

AN ABSTRACT OF THE THESIS OF

Ashley H. Roorbach for the degree of Master of Science in Forest Science presented August 26, 1999. Title: The Ecology of Devil's Club (*Oplopanax horridum* (J. E. Smith) Miq.) in Western Oregon

Signature redacted for privacy.

Abstract approved: _____

David E. Hibbs

Signature redacted for privacy.

Nan C. Vance

Devil's club (*Oplopanax horridum* (J. E. Smith) Miq.) is an indigenous shrub of the Pacific Northwest, often found in the *Tsuga heterophylla* (western hemlock)/Devil's club association in western Oregon. In the same family as ginseng, Devil's club is gaining attention for its medicinal properties. While traditional uses of Devil's club are well known, little biological research on the plant has been documented. This study is intended to increase the ecological knowledge of Devil's club in western Oregon, and provide an ecological basis for developing conservation guidelines.

Devil's club's ecological niche, adaptive limitations and growth patterns were studied in the Oregon Cascade Mountains and Oregon Coast Range. Devil's club sub-populations in western Oregon typically grow as patches in canopy gaps. The ecological niche of Devil's club is best characterized as shaded, moist and riparian. Although Devil's club was observed growing throughout a wide range of light environments, its highest micro-site percent cover value occurred in a low-light environment of 0.05 DIFN (diffuse non-interceptance). Soil moisture averaged 56.8% on a dry weight basis, ranging from 36.3% to 82.2%. Common overstory

tree associates include western hemlock, *Alnus rubra* (red alder), and *Pseudotsuga menziesii* (Douglas-fir); common understory shrub associates include *Rubus spectabilis* (salmonberry), *Vaccinium sp.* (huckleberry) and *Acer circinatum* (vine maple).

Devil's club stem complexes maintain a multiple-aged distribution of stems. A negative correlation between elevation and stem elongation suggests length of growing season limits potential annual stem elongation rates. Measurements of past and current stem branching patterns showed that occupation of growing sites is achieved primarily through layering of aerial stems. There were no observations of Devil's club producing rhizomes or root sprouts, and in two field seasons, there were only two observations of Devil's club seedlings. Stem elongation averaged 17.8 cm per year, with the longest growth occurring in low light environments. A stem lopping experiment in the field found strong apical dominance in vertical, aerial stems; damage to a stem will trigger bud break. A greenhouse experiment with stem cuttings indicates that production of Devil's club rooting stock should not be difficult.

The Ecology of Devil's Club (*Oplopanax horridum* (J. E. Smith) Miq.) in Western
Oregon

by

Ashley H. Roorbach

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed August 26, 1999
Commencement June, 2000

ACKNOWLEDGEMENTS

I wish to extend a sincere and wholehearted thank you to my major professors, David Hibbs and Nan Vance, for their support and guidance as I prepared, researched and wrote this thesis. Nan and Dave's patience, accessibility, vision and critical thinking were invaluable. John Tappeiner generously shared his expertise, helping to fit the thesis into the 'bigger picture.'

I appreciate as well support provided by the Pacific Northwest Research Station of the US Forest Service, the Sustainable Forestry Partnership and the Coastal Oregon Productivity Enhancement Project.

My parents' encouragement and support have, like always, been a huge help. My Corvallis *in situ* family, the MTH, has been a constant source of camaraderie and support. I especially want to thank Kim Kittredge for her enthusiasm as I plodded through this thing called graduate school. Likewise, Lisa Brown's compassion, hard-work and uncompromising principles will always be an inspiration.

Thank you to all the professors, researchers and research assistants who generously shared their time and expertise with me. I would like to mention by name the following: Steve Radosevich, Bill Emmingham, Mike Newton, Dina Brown, Nobi Suzuki, Joe Karchesey, Sam Chan, Mark Wilson, Steve Sharrow, and Barbara Bond. I would like to also make special mention of the wizards at QSG - much like navigating through patches of Devil's club, Manuela Huso and Lisa Ganio patiently led me through several thorny statistical problems.

Finally, I am indebted to the friendship I developed with my fellow students, whose unfailing good cheer and enthusiasm will always be remembered and appreciated.

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The Ecology of Devil's Club (*Oplopanax horridum* (J. E. Smith) Miq.) in Western Oregon

CHAPTER 1 INTRODUCTION

Devil's club (*Oplopanax horridum* (J. E. Smith) Miq.) (Hitchcock and Cronquist 1973) is gaining attention as a potentially useful medicinal plant. Aboriginal uses of Devil's club are well-documented (Willard 1992, Gunther 1988, Turner 1979, Smith 1983), and research is being conducted to determine the plant's modern pharmaceutical uses (Kobaisy et al. 1997; McCutcheon et al. 1995), but it has attracted little ecological research. What is known about Devil's club in western Oregon remains mostly descriptive (Hitchcock and Cronquist 1973, Pojar and MacKinnon 1994, Moore 1993): A sprawling shrub with erect aerial stems, each fiercely armed with 5 – 10 mm long yellow spines. Stems are typically topped with single crowns of spreading leaves (Figure 1.1). Leaves are large (to 40 cm width) alternate and deciduous, maple leaf shaped and palmately veined with spines protruding from underneath. Aerial stems grow from lateral, layered stems and can be over 4 meters in height. Reproduction is primarily vegetative by layering.

OBJECTIVES

The objectives of this study were to investigate the ecology of Devil's club, in particular its:

- Habitat and competitive niche;
- Growth, branching and reproduction patterns;
- Sub-population (patch) characteristics.



FIGURE 1.1 Individual stem of Devil's club (approximately 3 meters in height) in western Oregon.

LITERATURE REVIEW

Background

Devil's club is a member of the family Araliaceae that includes ginseng (*Panax ginseng* and *Panax quinquefolius*). Devil's club has been utilized by native people throughout the Pacific Northwest (Willard 1992, Gunther 1988, Turner 1982). On the British Columbia coast it is considered one of the native people's most important medicinal and sacred plants (Pojar et al. 1994, Turner 1982), and historically was traded widely throughout the region (Willard 1992). Most tissues of the plant are used, including the stem, roots, and bark (Moore 1995, Pojar et al. 1994, Willard 1992, Gunther 1988). Table 1.1 lists some of Devil's club traditional uses.

Table 1.1 Traditional uses for Devil's club (Willard 1992, Gunther 1988, Turner 1982).

Medicinal	
colds, sore throats, fevers	menstruation flow regulator
pneumonia	excessive milk flow reduction
rheumatism	as an emetic
tuberculosis	arthritis
adult onset of diabetes	stomach ulcers
cancer	gallstones
constipation	chest pains
head lice, dandruff	dental and topical painkiller
Other	
Fishing hooks and bobs	appetite suppressant
aid in seeking visions	ink for tattoos, ceremonial face painting and dying baskets
deodorant	perfumed baby talc
charm against evil spirits	

The most common modern use for Devil's club is for treating diabetes (Moore 1995, Willard 1994), though there are conflicting clinical results regarding the efficacy of Devil's club hypoglycemic properties (Smith 1983). Devil's club can also be used as an expectorant, a respiratory stimulant and for chest colds (Moore 1995). Moore (1995) also recommends its use to treat rheumatoid arthritis and other autoimmune disorders.

Distribution

Devil's club ranges from the north and western half of Oregon, through western Washington and British Columbia, Canada and into southern, central Alaska, and east through the higher elevations of Montana and Idaho. Further east in southern Ontario, around Lake Superior and on Isle Royal in upper Michigan are isolated populations. In the Pacific Northwest, north from mid-Washington, Moore (1993) describes Devil's club as often growing in full sunlight, and when in the understory able to completely fill forest 'hollows', entirely occupying and obscuring stream and river banks. In the southern and eastern edges of its range, Moore (1993) describes the plant as being mostly confined to deep, wet, and shady places, observations supported in Oregon by Franklin and Dyrness (1973), Hemstrom et al. (1982), and Hemstrom and Logan (1986). Devil's club patches in Oregon can be extensive, though more typically are small and scattered, appearing inconsistently, if at all, within a drainage. Devil's club in Oregon has been observed favoring north facing slopes (Hemstrom and Logan 1986), and cooler spots (Moore 1993).

Climate of Western Oregon and Washington

The climate of western Oregon and Washington is controlled largely by the Pacific Ocean and two mountain ranges, both parallel to the Pacific coastline. The most western of these, the Coastal Range, averages about 300 meters elevation in Washington (excluding the Olympic Mountains in the north part of the Olympic

Peninsula) to about 1,000 meters in Oregon. Eastward moving air masses from the Pacific Ocean passing over the Coast Range are uplifted and cooled, releasing prodigious amounts of precipitation. Rainfall in the western slopes of the Coast Range are some of the heaviest in the continental United States, averaging around 500 cm a year on the upper western slopes of the Oregon Coast Range (Weather America 1996).

About 95 miles east of the Pacific coast line the second mountain range, the Cascade Mountains, rises to an average of 1,500 meters in Oregon and slightly more in Washington. Eastward moving Pacific air masses are again uplifted and cooled, resulting in heavy precipitation along the western slopes, though not as much as on the Coast Range. Rainfall on the western slope of the Oregon Cascade average about 190 cm a year. Moving further east from the crest of the Cascades, precipitation decreases and a much drier climate dominates, characterized by hot summers with cool and dry winters in the eastern part of the two states. Sites for this study were located on the west and eastern slopes of the mid-Oregon Coast Range, as well as on the western slope of the mid-Oregon Cascade Mountains.

In southern Oregon, the Coast Range and Cascade Mountains merge and form the Siskiyou Mountains. These mountains are drier and warmer than either the Coast Range or Cascade Mountains (Table 1.2). They also mark the southern limit of Devil's club distribution in Oregon (Moore 1993).

The Pacific Ocean moderates and cools both the summer and winter temperatures in western Oregon and Washington. In the Willamette Valley, which separates the Oregon Coast Range and the Oregon Cascades Mountains, the average temperature ranges from only 3°C in the coldest month of February to 19°C in the hottest month of July (Weather America 1996). The influence of the ocean is not as strong in the interior in the Siskiyou Mountains. The valleys of these mountains average about 2.8°C warmer than valleys directly north, with maximum temperatures exceeding 32.2°C (90°F) 40 to 50 days a year (Weather America 1996).

Table 1.2 Range of average maximum August temperatures (1964-1995) from north to south in western Washington and Oregon.

Site ¹	Latitude // Longitude	Elev. (m)	Mean daily maximum temperature for Aug. C°(F°)	Mean # days >32.2°C (90°F)
Clearwater, WA	47° 35' N // 124° 18' W	24	21.8 (71.2)	1
Port Angeles, WA	48° 7' N // 123° 24' W	12	20.4 (68.8)	0
Monroe, WA	47° 51' N // 121° 59' W	37	24.8 (76.6)	1
Diable Dam, WA	48° 43' N // 121° 9' W	266	21.4 (70.6)	4
Grayland, WA	46° 46' N // 124° 2' W	6	19.4 (67.0)	0
Elma, WA	47° 0' N // 123° 24' W	21	25.7 (78.2)	3
Olympia, WA	46° 58' N // 122° 54' W	66	25.4 (77.7)	3
Cedar Lake, WA	47° 25' N // 121° 45' W	469	22.6 (72.7)	1
Long Beach, WA	46° 22' N // 124° 2' W	9	19.4 (66.9)	0
Grays River, WA	46° 23' N // 123° 34' W	31	23.2 (73.7)	2
Toledo, WA	46° 28' N // 122° 50' W	99	26.3 (79.4)	4
Packwood, WA	46° 27' N // 121° 40' W	318	26.2 (79.2)	4
Tillamook, OR	45° 29' N // 123° 51' W	12	20.5 (68.9)	0
McMinnville, OR	45° 12' N // 123° 12' W	46	28.3 (82.9)	7
N. Willamette Exp. Stat., OR	45° 17' N // 122° 45' W	46	27.1 (80.7)	5
Government Camp, OR	45° 18' N // 121° 45' W	1195	20.1 (68.2)	0
Newport, OR	44° 38' N // 124° 3' W	37	18.7 (65.6)	0
Tidewater, OR	44° 24' N // 123° 53' W	12	24.6 (76.3)	1
Corvallis Water Bureau, OR	44° 30' N // 123° 27' W	156	26.2 (79.2)	3
Cascadia, OR	44° 23' N // 122° 30' W	240	26.4 (79.5)	3
N. Bend, OR	43° 25' N // 124° 15' W	9	19.7 (67.4)	0
Elkton, OR	43° 39' N // 123° 36' W	40	29.1 (84.3)	7
Cottage Grove Dam, OR	43° 43' N // 123° 3' W	250	26.6 (79.8)	4
Wickiup Dam, OR	43° 41' N // 121° 42' W	1300	26.7 (80.1)	4
Brookings, OR	42° 3' N // 124° 17' W	32	19.8 (67.6)	0
Cave Junction, OR	42° 10' N // 123° 39' W	406	31.4 (88.6)	15
Ashland, OR	42° 13' N // 122° 43' W	543	30.1 (86.1)	12
Howard Prairie Dam, OR	42° 13' N // 122° 22' W	1372	26 (78.8)	3

¹ Each group of four recordings are located at approximately the same latitude, moving west to east longitudinally from the coast. Temperatures tend to increase farther away from the coast. The bottom three Oregon temperature readings are in the Siskiyou Mountains, which reportedly do not contain Devil's club (Moore 1993). Temperatures in these mountains, especially the number of days greater than 32.2°C (90°F) increase dramatically, even though they were recorded at higher elevations (Weather America 1996).

There is a pronounced wet season in western Oregon and Washington. West of the Cascade Mountains in Oregon about half the annual total precipitation falls from December to February (Weather America 1996), with most of the remainder falling during the Spring and Fall months. Summers are sunny but droughty. As a result many deciduous plants in the region, such as Devil's club, crowd into riparian areas where there is sufficient moisture to support competitive growth during the sunny but relatively short growing seasons.

Plant Community

Devil's club appears as an indicator of moist, poor or well drained sites in many plant community classification systems in the Pacific Northwest (Franklin and Dyrness 1973, Hemstrom et al. 1982, Hemstrom and Logan 1986). Based on Franklin and Dyrness (1973), Devil's club generally forms plant communities and associations in three major forest types in western Oregon: the coastal *Picea sitchensis* (Sitka spruce) Zone, the interior *Tsuga heterophylla* (western hemlock) Zone, and the higher elevation *Abies amabilis* (Pacific silver fir) Zone.

Picea sitchensis Zone

Franklin and Dyrness (1973) include in the *Picea sitchensis* Zone the coastal forests of Oregon and Washington up to a few kilometers inland, extending slightly further in coastal valleys. The Pacific Ocean moderates the climate throughout the zone, making it uniformly wet and mild.

Devil's club in this zone forms the *Tsuga Picea/Oplopanax, Athyrium* community (Franklin and Dyrness 1973). Major understory plants in this community include *Polystichum munitum* (sword fern) and *Oxalis oregana* (oxalis). Minor understory plants include:

Shrubs:

Vaccinium ovalifolium - ovalleaf huckleberry
Vaccinium parvifolium - red huckleberry
Menziesia ferruginea - rusty leaf
Acer circinatum - vine maple
Rubus spectabilis - salmonberry

Herbs:

Blechnum spicea - deerfern
Disporum smithii - Smith's
 fairybell's
Athyrium filix-femina - lady fern
Maianthemum dilatatum - false lily
 of the valley

Hemstrom and Logan (1986) describe the *Picea sitchensis*/*Oplopanax horridum* association as an indicator of very moist soils in seeps or impeded drainages. The southern limit of this association is reported to be the Waldport Ranger district (latitude ~ 44°), becoming more common further north into Alaska (Hemstrom and Logan 1986).

Tsuga heterophylla Zone

Franklin and Dyrness (1973) describe the *Tsuga heterophylla* Zone as a low to mid-elevation zone extending from the Oregon and Cascade Ranges north through the Olympic Peninsula into British Columbia. Often *Psuedotsuga menziesii* (Douglas-fir) dominates or co-dominates the overstory in these forests. Elevation of the *Tsuga heterophylla* Zone range from sea level to 600 or 700 meters in the Cascades at 49° latitude, and from 150 to 1,000 meters at 45° latitude (Franklin and Dyrness 1973). It encompasses all of the Coast Range except areas recognized as part of the *Picea Sitchensis* Zone. Franklin and Dyrness (1973) describe the *Tsuga heterophylla* Zone as the most extensive forest type in western Oregon and Washington, characterized by a wet and mild climate, with greater temperature extremes than in the *Picea sitchensis* Zone.

Within the *Tsuga heterophylla* Zone, Hemstrom and Logan (1986) and Hemstrom and Logan (1987) recognize a *Tsuga heterophylla*/*Oplopanax horridum* Association when Devil's club cover is greater than 5 percent in a site. Hemstrom et al. (1982) report that Devil's club in the mid-Oregon Cascade Mountains is found mostly along streams and in poorly drained, isolated wet spots in sites

subject to frequent rainfall, particularly in higher elevations. In the mid-Oregon Coast Range Hemstrom and Logan (1986) describe Devil's club as typically growing on northerly facing slopes in poorly drained, concave and seepy topography, as well as near streams. The *Tsuga heterophylla*/*Oplopanax horridum* Association becomes more common in both the Coast Range and Cascade Mountains with increasing latitude (Hemstrom et al. 1982, Hemstrom and Logan 1986).

Franklin and Dyrness also identify a lower-elevation *Thuja plicata* (western red cedar)/*Oplopanax horridum* Association on the east side of the Cascade Mountains within in the *Tsuga heterophylla* Zone.

Abies amabilis Zone

Franklin and Dyrness (1973) describe the *Abies amabilis* (Pacific silver fir) Zone as occurring on the western slopes of the Cascade Mountains from mid-Oregon (~ 44° latitude) north to British Columbia. Elevation of the Pacific silver fir forests range from 600 to 1,300 meters in northern Washington, 900 to 1,300 meters in southern Washington, and 1,000 to 1,500 meters in Oregon.

Hemstrom et al. (1987) recognize an *Abies amabilis*/*Oplopanax horridum* association when Devil's club cover is greater than 5 percent in a site. In the Washington Cascades, the presence of Devil's club is associated with wet, relatively warm sites, whereas in the central Oregon Cascades it is more commonly associated with wet and cool higher elevation sites (Hemstrom et al. 1987).

Franklin and Dyrness (1973) describe Devil's club growing in an *Alnus sinuata* (Sitka alder) Community, where Devil's club is often found as an important understory plant. The community is characterized as subject to deep winter snows - in Washington it is often found in avalanche chutes, though in Oregon it is more typically associated in sites with an abundance of seeping water. The only conifer found in this community is *Chamaecyparis nootkensis* (Alaska cedar).

Devil's club is also reported to occur in the wet, cool and high elevation *Tsuga mertensiana* Zone (Franklin and Dyrness 1973). In this zone, Devil's club in British Columbia is found in the *Tsuga mertensiana*/*Cladothamanus pyrolaeiflorus* (copper brush) Association, where it often grows with *Athyrium filix-femina*. The association reportedly indicates wet sites within drier than normal areas (Franklin and Dyrness 1973).

In the Tongass National Forest of coastal Alaska, Devil's club is more extensive than in western Oregon and forms recognized associations with wide range of plants, including western hemlock, sitka spruce, Alaska cedar, skunk cabbage (*Lysichitum americanum*), salmonberry, black cottonwood (*Populus trichocarpa*), and blueberry (*Vaccinium* sp.) (Shephard 1995, Martin et al. 1995). Devil's club occupies sites the Tongass National Forest that are productive, wet, and generally well drained; saturated soils are common (Shephard 1995, Martin et al. 1995). Both Shephard (1995) and Martin et al. (1995) observe that in sites where both salmonberry and Devil's club grow, the cover of salmonberry increases while cover of Devil's club decreases after clear-cuts.

SUMMARY AND OVERVIEW OF THESIS

As noted, little ecological research has been conducted on Devil's club in western Oregon. Most information is anecdotal, but consistent. The association with moist soil conditions is so strong that Devil's club is often used to identify seeps and draws in plant association guides. It is known that Devil's club can and does reproduce vegetatively, but to what extent has not been explored. The relationships between Devil's club and light, and other environmental factors including understory competition have not been documented. Given the current interest in Devil's club medicinal properties, increased biological understanding of the plant can enhance development of ecologically based conservation and management strategies.

There are two main chapters in this thesis. Chapter two describes Devil's club growth, morphology, and competitive response to micro-environmental conditions, including overstory trees, soil moisture and associated understory plants. Chapter three describes growth patterns, particularly vegetative reproduction patterns, and how they relate to Devil's club environmental adaptations. Chapter 4 briefly summarizes the preceding two chapters and discusses how Devil's club may be responding to its environment on a regional scale.

CHAPTER 2

ENVIRONMENTAL NICHE AND GROWTH PATTERNS OF OPLOPANAX HORRIDUM (J.E. SMITH) MIQ. (DEVIL'S CLUB) IN WESTERN OREGON

Ashley H. Roorbach

INTRODUCTION

Devil's club (*Oplopanax horridum* (J. E. Smith) Miq.) (Hitchcock and Cronquist 1973) is gaining attention as a potentially useful medicinal plant. Aboriginal uses of Devil's club are well-documented (Willard 1992, Gunther 1988, Turner 1982, Smith 1983), and research is being conducted to determine the plant's modern pharmaceutical uses (Kobaisy et al. 1997; McCutcheon et al. 1995), but it has attracted little ecological research. What is known about Devil's club in western Oregon remains largely descriptive (Hitchcock and Cronquist 1973, Pojar et al. 1994, Moore 1993): A sprawling shrub with erect aerial stems, each fiercely armed with 5 – 10 mm long, yellow spines. Stems are typically topped with single crowns of spreading leaves (Figure 1.1). Leaves are large (to 40 cm in width) alternate and deciduous, maple leaf shaped and palmately veined with spines protruding from underneath (Appendix B). Aerial stems grow from lateral, layered stems and can be over 4 meters in height. Reproduction is primarily vegetative, by layering.

Devil's club is considered a riparian associate and its presence is often used as an indicator of moist soil conditions (Hemstrom and Logan 1986, Hemstrom and Logan 1987, Franklin and Dyrness 1973, Hemstrom et al. 1982). In *Tsuga heterophylla* and *Picea sitchensis* plant associations in the Tongass National Forest of Alaska, subsurface flooding is common in many sites that contain Devil's club (Martin et al. 1995, Shephard 1995). In western Oregon, Devil's club is generally described as being confined to seeps and draws on north, shady aspects, or perched in a thin band along stream banks (Franklin and Dyrness 1973, Moore 1993). Pabst and Spies (1998) describe Devil's club in coastal Oregon as occupying moist though not saturated sites on stream terraces, transition slopes, and narrow draws.

The ecology of associated plants, particularly shrubs, can offer insights into the ecology of Devil's club (Grime 1989). Common shrub associates in western Oregon include salmonberry (*Rubus spectabilis*), huckleberry (*Vaccinium sp.*), vine maple (*Acer circinatum*), and stink currant (*Ribes bracteosum*) (Franklin and Dyrness 1973, Pabst and Spies 1998). Many of these shrubs are shade-tolerant, but

prolonged exposure to extremely low-light environments often reduces their populations, eventually causing many to disappear from a site (O'Dea et al. 1995, Ruth 1970, Tappeiner et al. 1991, Alaback and Herman 1988, Barber 1976). Stem elongation and cover of the shrubs typically increases with light, though in fully exposed environments, stem elongation generally decreases (Ruth 1970, Tappeiner et al. 1991, Minore et al. 1979).

Understory plants must be able to adapt to a wide range of environmental conditions to persist in a site. Shrubs in the Pacific Northwest are typically abundant in forest openings and gaps created by wind and fire disturbances (Tappeiner et al. 1986; Tappeiner et al. 1991, Fried et al. 1988; Alaback and Tappeiner 1991; Tappeiner and Zasada 1993, Ruth 1970, Stewart 1986). Tappeiner et al. (1991) suggest that salmonberry, vine maple and beaked hazel (*Corylus cornuta*) and other woody, clonal plants can persist in forest understories in low densities until the environment becomes more light favorable. When the overstory is removed or otherwise greatly reduced, these shrub species may quickly grow until they dominate the plant community (Tappeiner et al. 1991, Ruth 1970). In Alaska, salmonberry typically increases its cover in relation to Devil's club after clear-cuts in plant communities that include both plants (Martin et al. 1995, Shepard 1995). Layered stems of trampled vine maple sprout vigorously after stands in western Oregon have been clear-cut (O'Dea et al. 1995). Even after the forest canopy closes, vine maple persists, to eventually thrive again when the aging stand begins to self-thin (O'Dea et al. 1995, Zasada et al. 1991).

