackberry often increases in cover following disturbance and becomes a dominant species soon after disturbance in Pacific Northwest forests (Halpern, 1989; Schoonmaker and McKee, 1988; Dyrness, 1973). It continues to increase in cover and remains a dominant understory species, sometimes well after canopy closure.

Schmid and Harper (1985) also found that the guerrilla species diminished in abundance when faced with high levels of interspecific competition. This leads to the conclusion that, while creeping snowberry and trailing blackberry were both capable of forming dense thickets, creeping snowberry, which employs a more phalanx-like growth form, may be more persistent in the presence of invading species because of their higher competitive ability at high density. This may lead to creeping snowberry thickets exerting a higher level of competition for a longer time period on invading species than trailing blackberry.

There are many advantages to clonal growth including the potential to effectively utilize spatially patchy resources (Harper, 1977), increased survival of new ramets compared to seedlings due to increased size and the ability to share resources between connected ramets (Cook, 1983), and an increased chance of survival of a genet due to its replication in many ramets (Cook, 1979). These advantages are controlled by the pattern of growth of a clonal plant. The pattern of growth is a function of a clonal plant's ability to maintain persistent cover through infilling and spread into new areas. The mechanisms through which the two clonal plants in this study accomplished these functions differed, as did the advantages of each species selected method of vegetative reproduction. Different patterns of spread and in-filling may lead to these shrubs functioning quite differently in the community, with trailing blackberry acting more as a colonizing species that may not be as persistent, and creeping snowberry spreading relatively slowly, but forming a more lasting cover. A better understanding of structure and growth of clonal individuals and populations will further our understanding of the advantages of clonal propagation and its influence on the dynamics of plant communities.

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CHAPTER 4. THE EFFECTS OF THREE DIFFERENT TREATMENTS ON COMMUNITY STABILITY ON ELECTRIC UTILITY RIGHTS-OF-WAY IN WASHINGTON AND OREGON

The selective removal of undesirable vegetation, in contrast to indiscriminant or non-targeted control methods, can create stable low-growing plant communities in some ecosystems (Bramble et al., 1991; Brown, 1994). A vigorous plant community may reduce the establishment of undesirable tall growing species through competition, increased density of seed predators, and other interactions (Caccia and Ballarè, 1998). The resulting vegetation may have both aesthetic appeal and wildlife habitat value (Bramble et al., 1992). The frequency and overall cost of management can be reduced over the long term while maintaining the protection to the power line (Niering, 1958). Achievement of the goal of stable, low-growing plant communities requires an understanding of several interacting factors: the individual plant species and their growth characteristics, the type of disturbance or control methods being used, and plant community response following disturbance.

Treatment Effects

This project allowed us to assess the effectiveness of several commonly used vegetation control methods. Their success or failure was based on their ability to reduce the density of undesirable species and to promote the development of low-growing plant communities. Treatments were applied during the summer of 2000 and included a) mechanical cutting, b) application of herbicide, and c) both in combination (See Chapter 2 for description of sites and treatments). Two types of plots were used to assess change in species abundance over time and compare them among treatments. 2x2 m transect plots were installed prior to treatment application and measured again two years later (Chapter 2). 1x1 m gap plots were installed post treatment application and measured in 2001 and 2002 (Chapter 2).

The selective treatments used in this study reduced the cover of tall target species by an average of 53% from their initial values in 2000 in the 2x2 m transect plots described in Chapter 2 (Table 4.1). No statistical difference in the effectiveness of reducing tall target cover among the three treatment methods was found in the short time period of this study (Kruskal-Wallis rank sum test, $p>0.1$, $n=3$).

Table 4.1. Percent change in average cover ((2002 cover- 2000 cover)/2000 cover x 100) in transect plots for Tall Target and Nontarget species (Chapter 2). "CS" is a manual cut treatment with an herbicide application to the stumps, "FO" is a foliar herbicide treatment with a follow-up basal herbicide application, and "MA" is a manual cut treatment with no herbicide applications (Chapter 2). "All Sites" indicates average value among all three sites. "All Treatments" indicates average value among all three treatments. See Chapter 2 for treatment definitions.