This pattern is also illustrated with striped maple (*Acer pensylvanicum* L.), an understory tree in the eastern United States. Small, suppressed seedlings of striped maple can persist for decades in the herbaceous layer until a disturbance opens the canopy, releasing it into a reproductive stage (Wilson and Fischer 1977, Hibbs et al. 1980). Gaps in the overstory need not be large to initiate release of the plant. Wilson and Fischer (1977) estimated solar irradiance need only increase to about 12% to 18% full sunlight, though optimal light levels for stem elongation was found to be between 32% to 62% of full solar radiation. Light levels above 62%

full solar radiation suppressed striped maple stem growth (Wilson and Fischer 1977).

OBJECTIVES

The objective of this study was to more fully describe and explain Devil's club environmental niche in mid-Oregon, the southern edge of its distribution. The inconsistent appearance of Devil's club in drainages and its patchy distribution suggests that within Oregon, the difference between suitable and unsuitable habitat is more pronounced than that observed at more northern latitudes where the distribution of Devil's club is more extensive and continuous (Moore 1993, Martin et al. 1995, Shepard 1995). Studying Devil's club and the microenvironment it occupies in Oregon can illustrate critical environmental conditions necessary for its survival, as well as help describe the limits of its ecological adaptability.

Specifically, the study was designed to answer the following questions:

1. What characterizes Devil's club habitat in western Oregon?
2. Which environmental variables significantly influence Devil's club growth patterns?
3. How do the ecological adaptations of Devil's club differ from the common associates salmonberry and vine maple?

METHODS

In the summer of 1997, five sites each in the Oregon Coast Range the Oregon Cascade Mountains were selected to cover a wide range of elevations (Table 2.1). At these primary study locations, the micro-environmental, growth and cover patterns of Devil's club, and the growth and cover patterns of salmonberry and vine maple were measured. Seven other secondary locations, all in the Coast Range, were selected for stem growth measurements (Table 2.1). Two sites in the Coast Range were selected for leaf morphology measurements (Table 2.1). Devil's club populations were located by exploration, word of mouth from

area botanists and foresters, as well as by referencing plant survey data sheets maintained by the Siuslaw National Forest.

Devil's club populations are distributed on the landscape frequently as patches. A Devil's club 'patch' was defined as a discrete collection of Devil's club stems that dominated the plant community in which it grew. At each of the ten primary sites, three patches of Devil's club were sub-sampled to measure Devil's club and its microenvironment in as wide a range of habitat conditions as possible. At one site, Wiley Creek in the Cascade Mountains, one of the selected patches was discarded from the data set because of the influence of a road directly above it. A collection of Devil's club stems was considered discrete when it was visually distinguishable from an adjoining plant community, at least 4 meters from another discrete collection of Devil's club stems. Generally Devil's club patches were widely separated within a site, though at some locations, particularly along stream banks and draws, Devil's club stems were not always distributed into neat, easily defined patches.

At the seven secondary sites, only one patch per site was selected and measured, except the Prairie Mtn. site where two adjacent patches were measured.

Two transects were installed on each patch (Figure 2.1). One transect ran perpendicular to the main slope of the patch, dividing the patch approximately in half. The other transect was fitted at a right angle to the first transect, again dividing the patch in half. The intersection of the two transects was designated patch center.

Sample points were placed along these transects (Figure 2.1). Five within-patch sampling points were designated, one directly at patch center and the other four along the four transects radiating from patch center, one meter within the patch edge. Four perimeter-patch sample points were designated along the same transects, but located two meters beyond the patch edge, for a total of nine sample points per patch.

At each of the seven secondary sites, a 20.9 m² square plot was located in the middle of a patch. Within this plot, a stem was randomly selected for measuring.

TABLE 2.1 Locations of primary, secondary and leaf morphology study sites.

Coast Range	Latitude // Longitude	Cascade Mts.	Latitude // Longitude
<u>Primary Sites</u>			
Beaver Creek	44° 26' N // 123° 25' W	Scott Creek	44° 32' N // 122° 37' W
Congdon Cr. 1	44° 10' N // 123° 33' W	Browder Ridge	44° 23' N // 123° 12' W
Congdon Cr. 2	44° 10' N // 123° 33' W	Canyon Creek	44° 20' N // 122° 21' W
Deer Creek	45° 3' N // 123° 55' W	Iron Mtn	44° 24' N // 122° 10' W
Square Creek	45° 19' N // 123° 38' W	Wiley Creek	44° 20' N // 122° 34' W
<u>Secondary Sites</u>			
Beaver Cr. 4	44° 26' N // 123° 25' W		
Bummer Creek	44° 18' N // 123° 35' W		
Nestucca R.	45° 18' N // 123° 40' W		
Nettle Creek	44° 29' N // 123° 46' W		
Oliver Creek	44° 20' N // 123° 22' W		
Prairie Mtn. 1	44° 16' N // 123° 35' W		
Prairie Mtn. 2	44° 16' N // 123° 35' W		
Rock Creek	44° 19' N // 123° 33' W		
Tobe Creek	44° 19' N // 123° 34' W		
<u>Leaf morphology Sites</u>			
Beaver Cr. 5	44° 26' N // 123° 25' W		
Yew Creek	44° 27' N // 123° 32' W		

Habitat variables

Habitat characteristics were measured on patch and point scales, and included: elevation, overstory age, plant community, aspect, canopy cover, soil moisture, slope, and duff thickness. Only elevation, slope and aspect were measured at the seven secondary sites.

Elevation of sites was estimated from 1:100,000 meter US Geological Survey topographic maps and USDA Forest Service Ranger District maps.

Stand ages were calculated by extracting core samples from trees bordering study patches and counting growth rings. If there was more than one age class,

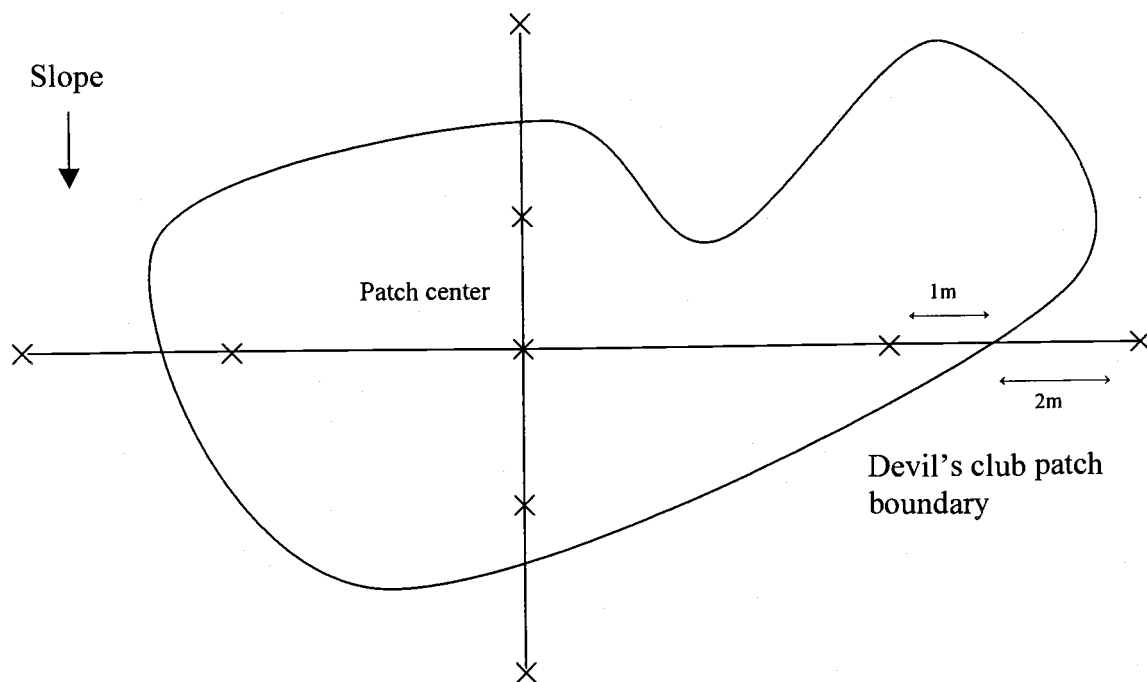


FIGURE 2.1 Plot design example at primary study sites. Sample points are marked with an X.

multiple trees were sampled and the oldest was selected to estimate age. In clear-cuts, branch whorls on saplings were counted to estimate stand age.

The overall cover of individual tree, shrub and herbaceous species within patches and in the perimeter of patches were visually estimated. Overall cover of broadleaf trees, conifer trees, shrubs and herbs in a stand were calculated by totaling the cover values of species within each group, within and in the perimeter of patches. Overstory tree data from Iron Mountain was discarded because visual estimates of the cover were considered potentially inaccurate; the trees in this higher elevation site were stunted and their distribution clumpy. Overstory tree data from one patch at the Congdon Creek 2 site was also discarded because the patch straddled two distinct stands, an older conifer-dominated stand, and a younger alder (*Alnus rubra*)/salmonberry-dominated stand.

Patch aspects were measured in the field with a compass. At a larger scale, drainages in which sites were located were estimated with 1:100,000 meter US Geological Survey maps. Aspect values were transformed from the circular degree scale of the compass to a linear scale. The transformation is based on Beers et al. (1966) as follows: $A' = \cos(A_{\max} - A) + 1$, where A_{\max} is a reference aspect and A is the measured aspect. Transformed values increased the closer the measured aspects came to the reference aspect of 45° , to a maximum of 2, so that all transformed values ranged from 0 to 2 according to how close they were to 45° . To maintain statistical balance when comparing patch aspects to drainage aspects, the transformed values of all aspects in a site were averaged to one value per site.

The primary slope of the patch was measured with a clinometer and read on a percentage basis.

An LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, Nebr.) was used to estimate canopy openness through measurements of relative diffuse non-interceptance (Welles and Norman 1991). Two light sensors filtered to measure wavelengths of diffused light were used in which one provided a reference, open canopy light measurement and the other a measurement at the sample point. When a sample point occurred at a Devil's club stem, the light sensor was placed directly above the crown of the plant. The view angle used was 148° from five zenith angles radiating in concentric bands from the light sensor lens, ranging from 0° (directly above) to 74° (16° above the horizontal plane). Diffuse non-interceptance (DIFN) was calculated from the ratio of paired light readings. DIFN is a relative measure of intercepted light through the canopy that can index canopy cover ranging from 0 (completely closed canopy) to 1 (completely open sky) (Welles 1990). A potential source of error with this procedure is the presence of reflected light in an understory, which can skew estimates of DIFN. To avoid this problem, measurements were taken only near sunrise (before 7:00 am) or near sunset (after 6:30 pm) in July, August and early September.

Soil moisture was calculated on a percentage basis using gravimetric analysis. Soil samples were collected during the later half of July and through August, when

soil conditions should be most dry, and brought into the lab. At each sample point in a plot, three separate 30 ml mineral soil samples from the A soil horizon were collected and combined, for a total of approximately 90 ml soil per sample point. Samples were weighed, dried for 24 hours at 38°C and then weighed again. Moisture content was determined on a dry weight basis (wet weight of the soil sample minus the dry weight, then divided by the dry weight). Duff thickness was measured to the nearest 0.1 cm with a metric ruler at each sample point.

In the beginning of the data collection, soil moisture content was measured with a Type ML1 theta probe (Delta-T Devices, Cambridge, England), but the instrument gave inconsistent results. As a result, soil moisture measurements at the Iron Mountain site, and two patches from both the Beaver Creek and Congdon Creek sites were discarded. Additionally, for a single patch at the Berlin Creek site, over half the material in the gravimetric samples was organic, skewing soil moisture estimates, and was not included in the analysis. Not all sites were sampled because soil collection ceased when fall rains arrived.

Growth patterns

Devil's club growth patterns were estimated for patches and individual plants. Current year's stem elongation, percent cover and patch sizes were measured. Also measured were current year's stem elongation and percent cover of salmonberry and vine maple. At the seven secondary sites, only current year's stem elongation was measured.

The nearest, dominant Devil's club stem to each within-patch sample point was selected and current year's elongation of the stem was measured to the nearest 0.1 cm. For salmonberry and vine maple, current year's elongation of the stem within-patches and in the perimeter of patches was measured when a stem was within a meter's distance of a sample point. As a result not every patch that contained salmonberry or vine maple had their stem elongation lengths measured.

At the seven secondary sites, current year's stem elongation was measured on all apical stems that were part of that stem complex, to the nearest 0.1 cm. (see Appendix C for field sketches and notes on these stems).

In the calculation of patch area, patches were assumed to have generally an elliptical shape. Their sizes were estimated by using the plot transect lengths in the formula, $\text{area} = \text{Pi} * (\text{length} * \text{width}) / 4$. A simple model to predict potential patch expansion over time, based on the mean stem elongation rate, was developed by using the above formula. Patch expansion was assumed to radiate outward from a central point in an elliptical shape ($\text{length} = 2 * \text{width}$). The mean of the current year's stem elongation measurements was used as a constant in the formula: $\text{area} = -1 + \text{Pi} * ((2 * \text{age} * \text{mean elongation (m)}) * (\text{age} * \text{mean elongation (m)})) / 4$. Negative 1 was included in the formula to delay predicted patch expansion until stems reached the height of at least 1 meter.

Leaf morphology

The length leaf petioles, angle of petioles off the stem, degree of leaf curl, and leaf color were measured from a single patch at Beaver Creek in an exposed environment and from two patches (at Beaver Creek and Yew Creek) in an understory environment. Leaf areas were measured in the lab and specific leaf areas were calculated. To select samples for measurements, five stems were selected following the procedure illustrated in Figure 2.1. A single leaf from each stem was then randomly selected, for a total of five samples per patch. Both field and lab measurements were made on these selected samples. Measurements and calculations were averaged to a per patch basis. A protractor was used to measure the angle of petioles to the main stem, and the degree of leaf curl, basing estimates on the angle of the leaf blade off the parallel from the leaf axis. The greenness of leaves was estimated on a scale of 1 to 6 (1=yellow; 6=dark green) from a color wheel. Leaf areas were calculated by bringing leaves into the lab and running them through a LI 3100 Area Meter. The dry weights of the leaves were measured after

drying them in an oven for 48 hours at 21°C. To calculate specific leaf areas, the surface area of the leaves was divided by their dry weights.

Statistics

Three different statistical tests were conducted on the data: regression, paired t-tests and logistic.

Multiple linear regression was used to explore which environmental factors significantly ($p\text{-value} < 0.05$) predicted patch size, stem increment and cover values of Devil's club, salmonberry and vine maple. The natural log transformation was used to normalize stem increment data for Devil's club and salmonberry.

Data were analyzed on three scales, from largest to smallest. Analysis that included elevation and drainage aspect were done on a 'site' scale to investigate their influence on growth patterns (Table 2.2). Mean patch size, stem increment and cover values for each site was calculated and used in the analysis.

TABLE 2.2 Habitat variables by site, stand and patch levels.

Site-level	Stand-level	Patch-level
1. Elevation	1. Stand age and density	1. Diffuse radiation levels
2. Drainage aspect	2. Plant community:	• within patch
	• % cover of overstory	• perimeter of patch
	• broadleaf and conifer	2. % soil moisture
	• trees in stand, by	• within patch
	• species	• perimeter of patch
		3. Thickness of duff layer
		• Within patch
		• Perimeter of patch
		4. Plant community:
		• Cover of shrubs, within and in
		perimeter of patch, by species
		• Cover of herbs, within and in
		perimeter of patch, by species
		5. Patch aspect
		6. % slope

Analysis that included overstory tree characteristics was done on a 'stand' scale (Table 2.2). For sites with homogenous overstories, the mean cover were used across the site. For sites with heterogeneous overstories patches were treated as separate sample units (Table 2.3). For example, at the Scott Creek site, Devil's club was sampled in three distinct stands - an older riparian stand with strong conifer presence, a younger riparian stand dominated by broadleaf trees, and a young regenerating clear-cut (Table 2.3). Each patch was treated as a separate sample unit.

Environmental variables that could vary between patches within a site were analyzed on a 'patch' scale (Table 2.2), where patches within site were analyzed as separate sample units. The means of sample points within each patch were used. These variables included light, soil moisture, and duff thickness (Table 2.2). Measurements also included whole-patch variables such as understory plant species cover values, patch aspect, and slope. Mean patch size, stem increment and cover of Devil's club were reported on this scale. Perimeter-patch stem increment and cover values for salmonberry and vine maple were also included analysis.

In the regression analysis, the three levels were combined in the following way: Stem increment, cover and patch size values were first analyzed at the site-level. Environmental variable(s) that significantly explained the most amount of variation were selected for model building. Significant response values (p -value < 0.05) were then run through the 'site' model to remove variation associated with elevation or drainage aspect while generating new predicted stand level values. These predicted values were analyzed using only stand-level environmental variables (i.e. no elevation) while weighted with the inverse of the standard error to remove variance skew associated with non-linear confidence intervals. The process was repeated for the patch-level environmental variables. If a response variable was found not to have significant relationships with an environmental variable at one level, original data were analyzed at the next lower level. Within-patch and perimeter-patch salmonberry and vine maple stem increment values were combined in analysis at the site and stand levels, but analyzed separately at the

TABLE 2.3 Study sites with elevation, stand age, drainage aspects and patch-level aspects. Transformed aspect values are based on a scale of 0 to 2 according to how close they are to 45°.

Site	# of patches	Elev (m)	Stand age ¹	Drainage aspect (°)	Drain. aspect (trans.)	Mean patch aspect (trans.)	% conifer in-patch	% conifer perim.	% brdlf in-patch	% brdlf perim.
Coast Range										
Beaver Cr.	4	265		100	1.6	1.7				
Patches 1,2,3			55				12	49	10	42
Patch 4			b							
Bummer Cr.	1	325	a	345	1.5	1.7				
Congdon Cr. 1	3	335	102	125	1.2	1.7	33	63	31	35
Congdon Cr. 2	3	335	7	125	1.2	1.7	8	10	7	22
Nestucca River	1	230	b	225	0.0	1.1				
Nettle Creek	1	460	b	315	1.0	0.2				
Oliver Creek	1	160	b	140	0.9	1.9				
Deer Creek	3	175	100	200	0.1	0.4	27	55	23	24
Praire Mtn	2	700	a	355	1.6	1.8				
Rock Creek	1	245	c	127	1.1	0.3				
Square Top Mtn	3	560	120	340	1.4	1.4	50	57	3.3	0
Tobe Creek	1	280	b	315	1.7	0.3				
Cascade Mountain Range										
Scott Creek	3	365		270	0.3	1.1				
patch 1			85				50	45	30	80
patch 2			19				3	8	13	25
patch 3			22				3	6	0	0
Browder Ridge	3	130		119	1.3	1.1				
patches 1, 2		0	90				15	70	8	0
patch 3			120+				40	70	0	0
Canyon Creek	3	590		340	1.4	1.8				
patch 1			35				0	12	95	95
patch 2, 3			35				18	75	0	0
Iron Mtn	3	134	23	135	1.0	1.9				
		5								
Wiley Creek	2	330	22	310	0.9	1.9	20	38	75	78

¹Stand ages in these patches were not measured except for visual estimates whether the stands were a) young, b) mature or c) old-growth

patch level. Only within-patch cover values for salmonberry and vine maple were used in regression analysis.

Paired t-tests were used to determine significant differences ($p\text{-value} < 0.05$) between environmental variables within a patch and in the perimeter of a patch.

Logistic regression was used to determine whether there was significant difference in the frequency of individual species within and in the perimeter of patches at the primary study sites.

Stem increment, cover and patch size values were plotted against environmental values to explore threshold relationships.

RESULTS AND DISCUSSION

Habitat

Devil's club consistently grew in canopy gaps (Table 2.4, Figure 2.2). The mean cover of overstory trees within-patches was 44% (SD 31.6%), ranging from 3% to 95%, while the mean cover of trees in the perimeter of patches was 73.8% (SD 35%), ranging from 6% to 125%. Paired t-test comparison showed significant difference ($n=13$) between overstory values within and in the perimeter of patches. The mean cover of conifer trees within-patches was 21.3%, (SD 17.3, $n=13$), ranging from 0% to 50%, and the mean cover in the perimeter of patches was 42.9 (SD 25.7, $n=13$), ranging from 6% to 75%. Data were not normally distributed enough to enable paired t-test comparison. The mean cover of broadleaf trees within-patches was 22.7% (SD 29.9%, $n=13$), ranging from 0% to 95%, and the mean cover in the perimeter of patches was 30.8% (SD 33.9, $n=13$), ranging from 0% to 95%. Data were not normally distributed enough to enable paired t-test comparison. The relatively high percentage of broadleaf to conifer tree cover highlights the tendency of Devil's club to grow in riparian areas, where broadleaf trees tend to be more common than in upslope areas (Nierenberg and Hibbs In press, Pabst and Spies In press).

The mean cover of all shrubs within patches (including Devil's club) was 105% (SD 31.7%) ranging from 53% to 163% while the mean cover of all shrubs in the perimeter of patches was 54.8%, (SD 36.5%, $n=29$) ranging from 5% to 135%

(Table 2.4). Paired t-test showed a significant difference between shrub cover within patches and in the perimeter of patches ($n=29$). Salmonberry was the most common shrub species, occurring in 76% of the studied patches.

The mean cover of all herbs within patches of Devil's club was 60% (SD 31.1%) ranging from 8% to 145%, while the mean cover of all herbs in the perimeter of patches was 69.3% (SD 29.7%), ranging from 19% to 134% (Table 2.4). There was no significant difference in cover of herbs within and in the perimeter of patches in a paired t-test comparison ($p\text{-value} = 0.1634$). Swordfern (*Polystichum munitum*) was the most common herb, occurring in 76% of the patches. There was a significant difference in the cover of swordfern within patches (18.9%) and in the perimeter of patches (24%) in a paired t-test ($n=29$), indicating that the presence of Devil's club may reduce the cover of swordfern, likely through shading. There were significant differences in the frequencies of lady fern (*Athyrium filix-femina*) and trillium (*Trillium ovatum*) within and in the perimeter of patches (20.7% vs. 44.8% for lady fern, and 6.7% vs. 24.1% for trillium).

For a complete list of plants, frequency and cover values see Appendix A.

There was a slight though biologically insignificant difference between DIFN (Diffuse Non-interceptance) measured within patches and in the perimeter of patches, suggesting similar understory diffuse light environments despite significant differences in overstory tree covers. Based on a sample size of 29, the within-patch DIFN mean was 0.19 (SD 0.2), ranging from .016 to 0.7. The perimeter-patch DIFN mean was 0.16 (SD 0.2), ranging from .02 to 0.69. Data were not normally distributed enough to enable paired t-test comparison.

Devil's club consistently grew in moist soil conditions (Figure 2.3). Based on a sample size of 18 across 8 sites, within-patch soil moisture levels averaged 56.8% (SD 11.9), ranging from 36.3% to 82.2%. The average perimeter-patch soil moisture level was 62.81% (SD 17.9), ranging from 23.7% to 100.6%. There was no significant difference between within-patch and perimeter-patch soil moisture levels ($p\text{-value} = 0.9132$ in a paired t-test), though there was a wider range of

100.6 % vs. 36.6% - 82.2%, Figure 2.3). The root system of Devil's club may help explain the association with high moisture. Qualitative observations of layered Devil's club stems suggests that rooting generally consists of long, thin roots that occur irregularly along the stems, often at rings of bud scale scars. To provide sufficient water to maintain transpiration for competitive growth in a shrub with

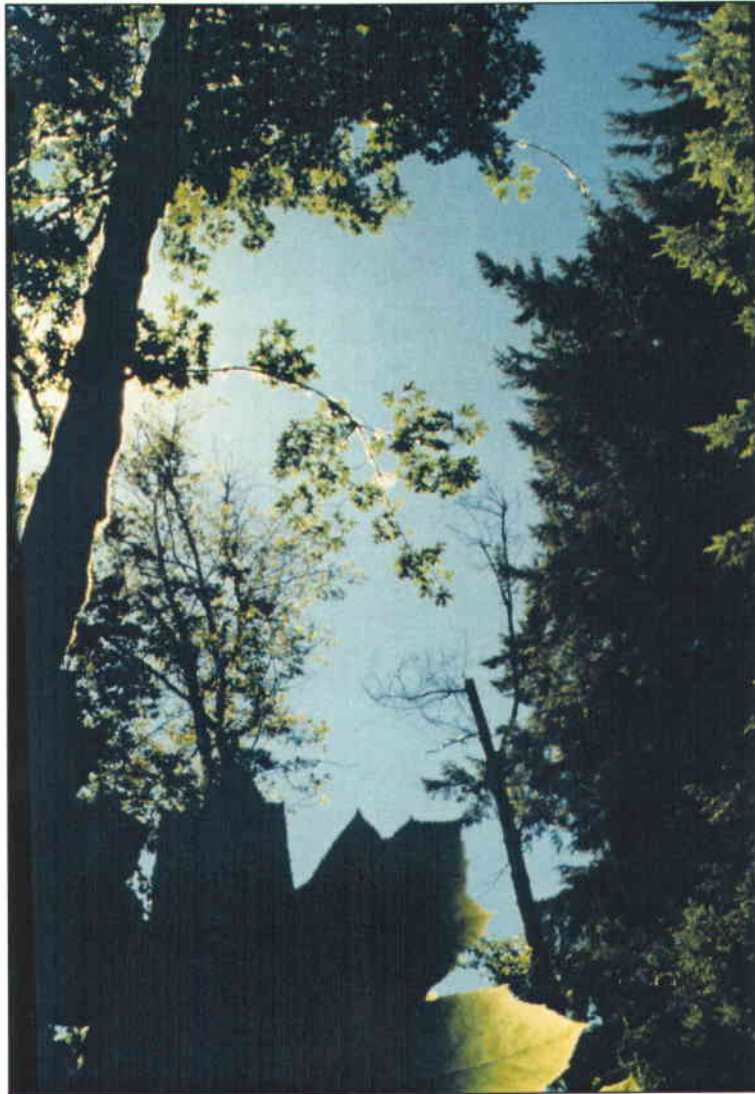


FIGURE 2.2 Gap above Devil's club patch. Devil's club leaf is in lower foreground.

TABLE 2.4 Summary of common plant species associated with Devil's club in western Oregon.¹

	Perimeter-of-patch		Within-patch	
	frequency	cover	frequency	cover
Tree				
Western Hemlock (<i>Tsuga heterophylla</i>)	100%	28.6%	92.3%	14.3%
Red alder (<i>Alnus rubra</i>)	53.8%	22.1%	61.5%	14.7%
Douglas fir (<i>Pseudotsuga menziesii</i>)	61.5%	8.2%	53.8%	3.9%
Big leaf maple (<i>Acer macrophyllum</i>)	46.2%	8.7%	46.2%	7.3%
All trees*	--	73.8%	--	44%
Shrub				
Devil's club (<i>Oplopanax horridum</i>)	--	--	100%	63.3%
Salmonberry (<i>Rubus spectabilis</i>)	72.4%	15.4%	75.9%	14.1%
Huckleberry (<i>Vaccinium sp.</i>)	51.7%	5.9%	62.1%	4.6%
Vine maple (<i>Acer circinatum</i>)	62.1%	19.4%	51.7%	13.9%
Stink currant (<i>Ribes bracteosum</i>)	27.6%	2.1%	20.7%	1.0%
All shrubs*	--	54.8%	--	105%
Herb				
Swordfern (<i>Polystichum munitum</i>)*	79.3%	24%	75.9%	18.9%
Oxalis (<i>Oxalis Oregensis</i>)	65.5%	21.7%	69%	18.2%
Galium (<i>Galium triflorum</i>)	24.1%	0.7%	41.4%	1.1%
Deer fern (<i>Blechnum spicant</i>)	41.4%	1.9%	35.5%	2.6%
Tolmiea (<i>Tolmiea menziesii</i>)	20.7%	1.9%	27.6%	2.0%
Lady fern (<i>Athyrium filix-femina</i>)+	44.8%	2.6%	20.7%	2.2%
Wild ginger (<i>Asarum caudatum</i>)	17.2%	0.8%	17.2%	0.7%
False Solomon's seal (<i>Smilacina racemosa</i>)	6.9%	0.3%	10.3%	0.4%
Trillium (<i>Trillium ovatum</i>)+	24.1%	0.5%	6.7%	0.1%
All herbs	--	69.3%	--	60%

¹Tree overstory values are based on n=13; shrub and herb cover values based on n=29. * indicates significant difference in cover within and in the perimeter of patches, + indicates significant difference in frequency within and in the perimeter of patches.

high leaf surface area, occupation by roots of soils high in moisture may be necessary in areas with a droughty growing season.

Generally, Devil's club grew on moderately steep slopes; the average across all sites was 34.5% (SD 20.3%, n = 38), ranging from 20% to 72%.

At the scale of watersheds, Devil's club was found on all aspects (Figure 2.4), with an average transformed value of 1.1 (SD 0.5, n = 17), ranging from 0 to 1.7.

At the patch-scale, distribution was slightly skewed to northern aspects with an

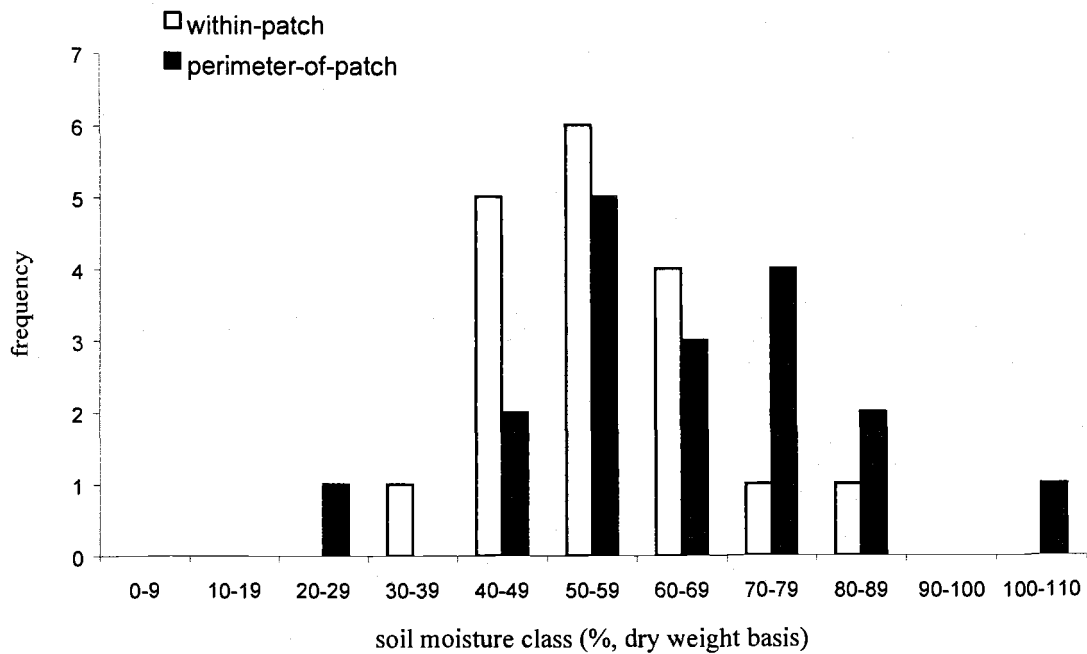


FIGURE 2.3 Comparison between within-patch and perimeter of patch soil moisture levels. Devil's club was consistently found in moist soils.

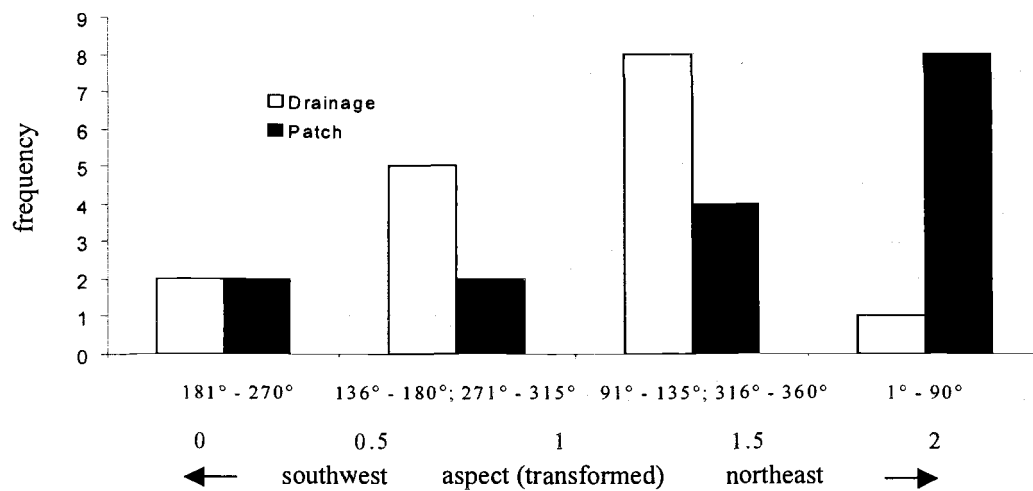


FIGURE 2.4 Frequency of Devil's club according to the aspects of drainages, and the distribution of patch aspects within drainages. Within drainages, Devil's club tended to grow on northeast aspects.

average transformed value of 1.3 (SD 0.7, $n = 17$), ranging from 0.2 to 1.9 (Figure 2.4). There was no significant difference between the two (p -value = 0.308 in a paired t -test).

A significant difference was detected between the duff thickness within patches and the thickness of the duff in the perimeter around patches (p -value = 0.026 in a paired t -test). The average thickness was 2.4 cm (SD 1.5, $n = 29$) within patches, and 2.9 cm (SD 1.6, $n = 29$) in the perimeter of patches.

Stem increment

The mean stem increment rate for Devil's club for the current year was 17.8 cm. (SD 6.3 cm; $n = 38$), ranging from 6.2 cm. to 36.4 cm. The mean stem increment rate for salmonberry for the current year was 78.8 cm. (SD 33.7 cm; $n = 40$), ranging from 18 cm. to 149 cm. The mean stem increment rate for vine maple for the current was 15.78 cm. (SD 17.8 cm; $n = 19$), ranging from 0.5 cm. to 78 cm.

Longest Devil's club stem elongation (36.4 cm) occurred under low light conditions (DIFN, 0.043) (Figure 2.5). Much of the variation observed in elongation rates occurred at light levels less than 0.1 DIFN as well.

Stem increment for salmonberry reached its maximum at a higher DIFN level than Devil's club, and maintained elevated stem elongation rates over a wider range as well (Figure 2.5). Stem increment of salmonberry was greater than 140 cm (140.75 cm. to 149 cm) in four patches where levels of DIFN ranged from 0.07 to 0.24 (Figure 2.5). The longest vine maple stem increment (78 cm) occurred at the much higher DIFN level of 0.56 (Figure 2.5).

At the site level, elevation provided the only significant prediction of current year's stem increment for Devil's club (Figure 2.6). The regression model (back-transformed) predicts median stem increment decreases about 5% for every 100 meter increase in elevation (Figure 2.6): $\ln(\text{increment}) = 3 - 0.009 * (\text{elevation})$, 95% CI = -0.0009 to -0.00019; p -value = 0.005, $r^2 = .44$, $n = 16$. The negative relationship between stem increment and elevation may be a response to a shorter growing season, though could also be a selective response to a harsher, windier

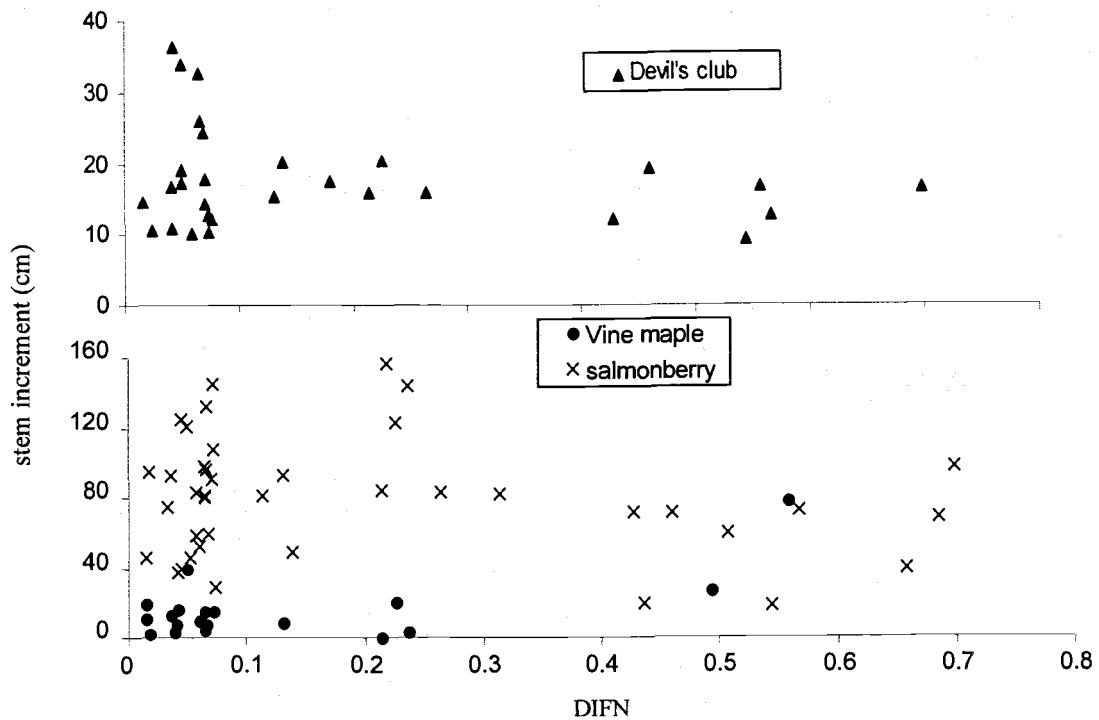


FIGURE 2.5 Devil's club, vine maple and salmonberry stem increment by DIFN. Devil's club and salmonberry increment values were highest at lower DIFN, where variation was also greatest.

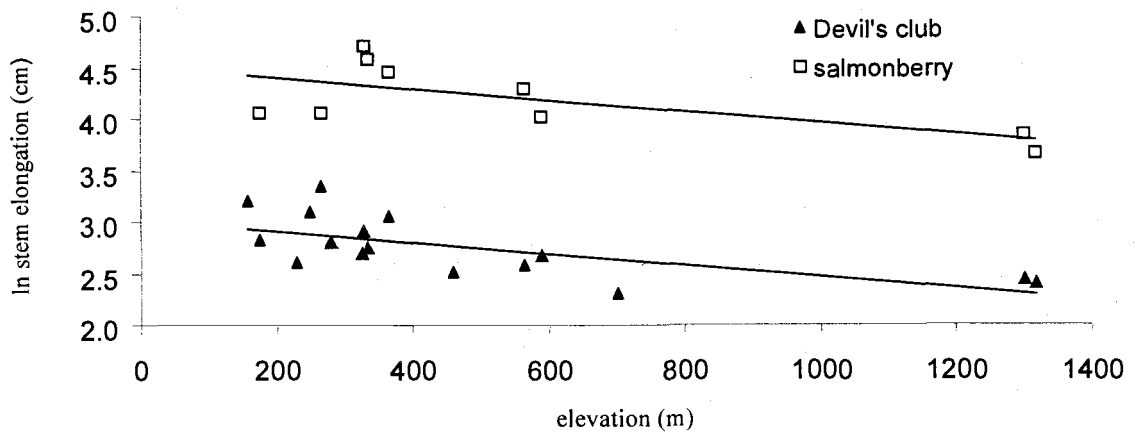


FIGURE 2.6 Site-level comparison between Devil's club and salmonberry current year's stem increment with elevation. Elevation had the strongest correlation with stem increment rates for both species.

climate (Woodward 1986).

After removing variation associated with elevation at the patch-level, the most significant predictor of stem increment was cover of shrubs within patches, not including Devil's club (Figure 2.7). The regression model predicts: $\ln(\text{stem increment}) = 0.881 + 0.522 * (\text{shrub cover})$, 95% CI = 0.08 to 0.96; p-value = 0.0226, $r^2 = .18$, $n = 29$.

The relationship between salmonberry stem increment and elevation is similar to the relationship between Devil's club and elevation (Figure 2.6). Regression analysis (back-transformed) predicts the median stem increment decreases about 5% for every 100 meter increase in elevation: $\ln(\text{growth}) = 4.5 - 0.00049 * \text{elevation}$, 95% CI = -0.0009 to -0.00012; $r^2 = .47$; $n = 9$; p-value = 0.0179, (Figure 2.6).

No environmental variables predicted salmonberry stem increment rates at the patch level, or vine maple stem growth at any level.

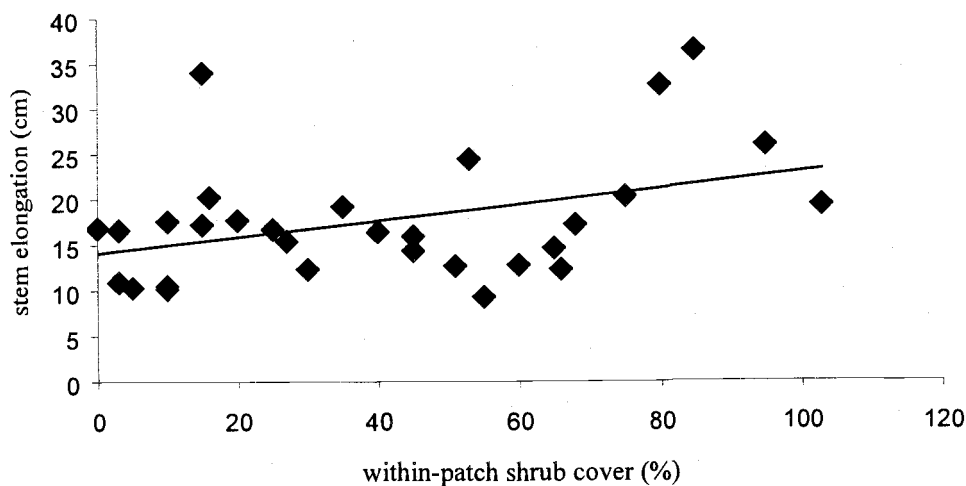


FIGURE 2.7 Stem increment of Devil's club plotted against shrub cover (not including Devil's club). Stem increment values are original, not predicted from elevation model.

Percent cover

Devil's club mean cover was 63.3 percent (SD 14.4, $n = 29$), ranging from 35% to 95% (Appendix A). Salmonberry grew in 22 of 29 Devil's club patches, with mean cover 14.1% (SD 17.4%, $n=29$), ranging from 0% to 60%. Salmonberry was observed growing in the perimeters of 21 of the 29 patches, with mean cover 15.4% (SD 19.1, $n = 29$), ranging from 0% to 70%. There was no significant difference between the mean percent cover within the patches and in the perimeter of patches (p -value = 0.104 in a paired t -test). Vine maple grew in 15 of 29 patches, with mean cover 13.9% (SD 20.8%, $n = 29$), ranging from 0% to 75%. Vine maple was observed in the perimeter of 18 of 29 patches, and averaged 19.1% cover (SD 24.9%, $n = 29$), ranging from 0% to 85%. Vine maple cover data were not normally distributed enough to enable paired t -test.

A DIFN less than 0.1 was calculated at most Devil's club patches (17 of 29 patches, or 59%) (Figure 2.8). Cover of Devil's club had maximum values and maximum variation at DIFN less than 0.1 (Figure 2.9) as well. Maximum cover

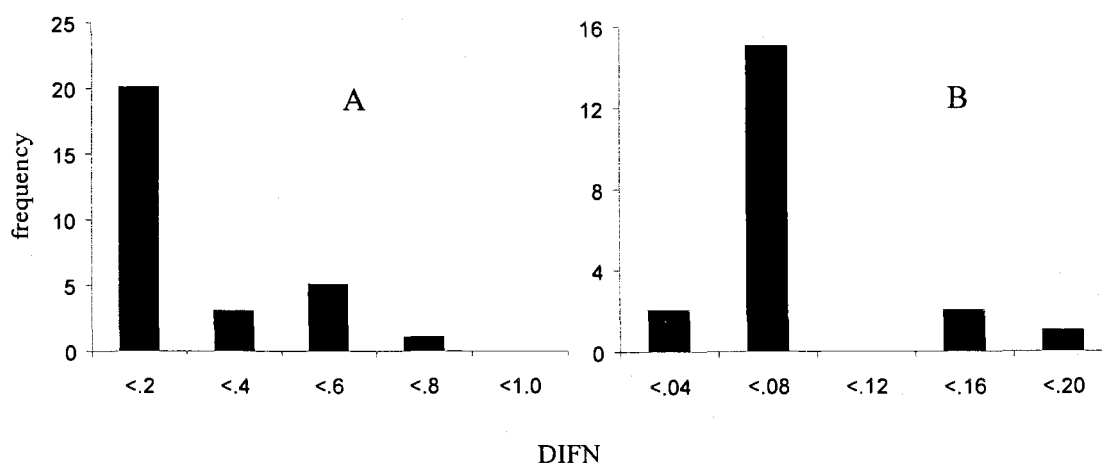


FIGURE 2.8 Distribution of Devil's club according to light classes, across the full range of DIFN (A), and between 0 to 0.2 DIFN (B). Fifty-nine percent (17/29) of Devil's club patches grew in light conditions below 0.1 DIFN.

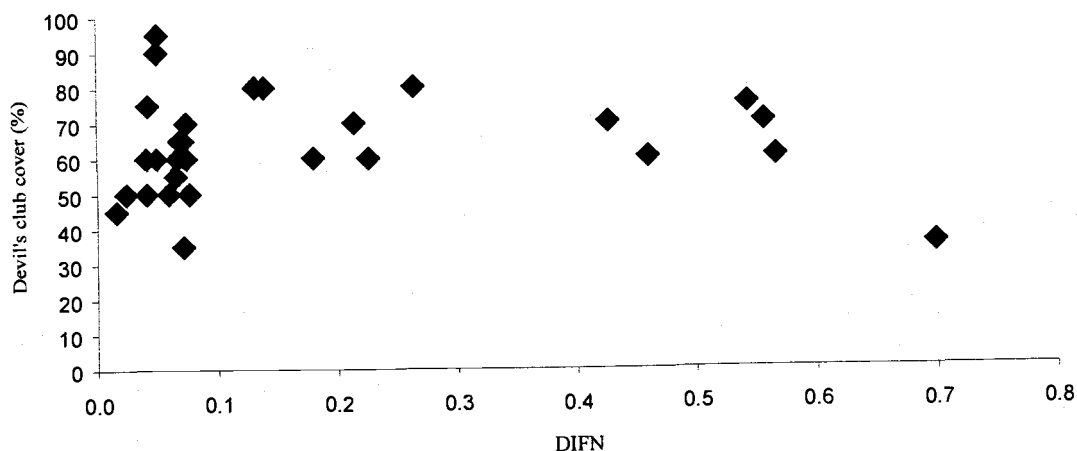


FIGURE 2.9 Cover of Devil's club related to DIFN levels. Variation was greatest in low-light environments, and maximum potential cover appeared to decline slightly with increasing DIFN.

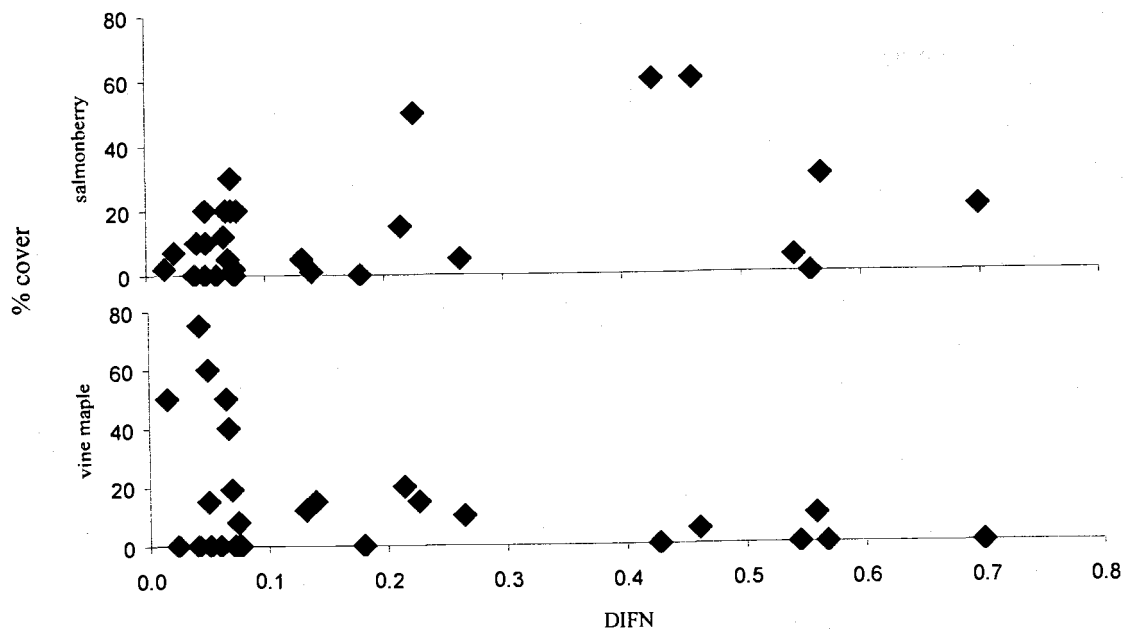


FIGURE 2.10 Salmonberry and vine maple cover related to DIFN. The graph suggests that while salmonberry has the potential to be more dominant in exposed environments, vine maple has the potential to more dominant in shadier environments.