Site	Block	Target	Nontarget
Brownsville	CS	-18	89
	FO	-56	63
	MA	11	63
Skamania	CS	-76	40
	FO	-57	82
	MA	-37	34
Tacoma	CS	-95	61
	FO	-74	64
	MA	-76	87
All Sites	CS	-63	63
	FO	-62	70
	MA	-34	61
Brownsville	All Treatments	-21	72
Skamania	All Treatments	-57	52
Tacoma	All Treatments	-82	71
All Sites	All Treatments	-53	65

Different types of tall target species were controlled more effectively by different treatment methods. Non-sprouting target species (alder (*Alnus rubra*) and Douglas-fir (*Pseudotsuga menziesii*)) were effectively controlled by both herbicide and non-herbicide treatments (Figure 4.1a). The manual cut method, however, reduced non-sprouting tall target cover more quickly, and to a lesser amount than the foliar herbicide treatment; 1x1 m plots, centered around treated tall target species that were treated by the foliar herbicide method still averaged 28% non-sprouting tall target cover in 2001 and 13% in 2002 after the follow up treatment

(Figure 4.1a). Non-sprouting tall target cover in the manual cut treated plots had been reduced to almost zero in 2001 and remained at this low level in 2002. No plots centered on non-sprouting targets were installed in the Cut Stump treatment (Table 4.2).

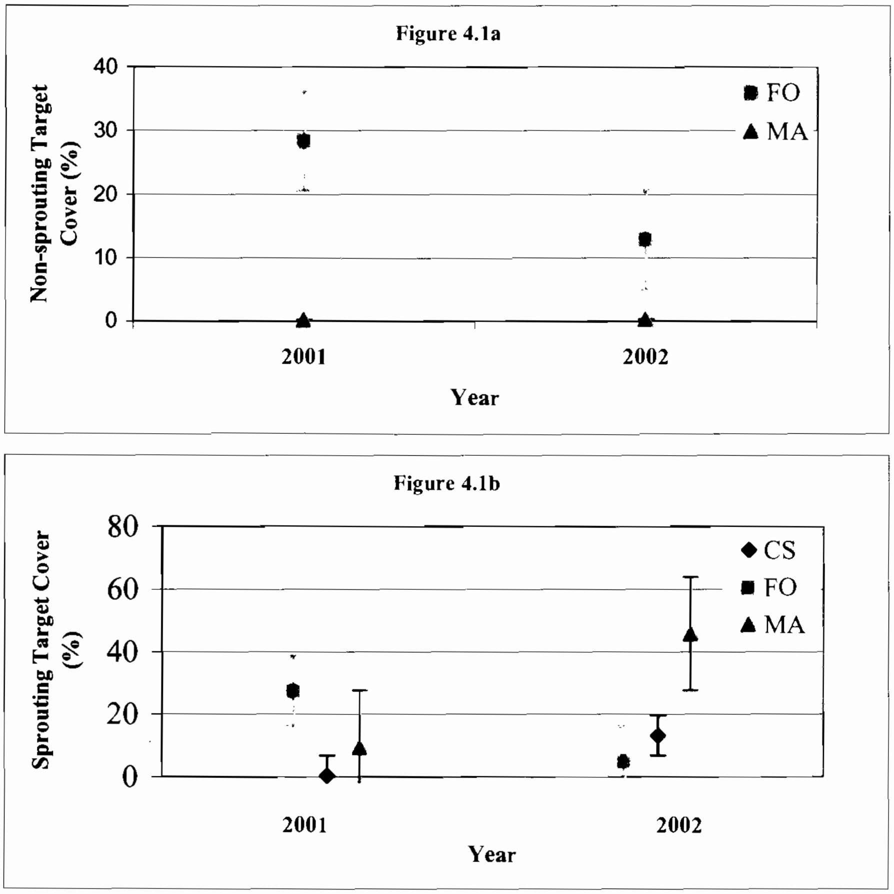

Figure 4.1. Comparison of the change in cover (%) of non-sprouting target species (alder (*Alnus rubra*) and Douglas-fir (*Pseudotsuga menziesii*)) (4.1a) and sprouting target species (vine maple (*Acer circinatum*), bigleaf maple (*A. macrophyllum*), hazel (*Corylus cornuta*), cascara (*Rhamnus purshiana*), and cherry (*Prunus emerginata*)) (4.1b) in 1x1 m plots from 2001 to 2002 between treatments (Chapter 2). No gap plots of non-sprouting species were installed in the cut stump treatment blocks. "FO" is a foliar herbicide treatment with a follow-up basal herbicide application, and "MA" is a manual cut treatment with no herbicide applications (Chapter 2). Error bars indicate the standard error.