(95%) was measured at 0.05 DIFN. At DIFN greater than or equal 0.15, cover ranged between 60% and 80%. Qualitative observations of Devil's club in exposed environments suggest it tends to grow along the shady side or underneath small trees or taller shrubs. Devil's club was observed growing in several clear-cuts, where DIFN values were as high as 0.7, suggesting that though understories are the usual habitat for Devil's club in western Oregon, the plant can persist, at least for a limited time, in exposed environments.

DIFN and Devil's club cover were not significantly correlated (p - value = 0.51). No other environmental variables significantly predicted Devil's club cover. The results did not reveal threshold relationships between cover and any environmental variable. The lack of a relationship may be a product of the study design. By measuring only populations of Devil's club where it was dominant, the range of potential cover values was too narrow to reveal any meaningful shift with changing environment.

Maximum potential cover values for salmonberry increased with increasing DIFN, reaching a maximum about 60% cover between .495 and .431 DIFN, and apparently dropping off after .5 DIFN (Figure 2.10). No environmental variable significantly predicted salmonberry or vine maple cover.

The relationship between vine maple cover and DIFN shows a threshold pattern, with the cover of vine maple limited at .1 DIFN (Figure 2.10).

Salmonberry and vine maple cover showed threshold patterns with aspect (Figure 2.11); when growing within patches of Devil's club, maximum potential cover of both plants were limited by southwest aspects. This relationship suggests that in plant communities where Devil's club is the dominant shrub, salmonberry and vine maple can best compete in sites most conducive to shrub growth in general, on north-east facing aspects.

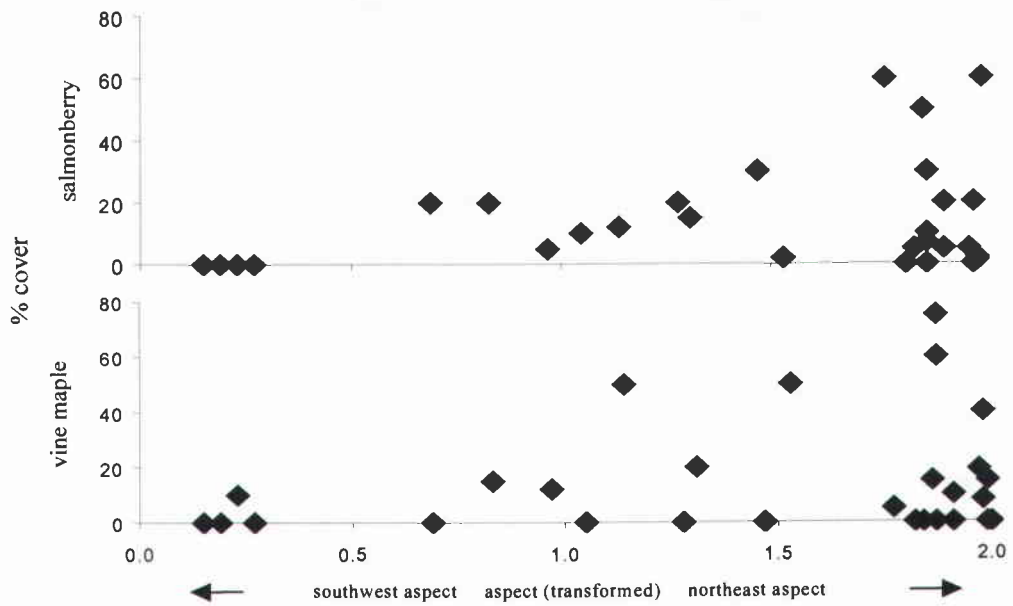


FIGURE 2.11 Cover relationships of salmonberry and vine maple with aspect. The ability of these two shrubs to compete with Devil's club appears to be limited by exposure to southwest aspects.



FIGURE 2.12 Sunfleck striking crown of Devil's club.

Leaf morphology

In the primary study sites, the largest leaves at their widest span averaged 41.1 cm (SD 6.2), ranging from 32 cm to 49 cm. Stem crowns typically contained 9 alternate leaves, arranged in understory environments in a mono-layer display. Crown widths averaged 109.5 cm (SD 23.1), ranging from 68.6 cm to 137.2 cm. Qualitative observations of stem crowns in understories suggest that leaves and stems lean towards angle of direct sunlight (Figure 2.13), displaying flat, monolayered surfaces. Often whole stems in understories grew in sweeping, arcing forms as well (Figure 2.14), suggesting that stem form follows the leaf crowns towards the source of greatest light. Many stems grew vertically as well (Figure 1.1). In exposed sites, qualitative observations suggest stems tend to remain vertical with little noticeable arc or lean.

Devil's club leaves displayed high plasticity in their form (Figure 2.15). Understory leaves exhibited commonly described characteristics of shade adaptation (Levitt 1980, Dale and Causton 1992, Young and Smith 1980, Givnish and Vermeij 1976), i.e. large, orbicular, thin and with a dark green color and high specific leaf area (Table 2.5, Figure 2.15) (see Appendix B for color Xerox copies of sun and shade leaves).

Leaves in exposed environments were sharply angled, both by the petioles and by their cup-shape, towards the direction of the sun (Table 2.5), minimizing exposure to radiation. Exposed leaves had less than half the size and specific area, and were much lighter in color than leaves observed in the understories (Table 2.5, Appendix B). In a Spring clear-cut, sun leaves had replaced shade leaves by mid-summer on the remaining few Devil's club stems. The shade leaves had expired after exposure to full sunlight.

In qualitative observations, it appears Devil's club used its petioles not just to support and angle leaves, but to adjust leaf extension according to different light and levels of competition. In understory environments, Devil's club leaf petioles were consistently just long enough to fully unfurl and angle their large, flat leaves,



FIGURE 2.13 Example of Devil's club leaves angling towards the path of direct light.



FIGURE 2.14 Devil's club as a sprawling shrub. Devil's club stems can grow vertically or horizontally, as illustrated here. See also Figure C.8.

TABLE 2.5 Comparison of Devil's club leaf morphology under high and low light conditions. Devil's club leaf characteristics varied with changed light conditions (n=5).

Site	Light envir.	Angle of petiole to stem (°)	Petiole length (cm)	Angle of leaf curl (°)	Leaf color	dry leaf wt.(g)	Leaf area (cm ²)	Specific leaf area
Beaver Creek	Exposed	40.2	20.2	33.0	2.6	2.7	312.2	120.91
Beaver Creek	Understory	67.0	28.2	3.4	5.3	3.2	782.0	246.09
Yew Creek	Understory	52.8	34.7	5.2	4.1	2.9	730.2	257.67

maximizing light interception while minimizing mutual leaf shading (Figure 2.12). In exposed environments, petiole lengths were more variable. Leaf displays were not as mono-layered, with shorter petioles often associated with smaller leaves (Figure 2.15B). There were also examples of Devil's club producing long petioles to extend its leaves into higher light conditions from stems buried under woody debris or the shade of competing shrubs and herbs. This pattern suggests that in exposed, non-light limiting environments where stems remain overtopped by debris or competing plants, petioles can be an important, even primary mechanism for Devil's club to extend its leaves to capture light (Givnish and Vermeij 1976). In understory environments where stems are able to attain maximum elongation (Figure 2.5), stem elongation and shoot thrust (Campbell et al. 1992) may instead be the more important mechanism for Devil's club to overtop competing plants or wind-throw material to capture light. The main function of petioles in these conditions is to angle and spread out the leaves to maximize light interception.

Patch size

Patches averaged 65.9 m² (SD 45.3, n = 29), ranging from 3.9 m² to 188.5 m². In upslope and less frequently disturbed areas where coniferous trees were relatively more abundant than broadleaf, deciduous trees, qualitative observations suggest Devil's club populations tend to be more contiguous and larger. Nearer



FIGURE 2.15 Comparison of Devil's club leaves in an exposed light environment (A), and an understory light environment (B).

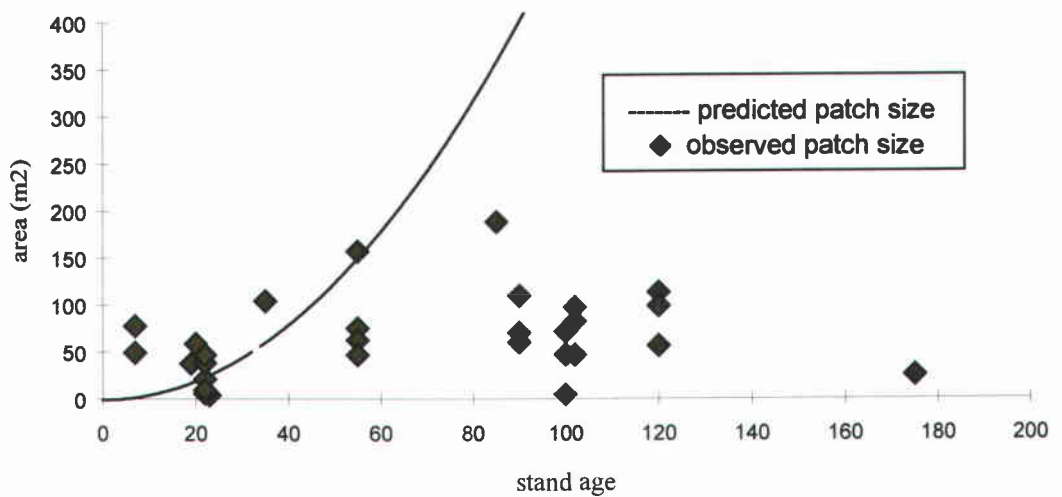


FIGURE 2.16 Model of Devil's club patch expansion based on mean stem increment rates. Actual patch size measurements reveal that stem increment rates are not a good predictor of patch expansion rates.

streams, the distribution of Devil's club appears more dispersed, with smaller patches intermixed in relatively more heterogeneous plant communities.

Figure 2.16 displays the results of the model predicting potential patch size over time based on mean annual stem increment (17.8 cm). Devil's club patch size did not correlate with stand age (p -value = 0.206, $n=13$). Observed patches tended to be larger than predicted in the first 30-40 years of a stand's growth, suggesting that patches typically initiate from more than one stem. After 30 to 40 years the model predicts patches could be larger than observed, suggesting that patch size is limited more by site conditions than by stem elongation rates. There were no correlations though between patch size and any measured environmental variable.

Summary

Moisture is the most consistent limiting environmental variable defining Devil's club habitat in western Oregon. Occupying high soil moisture sites (Figure 2.3) provides Devil's club (potentially) limited root system ready access to water. Pabst and Spies (1998) conclude that Devil's club occupies the base of destabilized, steep slopes near streams in part because of the accumulation of moisture in these sites during droughty summers. Soil moisture levels can also help explain the lower canopy cover directly above Devil's club patches. High moisture content (average 36%) and the generally steep slopes (average 38.6%) create unstable soil conditions susceptible to failure and tree fall. Martin et al. (1995) came to a similar conclusion about soil instability and susceptibility to windthrow from high moisture content within the *Tsuga heterophylla/Vaccinium sp.-Oplopanax horridum* Association in the Tongass National Forest.

Although DIFN levels did not distinguish difference in canopy cover within and in the perimeter of patches, overstory density and subsequent understory light conditions largely defines Devil's club competitive niche in western Oregon. Maximum stem growth (36.4 cm.) occurred at extremely low DIFN levels (.043), as did cover (95 % cover at .05 DIFN), suggesting that dominance by Devil's club of a plant community is favored in shadier environments. The positive relationship

of stem growth with overall shrub cover (Figure 2.7), along with the above patterns indicates that Devil's club is highly shade-adapted, that low-light environments are not injurious, and that low-light environments may actually be competitively advantageous. Indeed, the relationship of Devil's club to low-light environments almost suggests the plant is 'released' in these conditions, contrary to the typical tendency of understory shrubs and small trees to release with increasing light (Alaback and Tappeiner 1991, Fried et al. 1988, Hibbs et al. 1980, Ruth 1970, Stewart 1986, Tappeiner et al. 1986; Tappeiner et al. 1991, Tappeiner and Zasada 1993).

Results indicate that salmonberry and vine maple are more likely than Devil's club to dominate the plant community in higher light environments. Cover and stem growth of Devil's club peaked at a DIFN level just below those of salmonberry, and fell with increasing DIFN (Figures 2.5, 2.9 and 2.10). Salmonberry (and vine maple) stem elongation and cover values were greater at higher DIFN, and salmonberry maintained its cover over a greater range (Figures 2.10), suggesting that as in Alaska (Martin et al. 1995, Shephard 1995), salmonberry will dominate Devil's club in higher light environments.

Salmonberry and vine maple in western Oregon can grow vigorously in exposed conditions (Tappeiner et al. 1991, O'Dea et al 1995). Large disturbances that remove significant portions of an overstory can initiate aggressive growth of these shrubs (Tappeiner et al. 1991; O'Dea et al. 1995). Salmonberry is particularly competitive in exposed environments (Tappeiner et al. 1991, Ruth 1970), while in riparian areas, salmonberry cover under red alder can be so dense as to effectively exclude other species for an indefinite period of time (Carlton 1988). When in clear-cuts, vine maple can form large, thick mats of stems which persist only until a new overstory closes (O'Dea et al. 1995).

Much of the adaptability of these plants can be attributed to plasticity in their growth patterns. Tappeiner et al. (1991) found that the relative amount of salmonberry biomass allocated to rhizome production increased in open sites when compared to salmonberry in less open sites, enabling dominance of a site after a

disturbance with quick expansion of new shoots. With vine maple, dense thickets in exposed environments thin out in a closing stand to smaller numbers of longer stems, creating long bud banks for future layering (O'Dea et al. 1995).

Devil's club adaptations, while demonstrating similar plasticity, are qualitatively different. Its adaptations allow it to tolerate high-light environments, while maximizing growth and dominance in environments limited in light, such as forest understories. In many forest systems less than 2% of photosynthetically active radiation (PAR) present above a forest overstory penetrates to the understory (Chazdon 1988). Light that does penetrate is not uniform, its intensity and quality varies spatially and temporally according to elevation, aspect, slope, overstory density, absorptive capacity of overstory canopy layers, local weather patterns, season and time of day.

In general, plants under forest canopies intercept PAR as diffuse, scattered-radiation (low-intensity light reflected from the atmosphere and surrounding ground and plant surfaces), or as direct radiation (i.e. sunflecks). The amount of light provided by sunflecks is not insignificant; from 30% to 60% of the total carbon fixed daily in understories of tropical and temperate forests is contributed by sunflecks (Chazdon 1988). Canham et al. (1990) compared the light regimes in the understory of 5 forests types and found in Douglas-fir – Hemlock forests, sunflecks provided 47% (17% to 74%) of the available PAR, the lowest measured sunfleck percentage of the five forest types. Given the riparian quality of Devil's club habitat and the relatively high percentage of broadleaf trees in the overstory (Table 2.4), it would not be unreasonable to predict that in Devil's club growing sites in western Oregon, sunflecks account for a greater share than 47% of the total PAR (Canham et al. 1990).

Efficient capture and utilization of sunflecks can help explain Devil's club competitive success in low-light environments. Sunflecks' influence on Devil's club adaptations can be seen in its thin stems with long petioles and large leaves and the orientation of its stem and leaves towards direct light (figure 2.13) (Givnish and Vermeij 1976; Clearwater and Gould 1995). By contrast, in partially shaded

understories of New Zealand second-growth forests, little, narrow leaves of the juvenile *Pseudopanax crassifolius* are fixed, growing sharply angled downward along the sides of the plant's vertical stems (Clearwater and Gould 1995).

Clearwater and Gould (1995) conclude this morphology indicates *Pseudopanax crassifolius* adapts to low-light, understory environments by orienting its leaves to the strongest sources of diffuse light. If efficient utilization of diffuse radiation was the primary adaptation by Devil's club in western Oregon to understory light environments, similar leaf morphology might be expected. Instead, in conditions of low DIFN, increased stem elongation (Figure 2.5) places wide, mono-layered crowns above competing plants with leaves that turn towards the angle of direct light (Figure 2.13). Long petioles unfurl large, orbicular leaves unhindered, creating effective planes of leaves (Figure 2.12) that maximizes sunfleck capture (Givnish and Vermeij 1976).

Sunflecks may also help explain why patches in western Oregon do not expand to their full potential, as predicted by the mean growth rate in Figure 2.17. The angling of stems and crowns towards the direction of direct light indicates Devil's club actively forages for light. Canopy gaps were larger over patches of Devil's club (tree cover averaged 44% within patches and 73.8% in the perimeter of patches), which may increase the size, incidence and duration of sunflecks. In northern latitudes sunflecks tend to occur toward the center and northern portions of forest gaps (Chazdon 1988, Canham et al. 1990). In the perimeter of forest gaps, the incident or duration of sunflecks may lessen enough to effectively reduce Devil's club competitiveness so that stems avoid these spaces or expire when in them. There were at least two examples of recently expired leaf crowns located at patch edges (Figures C.1E, C.6B), even as interior crowns still flourished.

Conclusion

Devil's club has long been recognized as a riparian plant in western Oregon (Hichcock and Cronquist 1973, Franklin and Dyrness 1973), but it is now possible to more precisely compare its habitat niche with other western Oregon shrubs.

Devil's club occupies a relatively narrow, moist and shady niche. It is well adapted to shade - in moist, low-light environments it reaches the apex of its dominance (Figure 2.9). Salmonberry, vine maple, Oregon grape (*Berberis nervosa*), and salal (*Gaultheria shallon*) can all persist in a wide range of moisture and light environments, though their shade adaptations are not as strong as Devil's club. Instead they are more likely to be dominant in partial shade or exposed environments, such as clear-cuts (Tappeiner et al. 1991, Halpern and Franklin 1989, Huffman and Tappeiner 1997, O'Dea 1995). Salmonberry is one of Devil's club most common associates (Table 2.4), and is able to be dominant a wider range of environments, particularly when growing in association with red alder (Carlton 1988). In an appropriate site though Devil's club can be tenacious, able to out-compete even salmonberry. Upslope in dryer environments, Devil's club generally disappears while salmonberry becomes less dominant (Pabst and Spies In press). In these environments, salal and Oregon grape are more likely to dominate (Hemstrom and Logan 1986, Hemstrom and Logan 1987, Halpern and Franklin 1989).

Devil's club can persist in conditions of overstory removal, aided by the shade of residual trees and pioneering shrubs. Morphological plasticity contributes to Devil's club's persistence in these conditions until more favorable light environments develop. The capacity for clonal growth and reproduction, discussed in chapter 3, also helps Devil's club survive and grow in limiting environments.

CHAPTER 3

BRANCHING AND CLONAL GROWTH PATTERNS OF OPLOPANAX HORRIDUM (J.E. SMITH) MIQ. (DEVIL'S CLUB) IN WESTERN OREGON

Ashley H. Roorbach

INTRODUCTION

Most plants growing in aquatic environments and understories in temperate and boreal forests are able to form clones (Cook 1983). Heybroek (1984) and Pickett and Kempf (1980) conclude that clonal plants in general are better adapted than non-clonal plants to environments characterized by patchy resources. Pickett and Kempf (1980) view the capacity of shrubs to form clones as a significant adaptive distinction compared with most tree species. Advantages of clonal reproduction include:

1. More thorough dominance of favorable growing sites (Pickett and Kempf 1980). Seeds dispersed through sexual reproduction are more likely to travel away from favorable micro-environments, whereas ramets produced through asexual reproduction are likelier to spread and occupy nearby areas (Pickett and Kempf 1980). Hutchings and Bradbury (1986) hypothesized that smaller growth of stolons in areas with greater light allowed for more complete exploration and occupation of that environment, while longer growth in shadier sites increased the plants' chance of reaching a more light favorable environment. Hartnett and Bazzaz (1983) observed the same pattern with ramets of *Solidago canadensis*, which produced fewer though longer rhizomes in shaded environments.
2. Increased likelihood of survival from disturbance. Disturbance in understories, such as tree fall, floods, or landslides, tend to be intense but short in duration. Production of scattered ramets, particularly if the ramets become independent, lessen the risk of mortality to the whole plant (Cook 1983; Eriksson 1988). Clonal plants, supported by a network of connected genets and ramets are also able to grow back faster after such disturbances than non-clonal plants (Koop 1987; Stalter et al. 1997; Tappeiner et al. 1991, O'Dea et al. 1995; Hutchings

and Bradbury 1986; Hartnett and Bazazz 1983). Plants that rely primarily on sexual reproduction do not have as many stored resources to draw from when recovering from disturbance.

3. Better tolerance of limited or extreme environments (Koop 1987; Stalter et al. 1997). The interconnections and translocation of resources between genets and ramets effectively enlarge a clonal plant's resources capturing area, while limiting competition from other neighboring plants (Cook 1983). A plant is weakest and most vulnerable during its establishment and early growth phases. Newly established ramets can draw resources from mother genets to help insure early survival and growth (Hartnett and Bazazz 1983, Stalter et al. 1997). Populations of striped maple, which through most of its range in the northeastern United States reproduce sexually (Hibbs et al. 1980) was observed in the highlands of New York reproducing primarily through layering (Stalter et al. 1997). The authors hypothesized that the small gradually forming overstory gaps in these sites under which striped maple grow are not large enough for successful seed production and seedling establishment (Stalter et al. 1997). Another example is aspen (*Populus tremuloides*) in Colorado whose persistence may depend on clonal formation for reproduction, as the environment at present may be too harsh for seedling survival (Cheliak and Dancik 1982, Barnes 1975; referenced by Heybroek 1984).

Pacific Northwest forest shrub habitat

Forest openings and gaps created by wind, fire or other disturbances often contain dense populations of shrubs in the Pacific Northwest, (Tappeiner et al 1986; Tappeiner et al. 1991, Fried et al. 1988, Huffman et al. 1994, Huffman and Tappeiner 1997; Alaback and Tappeiner 1991; Tappeiner and Zasada 1993, Ruth 1970, Stewart 1986). Tappeiner et al. (1991) conclude that salmonberry (*Rubus spectabilis*) and other understory woody, vegetatively reproducing plants persist in

forest understories in low densities or as seed and bud banks until the environment becomes more light favorable. When the overstory is removed or greatly reduced, these shrub species quickly grow to dominate the plant community (Tappeiner et al. 1991, Ruth 1970, O'Dea et al. 1995).

Devil's club

Devil's club (*Oplopanax horridum* (J. E. Smith) Miq.) (Hitchcock and Cronquist 1973) is gaining attention as a potentially useful medicinal plant. Aboriginal uses of Devil's club are well-documented (Willard 1992, Gunther 1988, Turner 1982, Smith 1983), and research is being conducted to determine the plant's modern pharmaceutical uses (Kobaisy et al. 1997; McCutcheon et al. 1995), but it has attracted little ecological research. What is known about Devil's club in western Oregon remains mostly descriptive (Hitchcock and Cronquist 1973, Pojar et al. 1994, Moore 1993): A sprawling shrub with erect aerial stems, each fiercely armed with 5 – 10 mm long yellow spines. Stems are typically topped with single crowns of spreading leaves (Figure 1.1). Leaves are large (to 40 cm width) alternate and deciduous, maple leaf shaped and palmately veined with spines protruding from underneath (Appendix B). Aerial stems grow from lateral, layered stems and can be over 4 meters in height. Reproduction is primarily clonal by layering.

Devil's club is considered a riparian associate and its presence is often used as an indicator of moist soil conditions (Hemstrom and Logan 1986, Franklin and Dyrness 1973, Hemstrom et al. 1982). In Oregon, Devil's club is generally described as being confined to seeps and draws on north, shady aspects, or perched in a thin band along stream banks (Franklin and Dyrness 1973, Moore 1993). Pabst and Spies (1998) describe Devil's club in coastal Oregon as occupying moist though not saturated sites on stream terraces, transitions slopes, and narrow draws.

OBJECTIVES

The objective of this study was to characterize clonal stem growth and branching patterns of Devil's club in central Oregon Coast Range.

METHODS

In the summer of 1996, vegetative growth and reproduction patterns of Devil's club were measured in sites in and around the Siuslaw National Forest in the mid Oregon Coast Range. Devil's club populations were located by exploration, referral from area botanists and foresters, and by referencing plant survey data sheets maintained by the Siuslaw National Forest.

Aerial stem lopping experiment

The apical dominance and response to damage of Devil's club stems was tested by determining the budding potential of aerial stems at eight sites in the Oregon Coast Range. Treatment populations were selected roughly in an east-west transect across the Coast Range. At some locations, two separate and distinct sub-populations were treated (Table 3.1).

Five different treatments including a non-lopping control were applied to two sets of five stems at each site in the Spring of 1996 (Figure 3.1). At one site four sets of five treatments were applied. Treatments were based in part on the observation that bud swelling along the most recent year's stem growth section visibly diminished progressively down the stem, until towards the bottom of the annual increment it was non-existent, leaving only leaf scars.

TABLE 3.1 Study site locations for the aerial stem cutting experiment.

Population	Latitude // Longitude
Oliver Creek	44° 21' N // 123° 22' W
Beaver Creek 1	44° 26' N // 123° 25' W
Beaver Creek 2	44° 26' N // 123° 25' W
Yew Creek 1	44° 27' N // 123° 32' W
Yew Creek 2	44° 27' N // 123° 32' W
Boulder Creek (headwaters)	44° 27' N // 123° 50' W
Boulder Creek (confluence w/ Drift Cr.)	44° 29' N // 123° 52' W
Boulder Creek (up slope from confluence w/ Drift Creek)	44° 28' N // 123° 52' W

The mean response of each sub-population was calculated, for a total of eight replications. Treatments involved lopping the aerial stems at different locations relative to bud scale scar rings (Figure 3.1). From least to most removed, the treatments included 1) BS - lopping the current year's stem growth directly above the most recently formed ring of bud scale scars; 2) VB - lopping the aerial stem below the most recently formed ring of bud scale scars, above a visibly swollen bud in axil of leaf scar; 3) LS - lopping the stem below the most recently formed ring of bud scale scars, above a bud in axil of leaf scar that does not show any visible swelling; 4) PY - lopping the stem below the most recently formed ring of bud scale scars, directly above the prior year's ring of bud scale scar; and 5) NT - no treatment. The response variables were bud break at first bud proximal to the treatment; bud break of multiple bud; and the length of new shoot growth.

Logistic regression was used to analyze the results. T-test were used to test for significant difference (0.05 confidence) between the length of new growth of the different treatments.

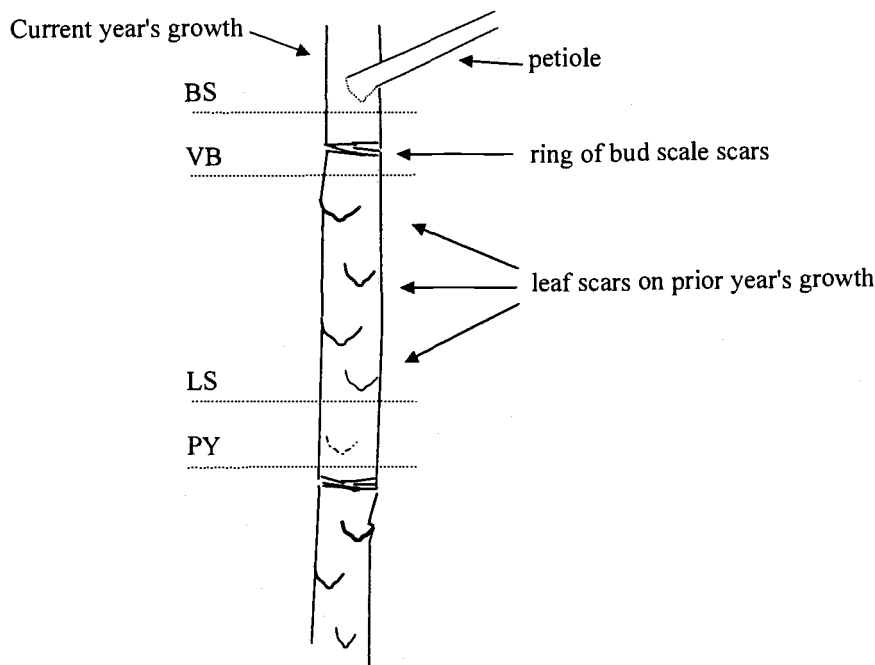


FIGURE 3.1 Treatment locations on stem samples. Stems were lopped in relation to the ring of bud scale scars. See text for description of treatments.

Branching and rooting experiment

Stem samples (12 cm length, approximately 2.5 cm diameter) were cut from layered horizontal Devil's club stems at 10 sites in the Oregon Coast Range in the Spring of 1996 and brought into the greenhouse for survival and growth experiments. Four different treatments, based on the combination of the presence and absence on the stem samples of pre-existent root or lateral shoot growth, were tested and compared. The four treatments included: 1) root and shoot - stem sample containing pre-existent root and lateral shoot growth; 2) root only - stem sample containing pre-existent root growth; 3) shoot only - stem sample containing pre-existent lateral shoot growth; and 4) stem only - stem sample containing neither pre-existent root nor lateral shoot growth. Altogether there were 50

samples, 10 each in treatments 1, 2 and 3, and 20 in treatment 4, the stem only treatment. When collecting stem samples, the amount of pre-existent root growth was not considered, though size of pre-existent shoot growth was limited to no more than 10 cm. in length.

Samples were planted in 200 mm by 160 mm polyurethane pots, in soil mixtures of 1 part loam soil, 1 part washed cement sand (1/4" screen), 1 part horticulture medium grade Canadian peat moss, and 2 parts #8 slow screen (3/8" screen) white pumice rock. Pot locations on the greenhouse bench were randomly allocated, and re-arranged twice during the experiment. Watering was done automatically with a mist system, keeping soil continuously saturated. The greenhouse was artificially cooled during the course of the summer to 27° Celsius. The experiment lasted 12 weeks.

Response variables included stem necrosis, and new shoot and new root presence and length. Locations of any new growth relative to bud scale scars was also noted, as was whether new shoots and roots grew attached.

Logistic regression was used to analyze the survival results. T-tests were used to test for significant difference (0.05 confidence) among the different treatments in new growth length.

Flowering, stem growth and branching

At eight patches in the Oregon Coast Range (Table 3.2), stems inside 20.9 m² plots were measured and counted. Plots were placed in the center of discrete Devil's club patches. Vertical heights above the ground and percentage of stems flowering were measured for each stem within the plot. At each site, one stem was randomly selected from within the plot, and annual growth (as indicated by rings of bud scale scars) was measured. (see Appendix C for field sketches and notes). Stem ages were calculated from these measurements. Slope and aspect of the plots were also measured. Elevation of sites was estimated from 1:100,000 meter US

Geological Survey topographic maps and USDA Forest Service Ranger District maps.

Table 3.2 Study site locations, plot aspects and elevations in the flowering, stem growth and branching study.

Site	Latitude // Longitude	Aspect (°)	Elevation (m)
Beaver Creek	44° 26' N // 123° 25' W	30	250
Bummer Creek	44° 18' N // 123° 35' W	360	325
Nestucca River	45° 18' N // 123° 40' W	320	230
Nettle Creek	44° 29' N // 123° 46' W	190	460
Oliver Creek	44° 20' N // 123° 22' W	19	160
Prairie Mtn. 1	44° 16' N // 123° 35' W	5	700
Prairie Mtn. 2	44° 16' N // 123° 35' W	9	700
Rock Creek	44° 19' N // 123° 33' W	177	250
Tobe Creek	44° 19' N // 123° 34' W	184	280

Stem maps

At three of the above sites (Beaver Creek, Oliver Creek, Prairie Mtn., all aerial stems within the plots were mapped, tracing stem branching and connections to each other and to their origins. One these sites (Prairie Mountain) consisted of two nearby stem complexes, which were mapped as two plots. In calculations involving ortet and stem densities, the means of the two plots were used.

RESULTS

Layering is the most common form of Devil's club reproduction in western Oregon. Over the course of two field seasons only two Devil's club seedlings were observed. There was no evidence of any rhizome production or of root sprouting. Observations in the field along with greenhouse results indicate that layering of

Devil's club is not difficult and will likely occur when aerial stems come in contact with ground (Figure 3.2).

Qualitative observations indicate that creation of independent ramets in Devil's club does occur, perhaps frequently, as Devil's club stems easily layer and are somewhat brittle. Many layered stems were observed damaged and broken from tree and branch fall. Patches of Devil's club usually contained large amounts of woody debris, indicating that tree and branch fall is responsible for much of the layering that occurs within patches in western Oregon. It was impossible to accurately determine the true age of a stem, or even how long it has been in a site. Current stem complexes may actually be independent ramets from much older, distant or now expired, genets.

Stem maps

Mean stem density was $2.22/\text{m}^2$; SD = $1/\text{m}^2$), ranging from $0.65/\text{m}^2$ to $3.88/\text{m}^2$ per patch. At the three mapped sites, the mean number of physically independent stems was $0.35/\text{m}^2$; SD = $0.44/\text{m}^2$). Many stems followed a 'sweeping' form where older stem sections most proximal to origin grew horizontal to the ground while distal sections grew with crowns curved upward in a more vertical position (Figure 3.3). On steeper slopes, stems tended to grow down slope; the plot of Figure 3.4, with a 65% slope illustrates this tendency.

There was no gradient in the density of crowns according to relative slope location within a patch (Table 3.3), as might be predicted by the above pattern, suggesting that as apical crowns grow outward, or downward (Figure 3.4), there is a steady recruitment of replacement crowns from new lateral shoot growth (Figures 3.3) in the interior of Devil's club patches.



FIGURE 3.2 Layered stem of Devil's club. There were no observations of rhizomes; all asexual reproduction of Devil's club occurs through layering of aerial stems.



FIGURE 3.3 New branch growth on lower section of aerial stem.

Oliver Creek

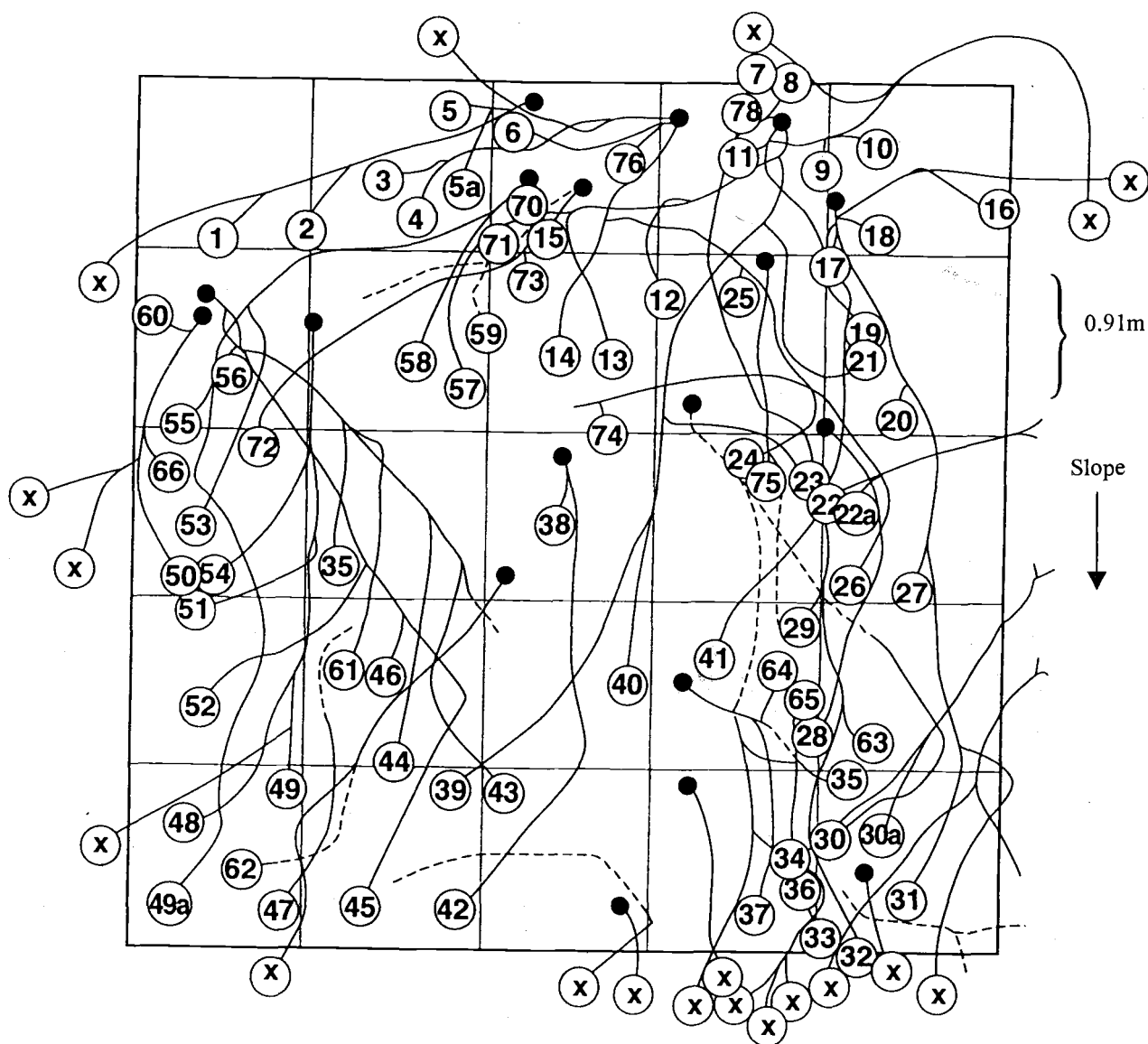


FIGURE 3.4 Aerial stem map of 20.9 m² plot of Devil's club population. Lines represent layered and non-layered aerial stems of Devil's club, circles with numbers in them indicate leaf crowns. Circles with 'x' in them indicate crowns that were out of the plot. Dotted lines represent rotted stems, darkened circles indicate stem origination points. Plot had a 19° aspect. See also Figure C.1.

TABLE 3.3 Mean number of stem crowns according to location within a patch (n=8). Crown number did not differ significantly according to whether stems were in the lower (downslope), middle, or upper (upslope) fifth of a patch.

	lower 5th	-	middle 5th	-	upper 5th
mean number of stems	8.2	8.2	8.8	8	8.6
standard deviation	6.9	4.6	3.7	4.6	6.0

Flowers and seed

Though seedlings are rare, seed production is dependable. Flowers are produced by the apical meristem (Figure 3.6). The next year's vegetative growth is from a lateral meristem, resulting in a characteristic crook in the stem. Flowering occurs on 22.84% (0% to 62.71%, SD 18.4, n=8) of the stems per patch and are generally limited to the taller stems (Figure 3. 5). Qualitative observations suggest that flowers tend to occur on stems in higher light environments. Devil's club stems produce bright red seed heads, which were observed to ripen through July and into August in western Oregon.

Stem growth

The mean age of eight measured stems was 24.7 years (SD - 8), ranging from 15 to 38 years. The mean diameter at the proximal end of the measured stems was 2.9 cm (SD 1.21), ranging from 0.8 cm to 4.57 cm. The mean diameter of the distal ends, just below the terminal bud, was 1.6 cm (SD 0.83), ranging from .8 cm to 3.7 cm. Mean vertical height of the stems was 124.8 cm (SD 35), ranging from 59.2 cm to 172 cm. There were stems outside of plots whose heights, though not measured, appeared to be significantly higher than these. Generally stems taller

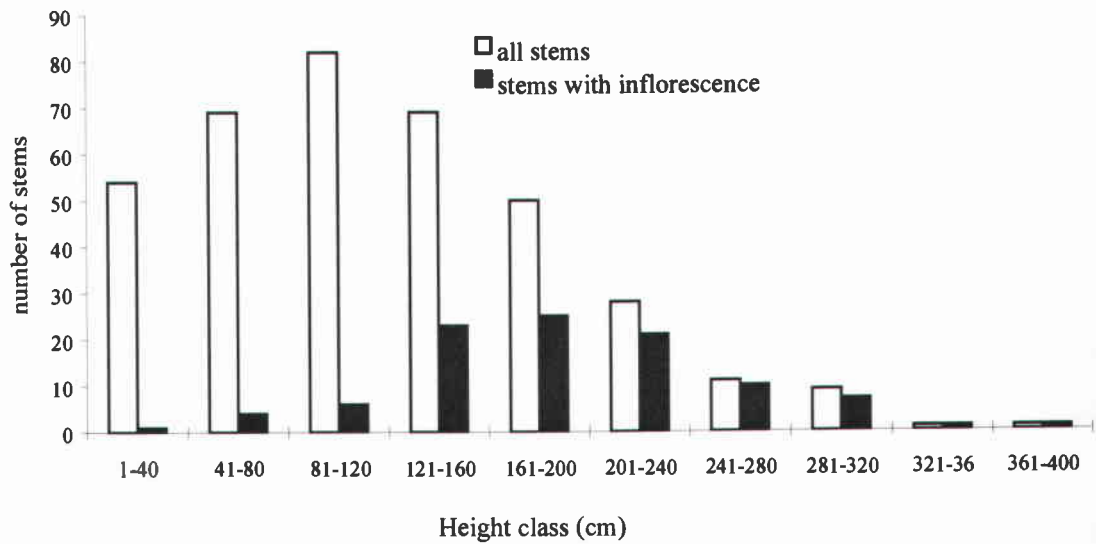


FIGURE 3.5 Stem height distribution and incident of flowering. Measured stem heights averaged 1.25 meters, ranging from 14 cm to nearly 4 meters. The graph displays the height distribution, as well as the distribution of all flowering stems. Flowering was typically associated with taller stems.



FIGURE 3.6 Devil's club flower. Inflorescence occurs directly from apical meristem.

than four meters height grow with the support of nearby tree branches and trunks. For example, one stem supported by the trunk of a Douglas-fir (*Pseudotsuga menziesii*) along Bummer Creek in the Oregon Coast Range was estimated to be 5 meters in height.

Aerial stem lopping experiment

New buds broke on all treated stems, either the first bud proximal to the cut (77.9% across all treatments, excluding control), or basipetal to the cut (Figure 3.7, Table 3.4). After lopping the stem below the most recently formed ring of bud scale scars (VB treatment), the visibly swollen bud in the axil of the first leaf scar broke in 100% the samples. After lopping the stem above the most recently formed ring of bud scale scars (BS treatment), the visibly swollen bud in the axil of the first leaf scar immediately below the ring of bud scale scars broke on 83.33% of the stems (95% C.I.- 59.1% to 94.5%).

Lopping stems above the previous year's ring of bud scale scars (PY treatment), resulted in 88.9% of the buds in axil of the first leaf scar immediately below the ring of bud scale scars breaking (95% C.I.- 64.8% to 97.2%). Less visibly swollen buds did not break as consistently. Lopping the stem several leaf scars below a markedly swollen bud but above a not visibly swollen bud in axil of a leaf scar (LS treatment) resulted in 44.44% (95% C.I.- 24% to 67%) of the buds in axil of the leaf scars immediately below the cut breaking (Figure 3.8). Buds in the other 55.6% of the stems broke in the axil of the of the first leaf scar immediately below the ring of bud scale scars. Without lopping (control treatment), there was new bud growth on only 5.88% of the stems (95% C.I.- .82% to 32%, Table 3.4).

Stem damage often initiated multiple bud breaks. More than one bud broke on 49% of the stems that were treated (Figure 3.7, Figure 3.9). Qualitative observations of Devil's club stems in exposed environments suggest that increased light levels can trigger lateral branching as well (Figure 3.10). There was no statistical evidence of significant difference in the length of new, first proximal bud

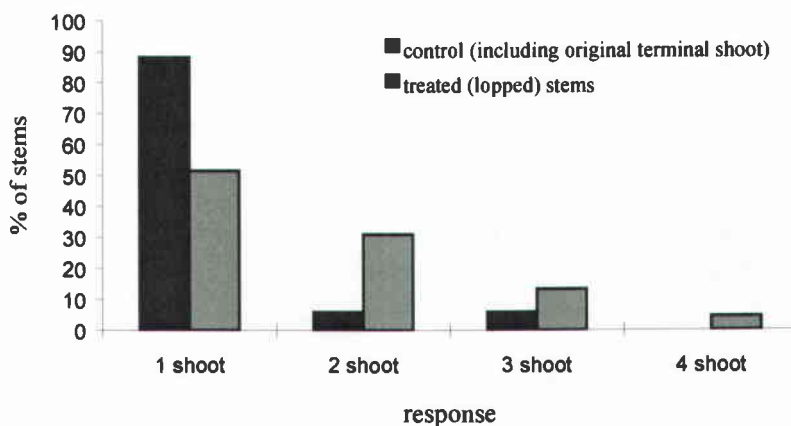


FIGURE 3.7 Number of aerial shoots per Devil's club vertical stem. In the absence of disturbance, branching is rare on vertical stem sections. New shoot growth is typical when stems are damaged. Multiple shoot growth after damage is also common.



FIGURE 3.8 New bud growth 2 weeks after lopping (LS treatment).

growth between treatments. Mean growth of the first proximal buds was 2.6 cm, ranging from 0.3 cm to 9.1 cm.

TABLE 3.4 Comparison of aerial stem cutting experiment results, by treatment. There was new bud growth in 100% of the treated samples, excluding control.

Treatment	% of 1st bud proximal to treatment to break	mean length (cm) of 1st bud proximal to treatment to break (SD)	% stems with multiple bud breaks	mean length of remaining, multiple bud growth
VB (n=14)	100%	1.89 (1.13)	21.43	1.27
BS (n=14)	83.33%	2.85 (2.09)	61.11	1.27
PY (n=14)	88.9%	2.83 (1.68)	38.89	1.22
LS (n=14)	44.44%	1.45 (.76)	66.67	1.37
NT (n=14)	5.88%	0.64 (-- ¹)	5.88	1.03

BS - lopping the current year's stem growth directly above the most recently formed ring of bud scale scars; **VB** - lopping the aerial stem below the most recently formed ring of bud scale scars, above a visibly swollen bud in axil of leaf scar; **LS** - lopping the stem below the most recently formed ring of bud scale scars, above a bud in axil of leaf scar that does not show any visible swelling; **PY** - lopping the stem below the most recently formed ring of bud scale scars, directly above the prior year's ring of bud scale scar; **NT** - no treatment.

¹ - Only one response, no standard deviation calculated.

Branching

Mean branching rates over 8 sites showed a near constant rate of increase with stem age (Figure 3.11). Rates for individual plants varied (Figure 3.12) suggesting damage from disturbance triggers new growth. New aerial stem increment growth reached its maximum potential within five years, remaining consistent thereafter (Figure 3.13). To the right of the schematic of the plot of Figure 3.4, a mature leaf maple tree (*Acer macrophyllum*) had recently fallen on that part of the patch, pinning many stems to the ground. Figure 3.14 shows the growth response of one of those stems to damage from the fallen big leaf maple. Stems in many different age

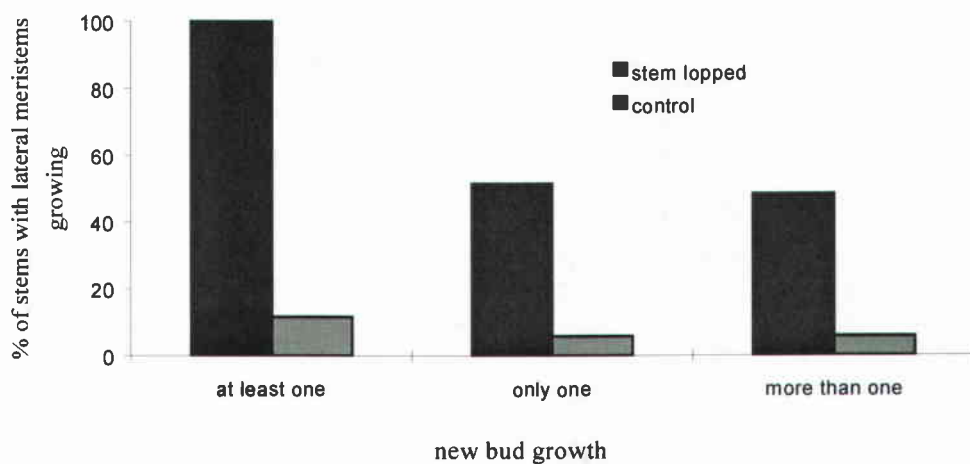


FIGURE 3.9 The rate of single versus multiple bud breaks between the treated stems and the control stems.



FIGURE 3.10 Multiple branching of Devil's club in high light environment. Qualitative observations suggest as well that flowering and seed set are more common in higher light environments.