Table 4.2. The number of 1x1 m plots distributed by site, treatment block, and target species type. Sprouting targets included vine maple (*Acer circinatum*), bigleaf maple (*A. macrophyllum*), hazel (*Corylus cornuta*), cascara (*Rhamnus purshiana*), and cherry (*Prunus emerginata*). Non-sprouting targets included alder (*Alnus rubra*) and Douglas-fir (*Pseudotsuga menziesii*). "CS" is a manual cut treatment with an herbicide application to the stumps, "FO" is a foliar herbicide treatment with a follow-up basal herbicide application, and "MA" is a manual cut treatment with no herbicide applications (Chapter 2).

Site	Block	Sprout	Nonsprout
BR	CS	10	0
	FO	6	0
	MA	24	0
SK	CS	11	0
	FO	15	0
	MA	16	3
TA	CS	11	0
	FO	7	8
	MA	5	5

The foliar with follow-up (FO) treatment resulted in the least tall target cover in plots centered on sprouting species (vine maple (*Acer circinatum*), bigleaf maple (*A. macrophyllum*), hazel (*Corylus cornuta*), cascara (*Rhamnus purshiana*), and cherry (*Prunus emerginata*)) in 2002 (Figure 4.1b). Vigorous re-sprouting of the target species was apparent in the manual cut treatment, with tall target cover reaching 46% by 2002 after being reduced to 9% in 2001. The cut stump treatment resulted in the lowest tall target cover in 2001, but had begun to increase slowly by 2002.

Nontarget cover increased by an average of 65% (Table 4.1) from 2000 to 2002. Again, no statistical difference was found in the change in average nontarget cover among treatments (Kruskal-Wallis rank sum test, $p>0.1$, $n=3$). The likely reason for the large increase in nontarget species cover was the replacement of tall target cover by nontarget cover where target plants had been killed.

Gap Size

The initial size of the gaps, measured as the area free of any live vegetation in 2001, did not differ significantly among treatments (Kruskal-Wallis rank sum test, $n=9$ $p>0.1$) and averaged 1.2 m^2 (Table 4.3). Gap area was calculated from measurements of the radial distance to live vegetation from the center of the gap plot in four directions. By 2002, just 1 ½ growing seasons after treatment, these gaps were almost completely closed by invading or regenerating vegetation. Some of the gaps were filled by the invasion of nontarget species while others, especially those treated by the manual cut method, were filled by re-sprouting target species.

Table 4.3. Average area (m^2) ± (SE) of gaps caused from the removal of target trees in 2001 and 2002 by treatment and site. "All" indicates average of all sites. "+" indicates value <0.05. One of the plots in the MA treatment block at Brownsville was an extreme outlier with a disturbance size in 2002 4x larger than the next largest value of any of the other plots and was not included in the analysis.

Site	Block	2001	2002
BR	CS	1.1 (0.2)	+
BR	FO	0.4 (0.1)	0.1 (0.1)
BR	MA	2.6 (0.7)	0
SK	CS	2.0 (0.8)	0.2 (0.1)
SK	FO	1.0 (0.5)	+
SK	MA	0.5 (0.2)	0
TA	CS	1.4 (0.3)	0.1 (+)
TA	FO	0.9 (0.5)	0.2 (0.1)
TA	MA	1.0 (0.5)	+
All	CS	1.5 (0.3)	0.1 (+)
All	FO	0.8 (0.2)	0.1 (0.1)
All	MA	1.4 (0.6)	+

The primary method of spread of many of the more common species, such as bracken fern (*Pteridium aquilinum*), trailing blackberry (*Rubus ursinus*), and thimbleberry (*R. parviflorus*), is through some type of vegetative reproduction (Haeussler et al., 1990; Daniels, 1985). Because the average size of the gaps created by the treatments were relatively small, non-target species were quickly able to fill in these areas through means of vegetative spread.