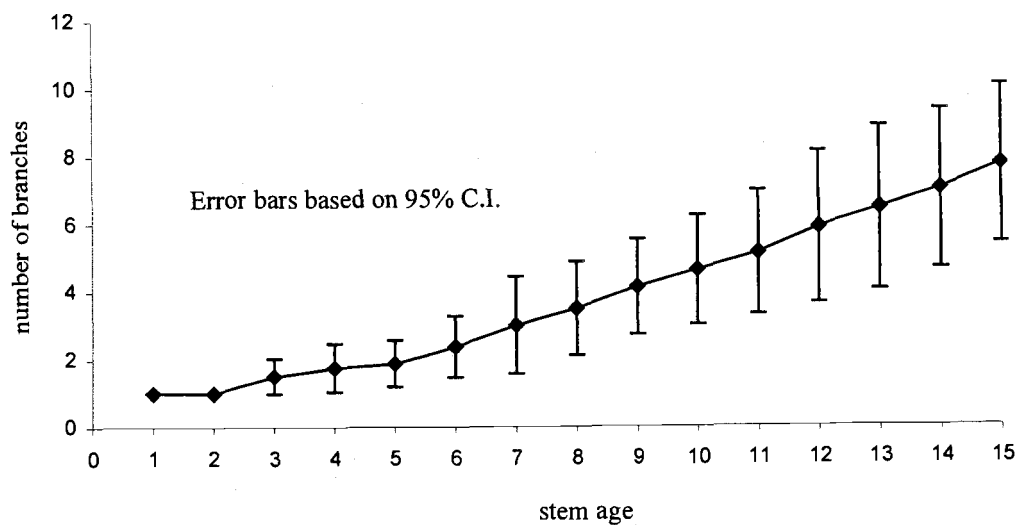


FIGURE 3.11 Mean number of branches as a function of stem age.

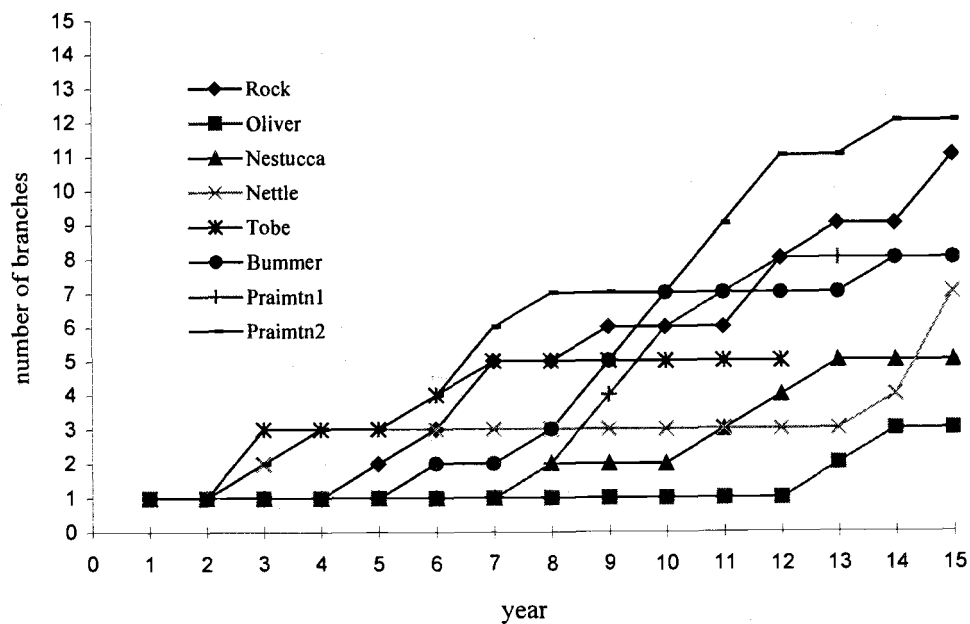


FIGURE 3.12 Branching of individual stems through the life of each stem.

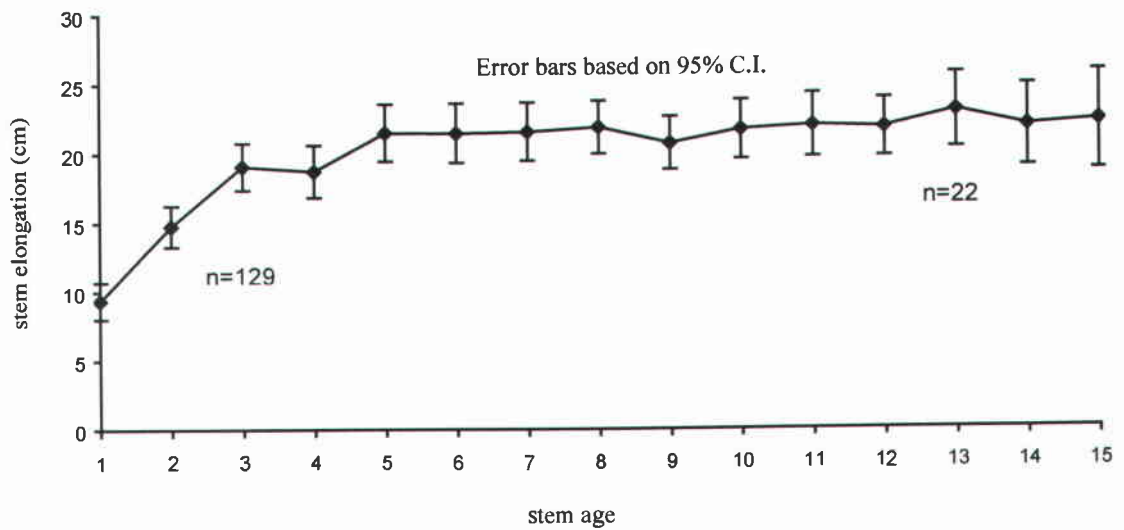


FIGURE 3.13 Mean stem increment rate as a function of stem age.



FIGURE 3.14 Growth of aerial stem after being knocked down by big leaf maple. See also Figure C. 1D in the appendix.

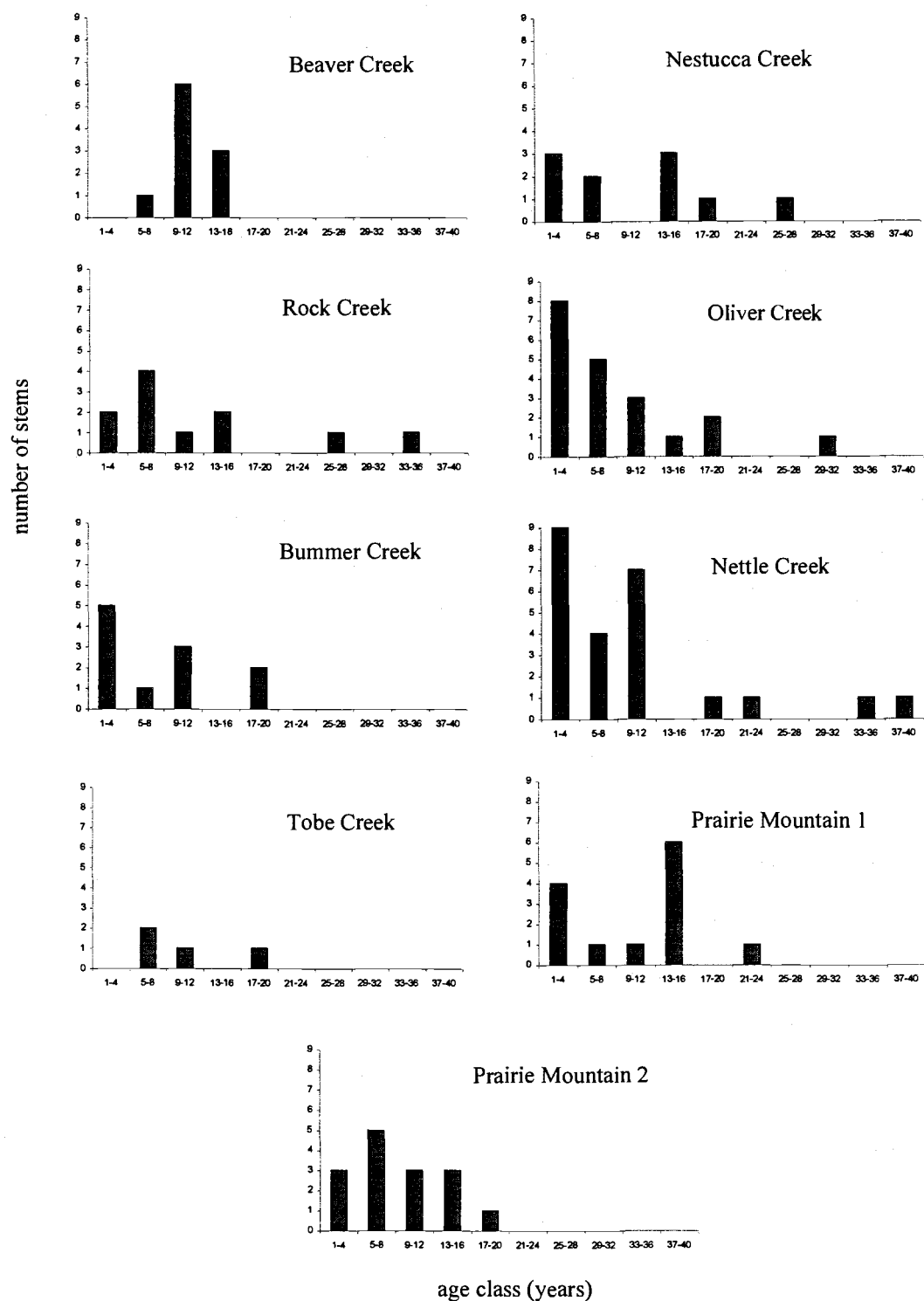


Figure 3.15 Distribution by age class of stems within individual stems complexes. Stems are distributed in a broad range of age classes, indicating continuous production of replacement stems.

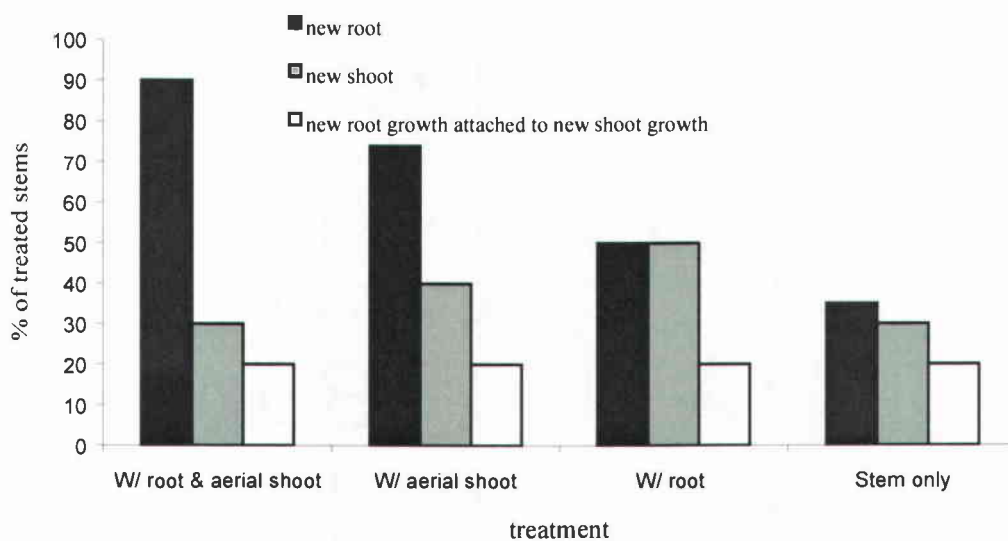


FIGURE 3.16 Percent of stems the grew new lateral shoots and roots, by treatment.



FIGURE 3.17 Sample of Devil's club stem after growing in greenhouse for three months. This sample contained a pre-existing lateral branching before being transplanted into the greenhouse.

classes (Figure 3.15), indicating a consistent recruitment of replacement stems as well.

Shoot and root initiation

Overall, the mean stem sample survival rate was 72.5% in the greenhouse experiment.

In stem samples that contained a pre-existing root and shoot, 90% survived (95% C.I.- 53% to 99%, $n = 10$, Table 3.5, Figure 3.16). Based on the median value, a stem sample with pre-existing root and lateral shoot growth is 13.5 times more likely to survive than a 'stem only' sample (95% C.I. - 1.4 to 128.3 times, p -value .0235). Thirty percent of the root and shoot samples grew new shoots as well (95% C.I.- 10% to 62%), and 90% of this treatments grew new roots (95% C.I.- 53.3% to 98.6%, $n = 10$, Table 3.5, Figure 3.16, see Figure 3.17 as an example of new root growth on stem sample at conclusion of experiment). Based on the median value, a stem sample in the root and shoot treatment is 16.7 times more likely to grow new roots than a 'stem only' sample (95% C.I. - 1.7 to 160.4 times, p -value .0146).

In stem samples that contained pre-existing shoot, 90% survived (95% C.I.- 53% to 99%, $n = 10$). Based on the median value, a stem sample with pre-existent shoot growth is 13.5 times more likely to survive than a 'stem only' sample (95% C.I. - 1.4 to 128.3 times, p -value .0235). Forty percent of the samples grew new shoots (95% C.I.- 15.8% to 70.3%, $n = 10$), and 80% grew new roots (95% C.I.- 45.9% to 95%, $n = 10$). Based on the median value, a stem sample with pre-existent shoot growth is 7.43 times more likely to survive than a 'stem only' sample (95% C.I. - 1.2 to 45 times, p -value .0291).

In stem sample that contained a pre-existing root, 60% survived (95% C.I.- 30% to 84%, $n = 10$). Fifty percent of the samples grew new shoots (95% C.I.- 22.5% to 77.6%, $n = 10$), and 50% grew new roots (95% C.I.- 22.6% to 77.6%, $n = 10$).

In stem samples that contained neither a pre-existing root nor shoot, 40% survived (95% C.I.- 21.4% to 62%, $n = 20$). Thirty percent of the stems samples grew new shoots (95% C.I.- 14.1% to 52.7%, $n = 20$), and 35% grew new roots (95% C.I.- 17.7.4% to 57.4%, $n = 20$).

Mean length of new shoots growth was 3.87 cm, ranging from 1.45 cm to 3.94 cm. Mean length of new root growth was 2.3 cm, ranging from 1.53 cm to 3.12 cm. New roots typically originated from either at the base and underneath pre-existing aerial stems, from pre-existing root system, or from primordial tissue along the stem sample, 'below' bud scale scars. On samples with pre-existing shoots, new aerial shoots typically grew from the base and underneath those shoots, also 'below' bud scale scars on the stems (Table 3.5, Figure 3.16).

TABLE 3.5 Comparison of survival and growth rates of stem samples by treatment.

Treatment	% survive	% grew new roots	mean length of new root growth (cm) of survivors (stdev)	% grew new shoots	avg. length of new shoot growth (cm) of survivors (stdev)	% samples in which new roots grew from new shoots
root and shoot (n=10)	90	90	3.12 (2.28)	30	1.45 (2.32)	20
shoot only (n=10)	90	80	2.52 (1.97)	40	3.25 (4.09)	20
root only (n=10)	60	50	1.53 (1.48)	50	3.94 (2.4)	20
neither root nor shoot (n=20)	40	35	2.02 (2.84)	30	3.37 (3.10)	20

New root growth was favored on stems that had pre-existing root and shoot growth (Table 3.5, Figure 3.16). The rate of overall stem sample survival (72.5%), indicates that production of Devil's club growing stock in greenhouses would not be difficult.

DISCUSSION

Disturbance events, mountainous terrain, and a climate that fluctuates between wet and dry seasons can create precarious growing environments for understory plants in western Oregon. In riparian areas where Devil's club is most common (Hemstrom and Logan 1986, Franklin and Dyrness 1973; Moore 1993; Hemstrom et al. 1982), conditions can be particularly difficult. Plants are subject to disturbances from fire, tree fall, floods, landslides and browsing, while facing strong competition above and below ground from both overstory and understory associates, often in light limiting conditions. It is not surprising then that clonal growth is so prevalent in understory shrubs of Oregon (Tappeiner et al. 1991); plants capable of asexual reproduction use clonal growth to expand and survive in limiting environments at the edge of their ecological and geographic range, in environments temporarily too limiting or competitive to persist through sexual reproduction (Cook 1983, Koop 1987, Stalter et al. 1997). This aspect of asexual reproduction can help explain growth patterns of Devil's club in western Oregon, including the creation and support of progeny, survival and recovery from disturbances, and competition with other shrubs.

Plants are most susceptible to mortality during their seed germination and seedling stages. Clonal formation effectively bypasses these two stages. Only two Devil's club seedlings were observed during the study's two field seasons, indicating that though sexual reproduction is possible, it is infrequent in western Oregon. Reproductive factors may include low seed production, viability and dispersal. A need for seed scarification, such as fire or passage through an animal's digestive system may also contribute to the low number of observed seedlings. Another limiting factor may be climate.

Clonal growth helps Devil's club respond positively to disturbances. Stems responded consistently to damage with new growth, though apical dominance may not be the only controlling mechanism for new branching. Shading may limit new

stem growth as well - observations of branching along unshaded, lower parts of aerial stems were common (Figure 3.3). In exposed environments, stems with multiple branches were common, even typical (Figure 3.10).

Layering and subsequent clone formation typically occurs when an aerial stem becomes pinned to the ground, often though not exclusively from branch or tree fall (results from chapter 2 suggest that Devil's club growing sites in western Oregon are prone to this type of disturbance). Another understory plant in western Oregon that reproduces primarily by layering is vine maple (*Acer circinatum*) (O'Dea et al. 1995), but this plant layers in a slightly different way. Like Devil's club, vine maple stems get pinned to the ground by woody debris, where they layer. Unlike Devil's club, layered stems often form arcs from the ortet to the point where they are pinned, much like the legs of a spider (O'Dea et al. 1995). Aerial stems of vine maple can become interlaced and knotted, and nearly impenetrable. The stems of Devil's club, because they often already grow parallel to the ground, tend to lay flat on the ground when they layer. Layered stems of Devil's club often overlap and cross each other into horizontal, tangled mats, but the vertical aerial stems remain relatively independent of each other.

Aerial stems represent a bud bank for Devil's club, similar to vine maple (O'Dea 1995). Even small independent stems pieces can layer, important because the brittleness of Devil's club stems leave them susceptible to breakage after a disturbance such as tree fall. Of the 20 samples in the greenhouse that contained neither a pre-existing root or shoot, 50% survived while 35% grew new roots. Stems that are knocked down layer *in situ*, or perhaps like the branches from poplar (*Populus*) and willow (*Salix*) species, can be carried down stream during floods to root and colonize new growing sites (Heybroek 1984).

New shoot growth results from damage to the stem. Buds, often multiple buds, broke on 100% of the cut samples in the stem cutting experiment, demonstrating that damage to stems typically results not in a decrease, but initially a net increase in the number of stems in a patch. The pattern of new stem initiation

seen in Figure 3.12, where the number of new stems increased in spurts suggests as well that stochastic events triggers new stem growth.

Even in an absence of disturbance, Devil's club produces a multiple-aged distribution of stems (Figure 3.3, Figure 3.15). In this manner it resembles other western Oregon shrubs (salmonberry, salal (*Gaultheria shallon*), Oregon grape (*Berberis nervosa*), and vine maple), which produce stems in many age classes to help spread laterally, maintain vigor and persist in a site (Tappeiner et al. 1991, Huffman et al. 1994, Tappeiner and Huffman 1997, O'Dea et al. 1995). Despite apparent similarities though, how these shrubs create and maintain multiple-aged stem distributions differ. For example, salmonberry and salal produce through rhizome expansion stems in many age classes to replace older clones that fragment and die (Huffman et al. 1994, Tappeiner et al. 1991). Stem production from sexual reproduction is slow and unreliable, particularly in exposed environments (Ruth 1970, Huffman et al. 1994). Oregon grape rhizome production is not as extensive as either salmonberry or salal, but vegetative expansion is supplemented with new stems through sexual reproduction (Huffman and Tappeiner 1997). Vine maple generally only reproduces vegetatively when stems layer after being knocked down and pinned to the ground from a disturbance (O'Dea 1995, Zasada et al. 1992), but is also able to produce new stems through sexual reproduction (Tappeiner and Zasada 1993). In exposed sites though, both vine maple and Oregon grape rely on vegetative reproduction (O'Dea 1995, Zasada et al. 1992, Huffman and Tappeiner 1997).

As a non-rhizomatous, clonal shrub, Devil's club shares many of the same reproductive attributes as vine maple, especially in its response to disturbance. Seedling production, however, is relatively rare, and Devil's club does not rely on disturbance to produce new stems from layering. Instead, light induced, horizontal stem growth (Figure 3.3) can facilitate vegetative expansion and a multiple-aged distribution of stems. Devil's club captures light in two ways - vertical growth raises leaf crowns above competition (see chapter 2), while sprawling growth

(Figure 2.14) enables Devil's club to explore a horizontal plane for understory light (Pickett and Kempf 1980). New shoot growth on 'sprawling' stems (Figure 3.3) is likely not so much a response to fragmentation or clone death, as seen with Oregon grape, salal or salmonberry (Huffman and Tappeiner 1997, Tappeiner et al. 1991) or from disturbance, such as with vine maple (Zasada 1992), but to an increase in available light (Figure 3.3) as older terminal crowns move horizontally and vacate growing space. This shoot growth in effect 'fills-in' Devil's club patches with replacement stems. The added weight of these branches, along with the accumulated weight of crossing stems from other sprawling stem complexes can exert enough downward force to press underlying stems into contact with the ground, enabling them to layer and the patch to keep expanding.

Once established, ramets benefit from their connection with the clonal network. In the dense shade typical of Devil's club habitat (see chapter 2), or during periods of high temperature and low moisture, translocation of photosynthates from mother genet to daughter ramet can assist in their growth and survival (Hutchings and Bradbury 1986; Hartnett and Bazazz 1983; Koop 1987). Translocation of resources within clonal networks of Devil's club can be inferred from retrospective measurements of stem elongation rates (Figure 3.13), where in five years new branches nearly attained their maximum potential growth rates. This kind of support is particularly important after disturbances like tree fall, as associated understory clonal shrubs like salmonberry and vine maple, which also respond vigorously to overstory disturbances (O'Dea et al. 1995, Zasada et al. 1992, Tappeiner et al. 1991, Ruth 1970) may be present and potentially displace Devil's club.

On layering stems, new root and shoot growth prepares Devil's club to create viable, independent clones. Greenhouse stem samples with pre-existing roots grew new roots and lateral shoots equally, on 50% of the samples (Table 3.5; Figure 3.16). Cook (1979) contends that developing independent ramets lessens the risk of mortality to a plant from intense but localized disturbances by dispersing risk to a

wider area. Hutchins and Bradbury (1986) speculate in turn that frequently disturbed sites select for fragmentation of clonal networks for this very reason. Certainly riparian areas of western Oregon are frequently disturbed, suggesting that the development of independent clones by Devil's club may be necessary for persistence in these sites, as much an adaptive reflection of disturbance patterns as a response to them.

Ultimately, growth patterns of Devil's club resemble growth patterns of other shrubs in the understory of western Oregon forests, where adaptive elasticity is critical to tolerate and reproduce in a wide range of fluctuating and often resource limiting environments (Tappeiner et al. 1986, Tappeiner et al. 1991, Fried et al. 1988, Alaback and Tappeiner 1993, Ruth 1970, Stewart 1986). Clonal growth is an important component of Devil's club adaptability, assisting it to survive and occasionally thrive at the edge of its ecological range.

CHAPTER 4 CONCLUSIONS

Devil's club in western Oregon grows in a wide range of environments - from low elevations to high elevations, from exposed environments to sites with dense overstories. Devil's club grows in forests that range from early seral to mature to old-growth, on slopes that range from nearly level to steep, and in association with a large number of plant species.

As an environment for Devil's club, Oregon's is best viewed as marginal, marking the shift from a cooler and moister north where the plant can and often does fill the forest understory (Moore 1993, Martin et. al 1995, Shephard 1995), to a warmer and drier south where it disappears altogether. This raises the interesting question of whether Devil's club in Oregon is a remnant from a cooler time period, and is in the process of retreating north.

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APPENDICES

APPENDIX A PLANT COMMUNITY LISTS

Within-patch														
Site	Cascade Range								Coast Range					
	Browder Ridge	Browder Ridge	Canyon Creek	Canyon Creek	Scott Creek	Scott Creek	Scott Creek	Wiley Creek	Beaver Creek	Congdon Creek 1	Congdon Creek 2	Deer Creek	Square Top	
Patch #	1, 2	3	1	2, 3	1	2	3	1, 2	1,2,3	1,2,3	2,3	1,2, 3	1,2,3	
<i>Acer macrophyllum</i>	0	0	15	0	0	10	0	40	1.7	20.7	7.5	0	0	
<i>Alnus rubra</i>	0	0	80	0	30	3	0	35	8.3	10	0	21.7	3.3	
<i>Cornus nuttallii</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	
<i>Abies amabilis</i>	7.5	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Picea sitchensis</i>	0	0	0	0	0	0	0	0	0	0	0	16.7	0	
<i>Pseudotsuga menziesii</i>	0	0	0	2.5	15	0	0	5	10	1.7	1.5	0	15	
<i>Tsuga heterophylla</i>	15	40	0	11.5	20	3	3	15	1.7	27.7	4	10	35	
<i>Thuja plicata</i>	0	0	0	3.5	15	0	0	0	0	3.3	2.5	0	0	

TABLE A.1. Tree list with cover values (%)

Perimeter-of-patch

	<u>Cascade Range</u>								<u>Coast Range</u>				
	Site Browder Ridge	Browder Ridge	Canyon Creek	Canyon Creek	Scott Creek	Scott Creek	Scott Creek	Wiley Creek	Beaver Creek	Congdon Creek 1	Congdon Creek 2	Deer Creek	Square Top
Patch #	1, 2	3	1	2, 3	1	2	3	1, 2	1,2,3	1,2,3	2,3	1,2,3	1,2,3
<i>Acer macrophyllum</i>	0	0	25	0	0	10	0	17.5	8.3	30	22.5	0	0
<i>Alnus rubra</i>	0	0	70	0	80	15	0	60	33.3	5	0	23.3	0
<i>Cornus nuttallii</i>	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Abies amabilis</i>	30	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pices sitchensis</i>	0	0	0	0	0	0	0	0	0	0	0	18.3	0
<i>Pseudotsuga menziesii</i>	0	0	0	2.5	10	5	0	15	45	5	2.5	0	21.7
<i>Tsuga heterophylla</i>	40	70	8	72.5	20	3	6	22.5	4.3	46.7	7.5	36.7	35
<i>Thuja plicata</i>	0	0	4	0	15	0	0	0	0	11.7	0	0	0

TABLE A.1 (continued)

Tree list with cover values (%)

Within-patch	Browder Ridge	Browder Ridge	Browder Ridge	Canyon Creek	Canyon Creek	Canyon Creek	Iron Mtn	Iron Mtn	Iron Mtn	Scott Creek	Scott Creek	Scott Creek	Wiley Creek	Wiley Creek
Patch:	1	2	3	1	2	3	1	2	3	1	2	3	1	2
<u>Shrub species</u>														
Oplopanax horridum	80	60	50	45	70	80	75	70	60	55	60	70	65	50
Acer circinatum	12	0	0	50	8	15	0	0	0	50	5	10	19	0
Arctostaphylos	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Berberos nervosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gaultharia shallon	0	0	0	0	30	0	0	0	0	0	0	10	0	0
Rhamnus purshiana	0	0	0	5	0	0	0	0	0	0	0	0	10	0
Ribes bracteosum	3	0	0	3	0	0	10	3	0	8	0	0	0	0
Rosa gymnocarpa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus parviflorus	0	0	0	0	0	0	0	0	0	0	7	0	0	0
Rubus spectabilis	5	2	0	2	0	1	5	60	30	12	60	0	5	0
Rubus ursinus	0	0	0	0	8	0	5	0	15	0	3	5	0	0
Salix spp	0	0	0	0	0	0	0	0	15	5	25	0	15	0
Sorbus spp	0	0	0	5	0	0	0	0	0	0	0	0	3	0
Vaccinium spp	7	3	10	0	5	0	35	0	0	5	3	0	1	3
<u>Herb species</u>														
Achlys triphylla	2	2	10	0	0	0	0	5	0	0	0	0	0	0
Adiantum pedatum	0	0	0	0	0	0	0	0	0	0	0	0	0	5

TABLE A.2

Cascade Mountains shrub and herb list with cover values (%)

Within patch	Browder Ridge	Browder Ridge	Browder Ridge	Canyon Creek	Canyon Creek	Canyon Creek	Iron Mtn	Iron Mtn	Iron Mtn	Scott Creek	Scott Creek	Scott Creek	Wiley Creek	Wiley Creek
Patch:	1	2	3	1	2	3	1	2	3	1	2	3	1	2
Adenocaulon bicolor	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anaphalis margaritacea	0	0	0	0	0	0	0	5	0	0	0	0	0	0
Asarum caudatum	2	0	0	0	0	5	0	5	0	0	0	0	0	3
Athyrium filix-femina	3	0	0	5	0	0	0	0	0	0	0	0	10	0
Blechnum spicant	0	0	20	0	9	12	0	3	0	8	0	0	0	0
Chrysosplenium glechomaefolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cirsium spp.	0	0	0	0	0	0	0	0	5	0	0	0	0	0
Cornus canadensis	0	2	15	0	0	0	0	0	0	0	0	0	0	0
Cornus canadensis	0	0	0	0	0	0	10	10	0	0	0	0	0	0
Equisetum spp	0	0	0	0	0	0	5	0	0	0	25	0	0	0
Galium spp	0	0	0	0	0	2	0	3	0	3	3	0	0	0
Grass spp.	0	0	0	0	0	0	15	20	35	0	0	0	0	0
Hypericum formosum	0	0	0	0	0	0	0	10	0	0	0	0	0	0
Hydrophyllum fendleri	0	0	0	3	0	0	0	0	0	0	0	0	0	0
Maianthemum diallatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxalis oregana	0	0	0	10	2	10	0	0	0	3	5	0	10	50
Petasites palmatus	0	0	0	0	0	0	0	0	0	0	5	0	0	0
Polypodium glycyrrhiza	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polystichum munitum	0	0	0	30	4	8	0	0	0	0	25	20	17	25
Pteridium aquilinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE A.2 (continued)

Cascade Mountains shrub and herb list with cover values (%)

Within-Patch	Browder Ridge	Browder Ridge	Browder Ridge	Canyon Creek	Canyon Creek	Canyon Creek	Iron Mtn.	Iron Mtn.	Iron Mtn.	Scott Creek	Scott Creek	Scott Creek	Wiley Creek	Wiley Creek
Patch:	1	2	3	1	2	3	1	2	3	1	2	3	1	2
<i>Smilacina racemosa</i>	0	0	0	0	0	0	0	0	0	3	5	0	0	0
<i>Smilacina stellata</i>	6	2	30	0	0	0	5	0	0	3	3	0	3	0
<i>Stachys</i> spp	0	0	0	0	0	4	0	0	0	6	0	0	0	0
<i>Tellima grandiflora</i>	0	0	0	0	0	0	0	0	0	3	0	0	0	0
<i>Tolmiea menziesii</i>	0	0	0	5	0	0	0	3	0	3	10	0	0	0
<i>Trillium</i> spp	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Vancouveria hexandra</i>	0	0	0	0	0	0	0	0	20	0	3	0	0	0
Bryophyte cover (%)	60	30	3	0	30	80	0	50	60	75	7	10	10	12
Perimeter of patch														
<u>Shrub species</u>														
<i>Acer circinatum</i>	15	0	4	50	30	15	0	0	3	80	25	40	20	0
<i>Berberos nervosa</i>	0	0	0	0	5	0	0	0	0	0	0	0	0	0
<i>Gaultharia shallon</i>	0	0	0	0	35	4	0	0	0	0	0	8	0	0
<i>Holodiscus</i> spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Oemleria cerasiformis</i>	0	0	0	0	0	0	0	0	0	3	0	0	5	0
<i>Rhamnus purshiana</i>	0	0	0	3	0	0	0	0	0	0	0	0	10	0
<i>Rhododendron</i> spp	3	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ribes bracteosum</i>	0	3	0	0	0	0	10	5	10	0	20	0	10	3

TABLE A.2 (continued)

Cascade Mountains shrub and herb list with cover values (%)

Perimeter of patch	Browder Ridge	Browder Ridge	Browder Ridge	Canyon Creek	Canyon Creek	Canyon Creek	Iron Mtn.	Iron Mtn.	Iron Mtn.	Scott Creek	Scott Creek	Scott Creek	Wiley Creek	Wiley Creek
Rosa gymnocarpa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus	0	0	0	0	0	0	0	0	0	0	0	10	0	0
discolor/lasiococcus														
Rubus parviflorus	0	0	0	0	0	0	0	5	0	0	30	0	0	0
Rubus spectabilis	15	5	0	0	0	7	0	60	15	40	15	5	5	3
Rubus ursinus	0	0	0	0	0	0	5	0	10	0	10	5	5	0
Salix spp	0	0	0	0	0	0	25	15	0	0	15	0	10	0
Sorbus spp	0	0	0	0	0	0	0	0	0	0	0	0	7	0
Vaccinium spp	0	25	10	0	35	2	0	0	10	0	20	4	0	0
<u>Herb species</u>														
Achlys triphylla	3	7	7	0	0	0	5	10	0	0	0	0	0	0
Adiantum pedatum	0	0	0	0	0	3	0	0	0	0	0	0	3	0
Anaphalis margaritacea	0	0	0	0	0	0	10	3	10	0	0	0	0	0
Asarum caudatum	1	0	0	0	0	0	0	10	5	0	0	0	0	0
Athyrium filix-femina	3	0	0	8	5	5	10	5	10	5	0	0	8	7
Blechnum spicant	3	3	15	2	0	8	0	0	0	3	5	0	0	0
Carax phyllomanica	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ciracea alpina	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Claytonia spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cornus canadensis	12	20	20	0	0	0	15	10	0	0	0	0	0	0

TABLE A.2 (continued)

Cascade Mountains shrub and herb list with cover values (%)

Perimeter of patch	Browder Ridge	Browder Ridge	Browder Ridge	Canyon Creek	Canyon Creek	Canyon Creek	Iron Mtn.	Iron Mtn.	Iron Mtn.	Scott Creek	Scott Creek	Scott Creek	Wiley Creek	Wiley Creek
Patch:	1	2	3	1	2	3	1	2	3	1	2	3	1	2
Epilobium angustifolium	0	0	0	0	0	0	0	0	0	0	0	5	0	0
Equisetum spp	0	0	0	0	0	0	0	0	0	0	10	0	0	0
Fragaria spp	0	0	0	0	0	0	20	0	0	0	0	0	0	0
Galium spp	0	0	0	0	0	1	0	0	3	0	3	0	0	0
Grass spp.	0	0	0	0	0	0	25	30	10	0	0	0	0	0
Hydrophyllum fendleri	0	0	0	0	0	0	0	0	5	0	0	0	0	2
Hypericum formosum	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Oxalis oregana	0	0	0	65	15	10	0	0	10	0	5	0	40	70
Maianthemum dialatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polystichum munitum	0	0	0	20	40	7	0	0	0	10	20	35	35	30
Pteridium aquilinum	0	0	0	0	0	0	0	0	15	0	0	0	0	0
Ranunculus spp	0	0	0	0	0	0	0	0	0	0	0	0	10	0
Smilacina stellata	3	7	33	0	0	0	0	3	0	0	0	0	0	0
Smilacina racemosa	0	0	0	0	0	0	0	0	0	3	7	0	0	0
Sorbus spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stachys spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tiarella trifoliata	3	10	10	0	0	0	0	0	0	0	0	0	0	0
Tolmiea menziesii		0	0	3	0	7	0	5	5	25	0	0	7	0

TABLE A.2 (continued)

Cascade Mountains shrub and herb list with cover values (%)

Perimeter of patch	Browder Ridge	Browder Ridge	Browder Ridge	Canyon Creek	Canyon Creek	Canyon Creek	Iron Mtn.	Iron Mtn.	Iron Mtn.	Scott Creek	Scott Creek	Scott Creek	Wiley Creek	Wiley Creek
Patch:	1	2	3	1	2	3	1	2	3	1	2	3	1	2
Trifolium spp	0	0	0	0	0	0	5	0	0	0	0	0	0	0
Trillium spp	3	0	0	0	0	0	0	0	0	3	0	0	1	0
Vancouveria hexandra	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Viola spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bryophyte cover (%)	5	20	3	5	3	12	10	20	70	30	3	50	30	30

TABLE A.2 (continued)

Cascade Mountains shrub and herb list with cover values (%)

Within patch:	Beaver Creek	Beaver Creek	Beaver Creek	Congdon Cr. 1	Congdon Cr. 1	Congdon Cr. 1	Congdon Cr. 2	Congdon Cr. 2	Congdon Cr. 2	Deer Creek	Deer Creek	Deer Creek	Square Top	Square Top	Square Top
Patch	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
<u>Shrub species</u>															
Oplopanax horridum	95	75	60	90	60	50	60	80	35	60	65	60	70	50	35
Acer circinatum	0	75	40	15	60	0	15	10	0	0	0	0	20	0	0
Arctostaphylos	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Berberos nervosa	0	0	25	0	5	0	0	0	0	0	0	0	0	0	0
Gaultharia shallon	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0
Rhamnus purshiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes bracteosum	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
Rosa gymnocarpa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10
Rubus parviflorus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus spectabilis	10	10	20	20	0	7	50	5	20	0	20	0	15	20	30
Rubus ursinus	0	0	0	0	0	0	10	0	10	0	0	0	0	0	0
Salix spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sorbus spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium spp	5	0	10	0	3	0	0	0	5	3	0	10	10	10	5
<u>Herb species</u>															
Achlys triphylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adiantum pedatum	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Adenocaulon bicolor	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0

TABLE A.3

Coast Range shrub and herb list with cover values (%)

Within patch:	Beaver Creek	Beaver Creek	Beaver Creek	Congdon Cr. 1	Congdon Cr. 1	Congdon Cr. 1	Congdon Cr. 2	Congdon Cr. 2	Congdon Cr. 2	Deer Creek	Deer Creek	Deer Creek	Square Top	Square Top	Square Top
Patch	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Anaphalis margaritacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asarum caudatum	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0
Athyrium filix-femina	0	35	0	0	0	0	0	0	5	0	0	0	0	0	5
Blechnum spicant	0	0	0	0	0	3	0	0	5	3	0	7	5	0	0
Chrysosplenium glechomaefolium	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0
Cirsium spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cornus canadensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cornus canadensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum spp	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Galium spp	3	0	3	1	3	0	5	0	0	3	0	0	1	1	0
Grass spp.	0	0	0	0	0	0	0	0	0	0	0	0	2	2	7
Hypericum formosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hydrophyllum fendleri	3	5	3	3	0	0	0	0	0	0	0	0	0	0	1
Maianthemum dialtatum	0	0	3	0	0	0	0	0	0	3	0	5	2	3	3
Oxalis oregana	0	65	0	22	20	7	30	20	15	40	75	13	25	35	70
Petasites palmatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Polypodium glycyrrhiza	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Polystichum munitum	30	5	20	40	40	5	35	60	60	20	20	10	35	25	15

TABLE A.3 (continued)

Coast Range shrub and herb list with cover values (%)

Within patch	Beaver Creek	Beaver Creek	Beaver Creek	Congdon Cr. 1	Congdon Cr. 1	Congdon Cr. 1	Congdon Cr. 2	Congdon Cr. 2	Congdon Cr. 2	Deer Creek	Deer Creek	Deer Creek	Square Top	Square Top	Square Top
Patch:	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
<i>Pteridium aquilinum</i>	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Smilacina racemosa</i>	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
<i>Smilacina stellata</i>	0	0	3	0	0	0	0	0	0	3	0	30	1	0	5
<i>Stachys</i> spp	0	0	0	5	0	0	0	0	0	0	5	0	0	0	0
<i>Tellima grandiflora</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tolmiea menziesii</i>	0	20	10	0	0	3	3	0	0	0	0	0	0	0	0
<i>Trillium</i> spp	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Vancouveria hexandra</i>	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bryophyte (%)	50	80	20	3	37	20	65	70	60	20	30	100	90	60	90
perimeter of patch															
<u>Shrub species</u>															
<i>Acer circinatum</i>	0	85	60	15	50	3	25	30	0	0	0	0	5	0	0
<i>Berberos nervosa</i>	30	0	20	0	5	0	0	0	0	0	0	0	0	0	0
<i>Gaultharia shallon</i>	15	3	0	0	0	0	0	0	5	0	0	0	0	0	0
<i>Holodiscus</i> spp	7	5	0	0	5	0	0	0	0	0	0	0	0	0	0

TABLE A.3 (continued)

Coast Range shrub and herb list with cover values (%)

Perimeter of patch	Beaver Creek	Beaver Creek	Beaver Creek	Congdon Cr. 1	Congdon Cr. 1	Congdon Cr. 1	Congdon Cr. 2	Congdon Cr. 2	Congdon Cr. 2	Deer Creek	Deer Creek	Deer Creek	Square Top	Square Top	Square Top
Patch:	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Oemleria cerasiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhamnus purshiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhododendron spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes bracteosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rosa gymnocarpa	3	0	3	0	0	0	0	0	0	0	0	0	0	0	3
Rubus discolor/lasiococcus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus parviflorus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus spectabilis	0	7	12	15	0	12	25	40	0	5	40	0	70	40	10
Rubus ursinus	0	0	3	0	0	0	15	0	5	0	0	0	0	0	0
Salix spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sorbus spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium spp	8	0	5	0	3	0	5	0	0	15	0	5	20	0	5
<u>Herb species</u>															
Achlys triphylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adiantum pedatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anaphalis margaritacea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Asarum caudatum	0	3	3	0	0	0	0	0	0	0	0	0	0	0	0
Athyrium filix-femina	0	0	0	0	0	0	0	0	5	0	0	0	0	1	3
Blechnum spicant	0	0	0	0	0	3	0	0	0	5	0	3	3	1	0

TABLE A.3 (continued)

Coast Range shrub and herb list with cover values (%)

Perimeter of patch	Beaver Creek	Beaver Creek	Beaver Creek	Congdon Cr. 1	Congdon Cr. 1	Congdon Cr. 1	Congdon Cr. 2	Congdon Cr. 2	Congdon Cr. 2	Deer Creek	Deer Creek	Deer Creek	Square Top	Square Top	Square Top
Patch:	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Carax phyllomanica	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Ciracea alpina	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Claytonia spp	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Cornus canadensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Epilobium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum spp	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
Fragaria spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium spp		3	3	0	0	0	3	0	0	0	3	0	0	0	0
Grass spp.	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0
Hydrophyllum fendleri	0	0	0	0	3	0	0	0	0	0	3	0	0	0	0
Hypericum formosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oxalis oregana	0	0	0	15	15	3	30	30	15	55	70	15	40	60	65
Maianthemum diallatum	0	0	0	0	0	0	5	0	0	0	0	3	0	0	5
Polystichum munitum	63	7	8	70	50	15	30	50	65	25	30	15	30	20	20
Pteridium aquilinum	10	0	3	0	0	0	0	0	15	0	0	0	0	0	0
Ranunculus spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Smilacina stellata	0	0	0	2	0	0	0	0	0	0	0	3	3	0	3
Smilacina racemosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sorbus spp	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0
Stachys spp	0	0	0	0	0	0	0	0	0	0	3	0	0	3	0

TABLE A.3 (continued)

Coast Range shrub and herb list with cover values (%)

Perimeter of patch	Beaver Creek	Beaver Creek	Beaver Creek	Congdon Cr. 1	Congdon Cr. 1	Congdon Cr. 1	Congdon Cr. 2	Congdon Cr. 2	Congdon Cr. 2	Deer Creek	Deer Creek	Deer Creek	Square Top	Square Top	Square Top
Patch:	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
<i>Tiarella trifoliata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tolmiea menziesii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trifolium</i> spp	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trillium</i> spp	0	3	0	2	0	0	0	0	0	0	0	0	0	1	1
<i>Vancouveria hexandra</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Viola</i> spp	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Bryophyte cover:	70	30	65	4	8	20	25	70	30	20	70	80	100	70	65

TABLE A.3 (continued)

Coast Range shrub and herb list with cover values (%)



Figure B.1 Section (adaxial) of a Devil's club shade leaf (actual size).

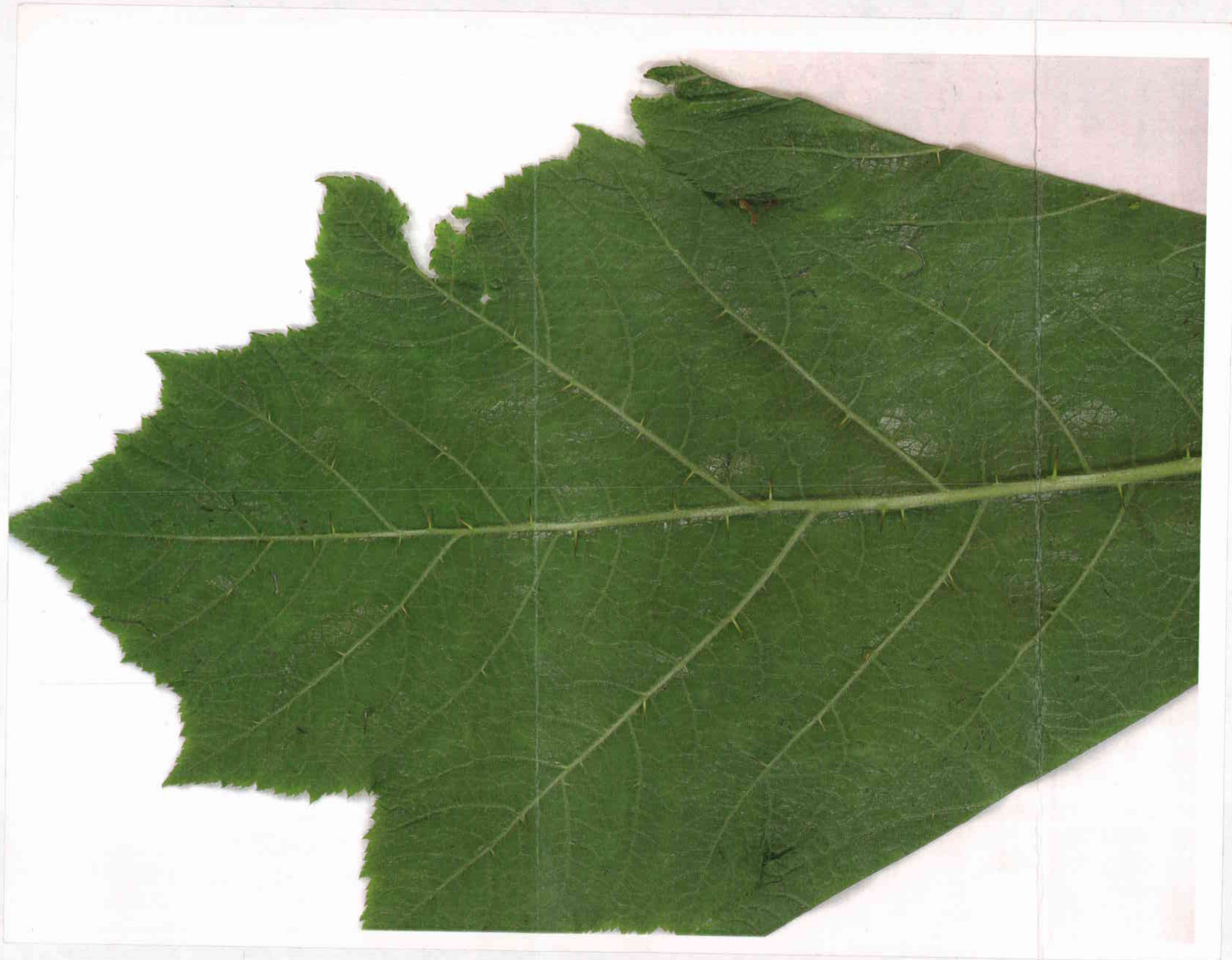


Figure B.2 Section (abaxial) of a Devil's club shade leaf (actual size).



Figure B.3 Section (adaxial) of a Devil's club sun leaf (actual size).

APPENDIX C FIELD NOTES AND SKETCHES OF FLOWERING, STEM GROWTH AND BRANCHING STUDY

Field sketches and notes primarily include stem increment lengths (cm) of layered/horizontal parts of stem sections. Some vertical stems are presented and are noted. Increments of vertical stems not presented were recorded on separate data sheets. Generally, branches were considered 'vertical' if not layered or growing generally horizontal to the ground. Stems were aged back to the origin of the stem complex.