Whether the observed increase in non-target cover persists over the next few years will depend on how well the invading nontarget vegetation is able to impede germination of new target species, as well as on the speed that target species not killed by the treatments re-sprout. Several of the low-growing shrub species found on these sites are capable of forming patches of vegetation with high stem densities

(Chapter 3). Other studies have found that once these shrubs are established and have formed dense thickets of vegetation, tree seedling establishment is greatly reduced (Hill et al., 1995; Niering and Goodwin, 1974; Meilleur et al., 1994).

This study did not find differences in the types of communities that resulted from the different treatment methods. Other studies that monitored sites for longer periods of time have found that the different treatment methods resulted in different assemblages of species (Bramble and Byrnes, 1983; Bramble et al., 1991; Dreyer and Niering, 1986; Luken et al., 1991). In particular, areas that are treated using the manual cut method have been found to increase in target stem density over time due to continual re-sprouting from cut stumps (Luken et al., 1991; Johnstone, 1990). There is some indication that this trend will be realized in our study as many of the target species that were treated with this method re-sprouted quite vigorously. However, a longer period of observation is necessary to confirm this trend.

Future Management

Based on the target and nontarget species response to the various treatments used in this study, I would recommend a combination of the current management strategies for future right-of-way maintenance. Whether or not a target plant will be killed by a manual cut treatment is largely dependent on its ability to re-sprout from cut stumps or roots. Many of the primary target species in the Pacific Northwest, including hazel, bigleaf maple, vine maple, cherry, and cascara display a superior ability to re-sprout following disturbance (Halpern, 1989; Haeussler et al., 1990;

Tappeiner, 1971; O'Dea et al., 1995). Therefore, a treatment method that involves the selective application of herbicide is often more effective at killing the target species. However, herbicide applications were often only partially effective at reducing target cover to low levels and required follow-up treatments to achieve the same reductions in target cover produced initially by the treatments that involved manual cutting. Two reasons for the mixed results produced by the foliar herbicide treatment include species resistance to the herbicide that was used and incomplete foliar coverage of the plant, often due to its large size. Therefore, my suggestion for future management of rights-of-way where both sprouting and non-sprouting targets are present would be an initial manual cut treatment, followed by a selective foliar treatment 1-2 years later.

The initial application of the manual treatment accomplishes several things. First, it kills all target species that are not capable of re-sprouting. Second, it initially reduces the size of target species that can re-sprout, temporarily eliminating their danger to the lines and makes them easier to treat with the follow-up selective herbicide treatment. The reduction in size of the target area also makes it less likely that herbicide drift will occur, reducing the risk of harm to nontarget vegetation. Third, it may weaken the surviving targets so that a follow-up herbicide treatment will be more effective.

There are many other management approaches that can also be considered when implementing a management strategy aimed at promoting stable, low-growing plant communities besides those that have been mentioned here. Several other approaches that have shown potential for creating stable communities include direct seeding of desirable species (Brown, 1995) and the incorporation of grazers or seed predators to control tree establishment. The method that is employed should be based on the existing plant community and environmental conditions of the area.

A goal of any ROW management strategy should be to keep the treatments as localized to the targets as possible. Low-growing shrubs have shown a propensity for forming communities resistant to tree invasion, as well as the ability to quickly spread into new space. These qualities make them desirable species on ROWs. A selective a management approach reduces the risk of harming low-growing nontarget cover in the vicinity of the target plants, making it more likely the gap that is created will be filled by the neighboring desirable nontarget species. A management strategy that aims to increase nontarget cover along with removing targets will be increasingly successful over time due to the resistance to tree seedling establishment displayed by many of the nontarget species. This leads to a reduced cost of management and increased safety to the lines.

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APPENDIX

Average cover of all species by site in each of the nine species groups in 2000. "TallT" is the average summed tall target cover and "Total" is the average total vegetative cover.

A. Brownsville

Group	**Black**	**GaSh**	**Grass**	**PoMu**	**Pomu/HoDi**	**PtAq**	**RuPa**	**RuUr**	**Sysp**
Count	**36**	**34**	**68**	**11**	**8**	**22**	**15**	**103**	**55**
AcCi	0.1	3.5	0.9	0	0.4	0	0	+	0
AcMa	0	0.3	0.1	0.1	3.0	+	0.1	+	0
AlRu	0	0	0	0	0	0	0	0	0
AmAl	0.5	0	+	0	0.4	0	0.3	0.2	0
BeNe	0	0	+	0	0	0	0	0	0
Black	19.1	1.4	1.7	4.4	3.5	1.3	5.6	1.5	1.8
CoCo	3.0	12.8	4.2	6.5	14.8	7.9	12.1	1.2	7.5
CySc	3.1	0.7	1.9	2.8	0	3.6	0.5	24.6	4.3
BlSp	0	0	0	0	0	0	0	0	0
Forb	0.7	0.7	1.8	0.5	1.6	0.8	1.9	1.1	0.9
GaSh	0.5	24.5	0.5	0.6	3.4	0.5	1.7	1.8	1.6
Grass	0.7	0.1	6.9	0.5	0.4	0.7	0.2	2.4	0.9
HoDi	0	0	0	0	6.3	0	+	0	0
Losp	0	0	0	0	0	0	0	+	0.4
AtFi	0	0	0	0	0	0	0	0	0
OeCe	0	0	+	0	0	0	0.1	+	0
PoMu	1.5	1.5	0.7	27.5	8.9	0.5	1.5	1.2	0.9
PrEm	4.1	3.5	0.9	4.6	3.5	0.8	5.9	0.8	1.0
PsMe	0.9	0.7	1.4	1.0	0	1.7	0.1	2.9	2.6
PtAq	2.6	3.8	2.4	2.5	1.9	17.9	2.9	2.5	3.8
Fruit	+	0	0.1	0	0	0.4	0.1	0.5	0.1
QuGa	0	0.3	0.2	0	0.3	0.5	0.5	+	0.1
RhPu	1.0	3.8	2.4	5.0	4.8	4.7	5.4	1.1	1.1
Rose	0.2	0.1	0.2	0	0	0.1	0.2	0.1	0.2
RuPa	1.8	6.7	0.6	2.8	0.4	4.2	25.3	0.1	0.8
RuSp	0	0	0	0	0	0	0	0	0
RuUr	5.3	1.9	2.9	2.4	3.3	3.5	2.1	12.5	2.3
Sasp	0.3	0.6	0.9	0.7	2.1	0.1	0.1	0.7	0.4
Sysp	3.9	1.5	3.2	2.0	0.7	2.2	1.6	1.9	34.5
ThPl	0	0	0	0	0	0	0	0	0
TsHe	0	0	0	0	0	0	0	0	0
VaPa	0	0	0	0	0	0	0	+	0
TallT	9.9	25.5	11.1	17.9	29.1	16.0	24.9	7.6	12.8
Total	49.3	68.4	33.8	64.0	59.3	51.3	68.3	57.3	65.1

B. Skamania

Group	Black	GaSh	Grass	PoMu	Pomu/HoDi	PtAq	RuPa	RuUr	Sysp
Count	-	67	60	27	67	26	4	18	56
AcCi	-	13.0	8.6	20.4	19.3	5.3	1.5	7.0	7.3
AcMa	-	1.7	1.6	2.0	1.1	1.6	8.5	1.9	0.7
AlRu	-	0.4	0.1	0	+	0	0	0	0
AmAl	-	0.1	0.5	0	0.8	0.1	0	0.3	+
BeNe	-	2.5	1.4	0.9	9.1	2.9	1.9	2.6	2.8
Black	-	+	0.1	0	0.2	0	0	0	0
CoCo	-	9.7	5.3	9.6	9.3	3.4	6.4	1.6	8.0
CySc	-	0.3	0.7	1.4	0.4	0.5	2.5	20.0	0.4
BlSp	-	0	0	+	0	0	0	0	0
Forb	-	1.1	4.4	2.3	1.1	1.2	1.3	1.1	1.1
GaSh	-	24.1	2.2	2.0	8.9	6.0	3.0	5.3	13.6
Grass	-	0.8	6.4	1.6	0.9	1.7	1.1	2.3	1.1
HoDi	-	0.2	0.4	0.5	2.6	+	0	0.1	0.1
Losp	-	0.3	0.1	0.2	+	0	0.1	0	0.1
AtFi	-	0.1	0.2	0.2	0	0	0	0	+
OeCe	-	0	0	0	0	0	0	0	0
PoMu	-	4.3	1.9	37.9	7.6	1.6	1.6	2.7	3.0
PrEm	-	0	+	0	1.2	0	0	0.6	+
PsMe	-	0.5	1.2	0.1	1.5	1.6	0	0.3	0.4
PtAq	-	5.6	2.6	2.3	3.6	15.5	6.9	3.2	4.3
Fruit	-	0	0.4	0	0	+	0	0	0
QuGa	-	+	0	0	0	0	0	0	0
RhPu	-	3.3	2.7	5.4	4.8	4.3	0.13	3.1	3.1
Rose	-	0.2	0.3	0.7	0.2	0.2	0	0.1	0.3
RuPa	-	1.5	1.3	2.4	0.6	1.9	32.5	1.6	3.3
RuSp	-	0	0	0	0	0	0	0	0
RuUr	-	1.2	1.6	1.4	1.0	1.6	1.3	4.4	1.6
Sasp	-	0.2	1.0	0.1	0.7	0.1	5.0	0	0.6
Sysp	-	3.5	5.8	3.4	4.8	2.0	7.0	3.4	29.5
ThPl	-	0	+	0	0	0	0	0	0
TsHe	-	0	0	0	0	0	0	0	0
VaPa	-	0.2	0.1	0.9	+	0	0	0	0.3
TallT	-	29.1	21.5	37.5	38.7	16.3	21.5	14.8	20.1
Total	-	74.8	50.8	95.5	79.7	51.3	80.6	61.5	81.6

C. Tacoma

Group	Black	GaSh	Grass	PoMu	Pomu/HoDi	PtAq	RuPa	RuUr	SyAl
Count	-	67	33	31	4	30	141	21	-
AcCi	-	6.0	3.6	4.3	5.0	6.5	6.3	3.9	-
AcMa	-	0.1	0	0	0	0	+	0	-
AlRu	-	4.1	2.4	12.1	0	9.5	5.6	2.5	-
AmAl	-	0	0	0	0	0	0	0	-
BeNe	-	0	0	+	0	0	0	0	-
Black	-	0.1	0	0	0	0	0.004	0	-
CoCo	-	0	0	0	0	0	0	0	-
CySc	-	0	0	0	0	0	0	0	-
BlSp	-	0.3	0.1	0.1	0	+	0.1	0.2	-
Forb	-	1.1	4.4	0.8	1.9	2.2	1.8	2.7	-
GaSh	-	24.3	0.3	2.5	8.0	1.3	0.7	1.7	-
Grass	-	1.3	12.09	0.3	1.3	2.7	0.9	1.0	-
HoDi	-	0.1	0	+	15.75	0	0	0	-
Losp	-	0	0	0	0	0	0	0	-
AtFi	-	0.2	+	0.2	0.1	+	0.1	0	-
OeCe	-	0.1	+	+	0	0.1	+	0	-
PoMu	-	2.0	0.5	26.7	4.3	1.2	3.8	2.6	-
PrEm	-	0	0.1	0	0	0	0.3	0.2	-
PsMe	-	3.0	1.9	3.3	0.8	0.6	0.9	3.5	-
PtAq	-	4.7	3.4	1.4	3.8	13.2	1.8	4.3	-
Fruit	-	0	0	0	0	0	0	0	-
QuGa	-	0	0	0	0	0	0	0	-
RhPu	-	0.1	0	0	0	0	0.1	0	-
Rose	-	0	0	0	0	0	0	0	-
RuPa	-	4.8	5.1	16.2	4.0	10.0	26.85	2.3	-
RuSp	-	0.4	1.2	1.7	0.8	1.7	3.3	1.2	-
RuUr	-	5.1	2.1	4.3	1.8	6.4	9.1	20.0	-
Sasp	-	0	0	0	0	0	0	0	-
Sysp	-	0	0.003	0	0	0	0	0	-
ThPl	-	2.0	0	0.3	0	0.5	0.7	0	-
TsHe	-	1.3	0.2	0.4	1.5	0.1	0.1	0.6	-
VaPa	-	0.4	+	0.2	0.8	0.5	0.2	0.8	-
TallT	-	16.8	8.1	20.4	7.3	17.3	14.0	10.6	-
Total	-	61.6	37.52	74.7	49.5	56.3	62.61	47.4	-