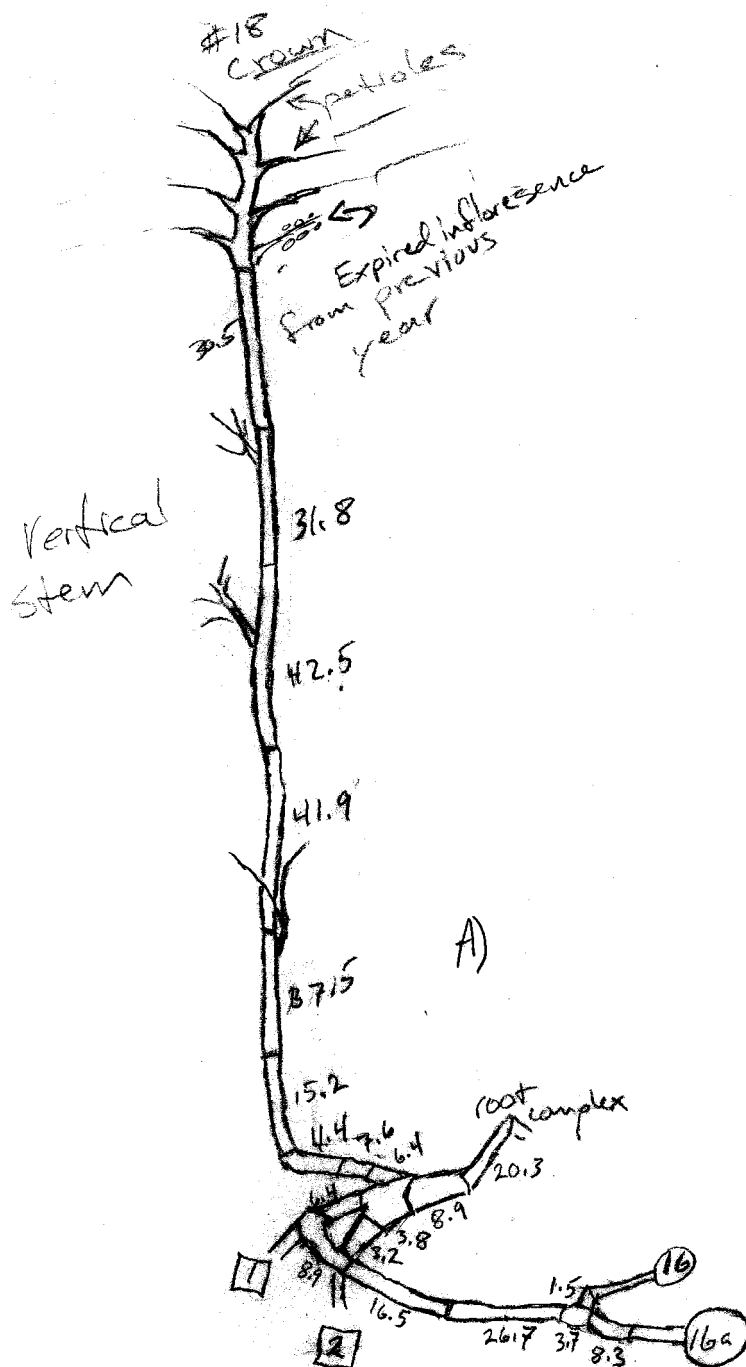


FIGURE C.1 Oliver Creek site. A) Field sketch and notes of vertical stem. Increment lengths are in centimeters. Circled numbers and letters are vertical stems (not presented). See Figure 3.4 for complete map of plot from which this stem was selected.

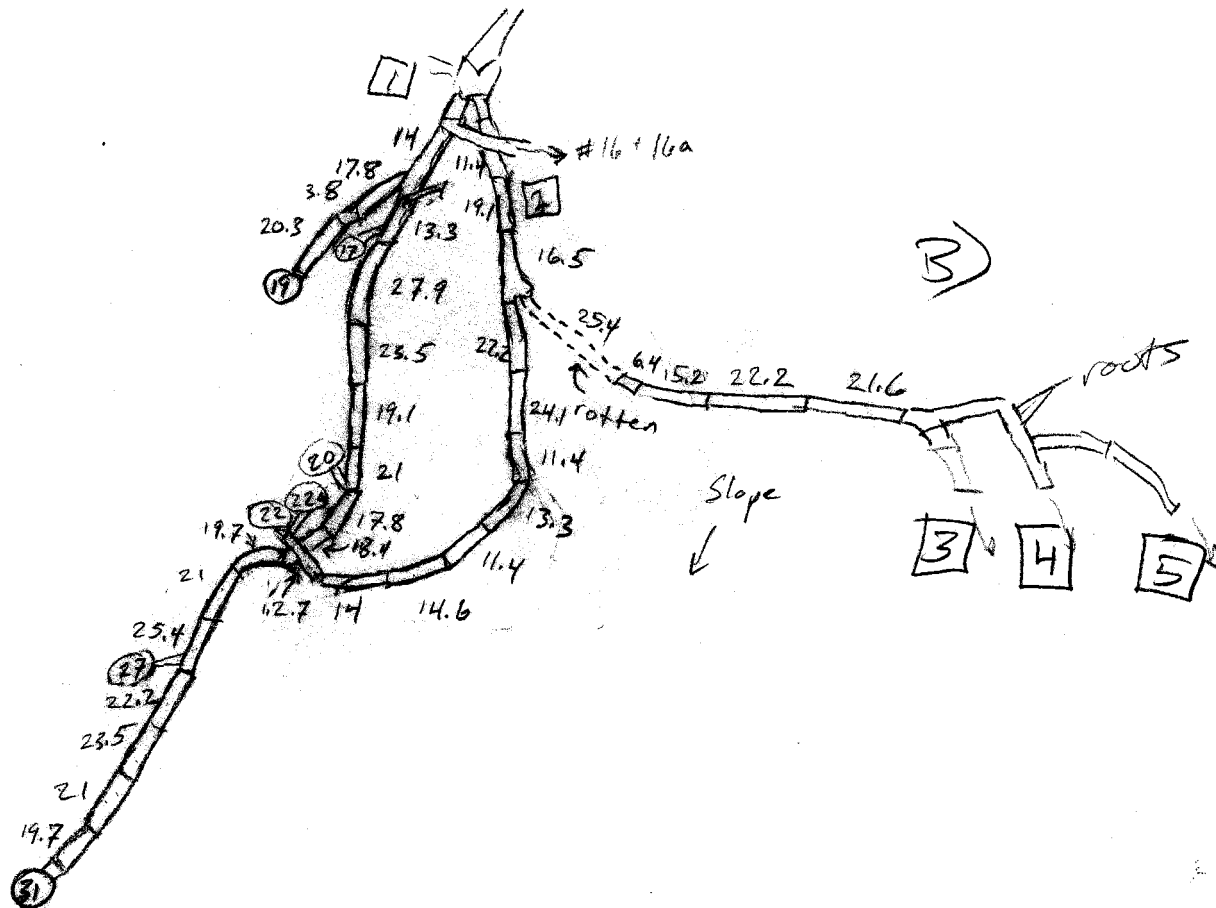


FIGURE C.1 (continued)

Oliver Creek site. B) Field sketch and notes of stem complex continued from A).

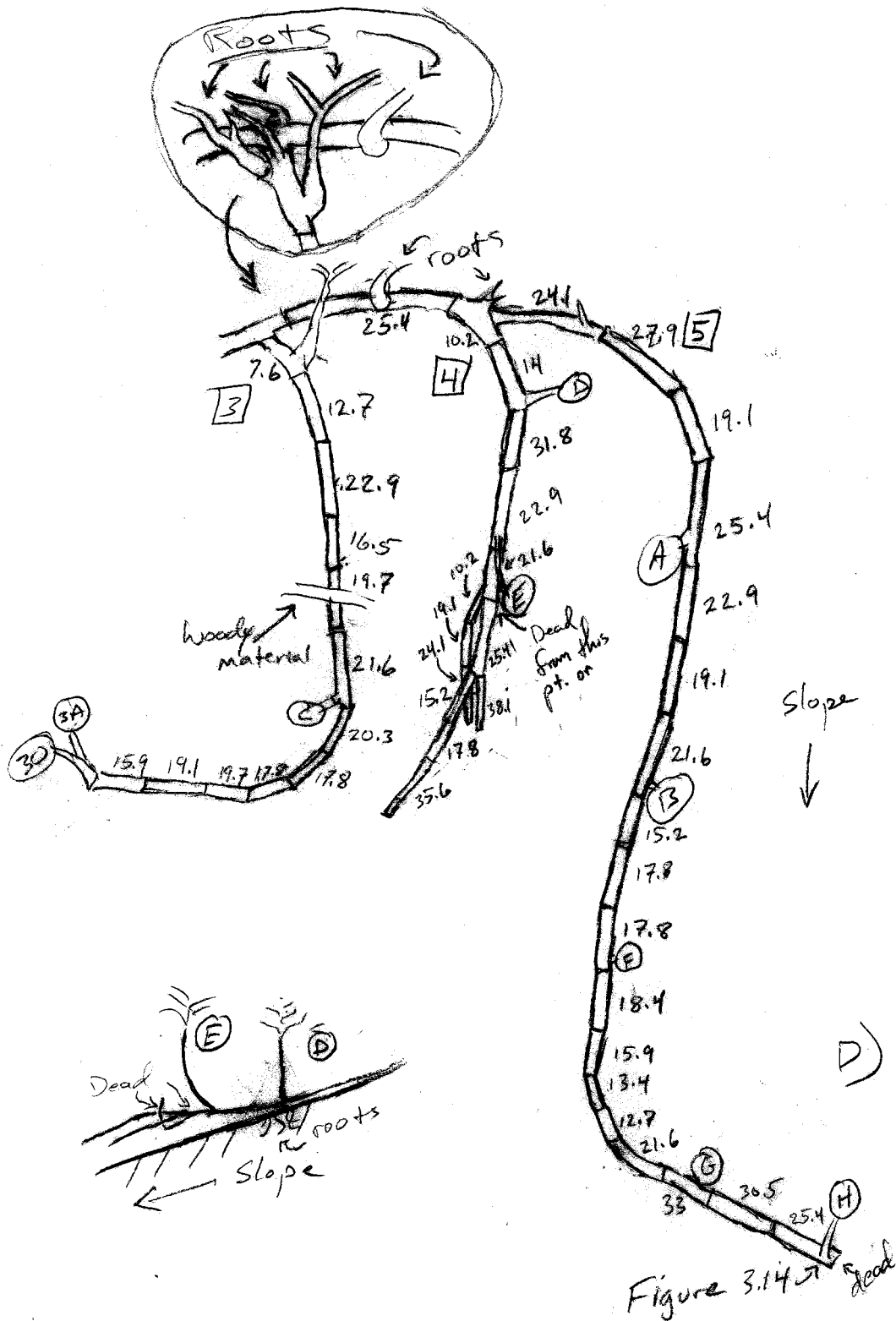


FIGURE C.1 (continued)

Oliver Creek site. D) Field sketch and notes of stem complex continued from B). E) Side view illustration of part of stem complex.



FIGURE C.1 (continued) Oliver Creek site. C) Diagram of whole stem complex.

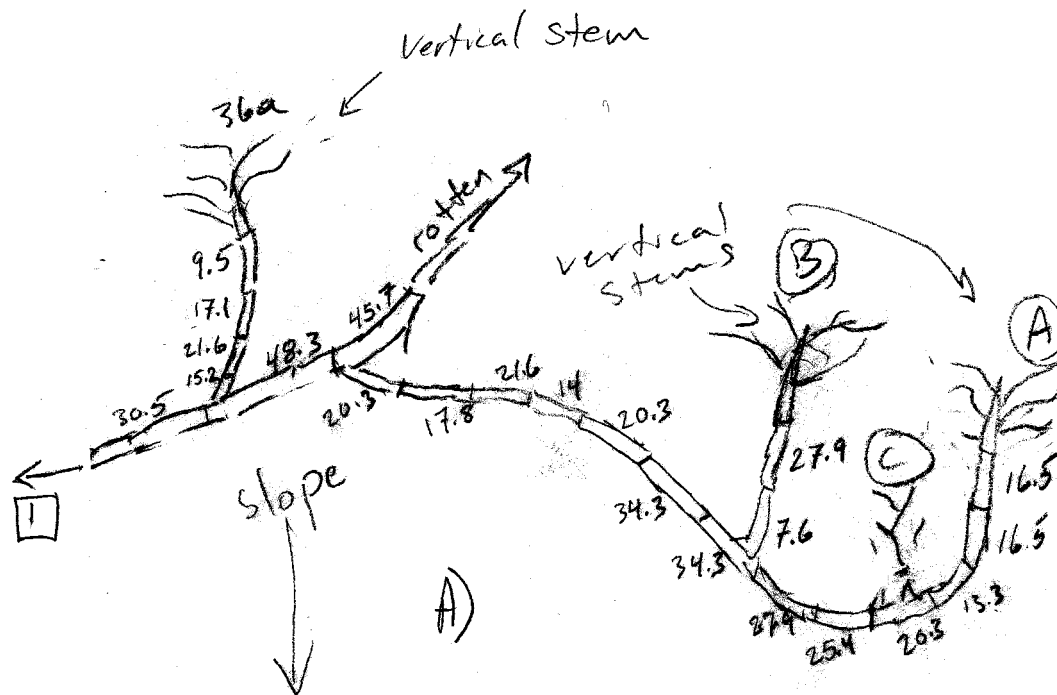


FIGURE C.2 Nestucca River site. A) Field sketch and notes of stem complex. Increment lengths are in centimeters.

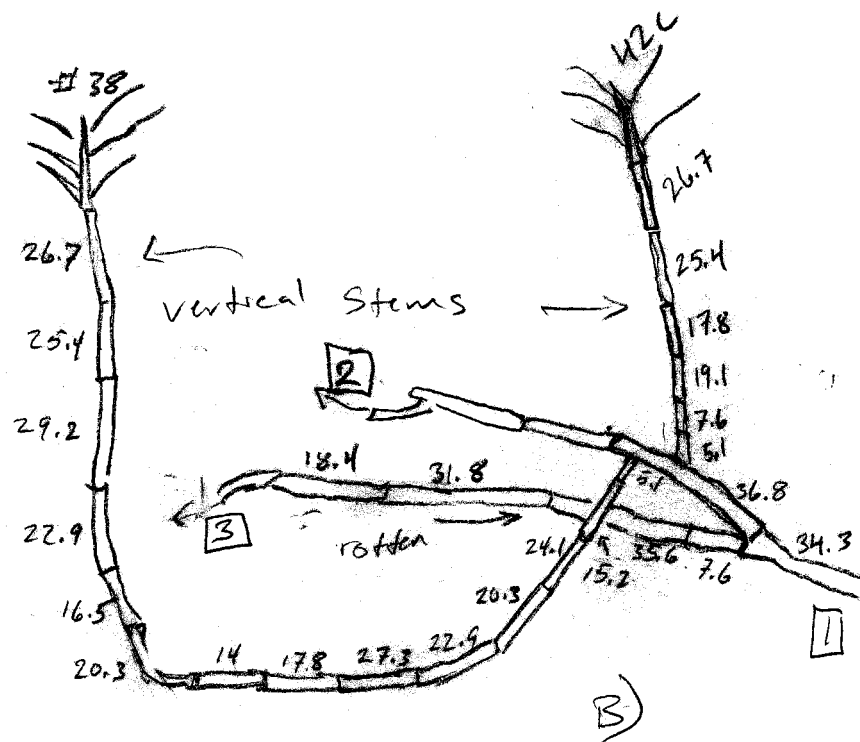


FIGURE C.2 (continued) Nestucca River site. B) Field sketch and notes of stem complex continued from A).

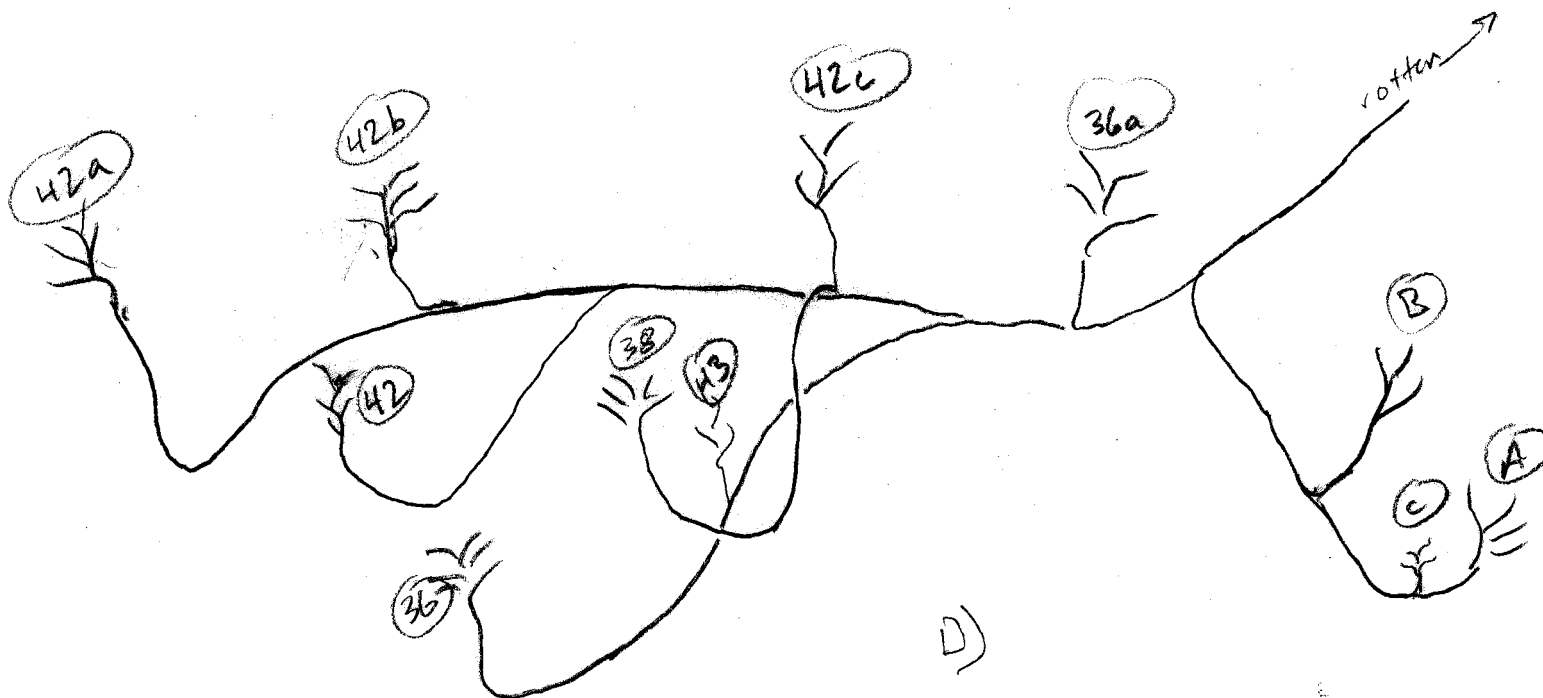


FIGURE C.2 (continued)

Nestucca River site. D) Diagram of stem complex.

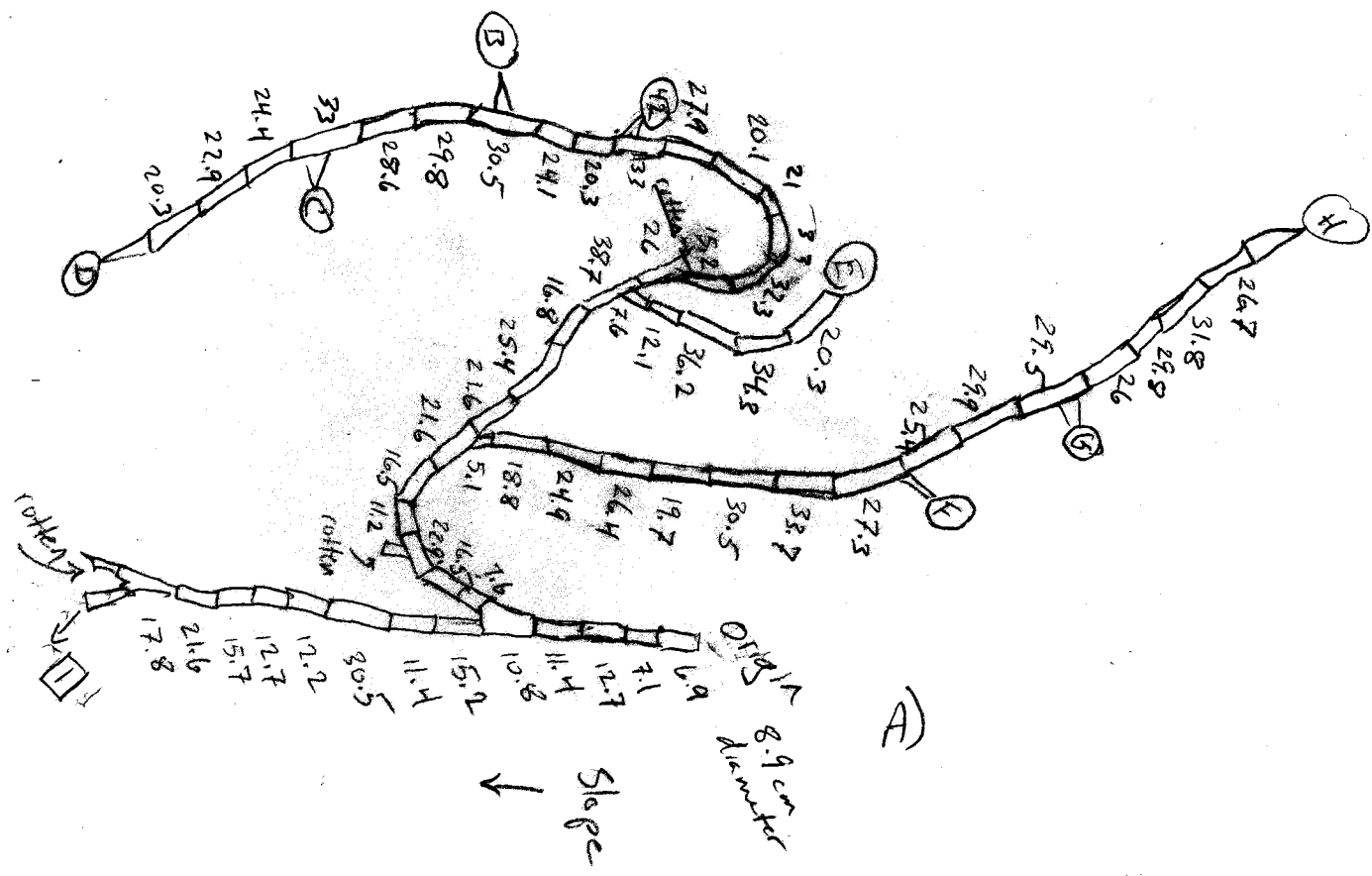


FIGURE C.3 Nettle Creek site. A) Field sketch and notes of stem complex. Increment lengths are in centimeters. Circled numbers and letters are vertical stems.

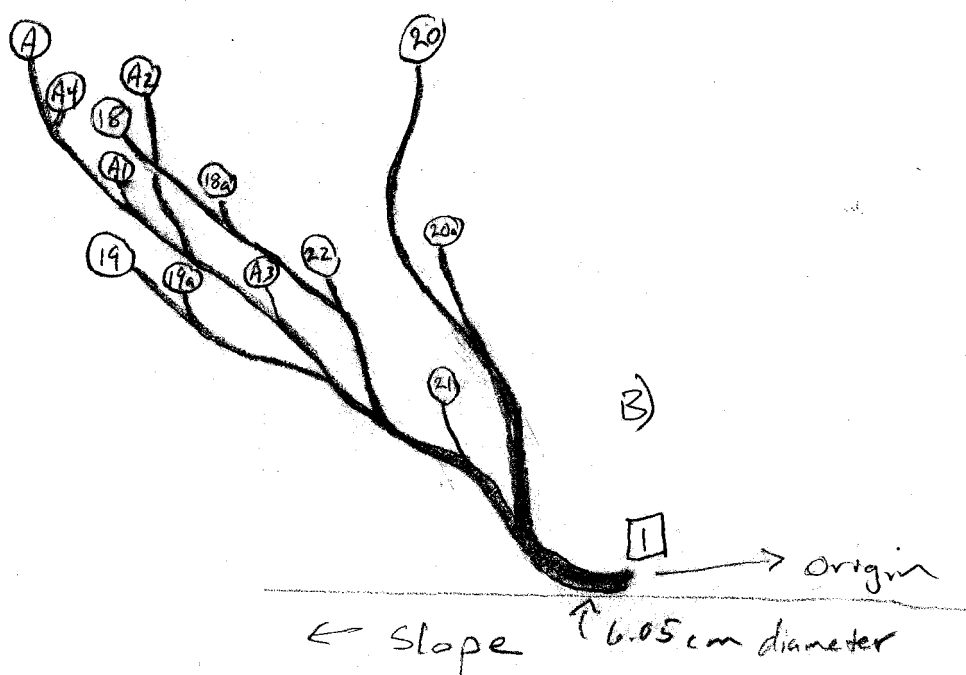


FIGURE C.3 (continued)

Nettle Creek site. B) Side view illustration of aerial section of stem complex.

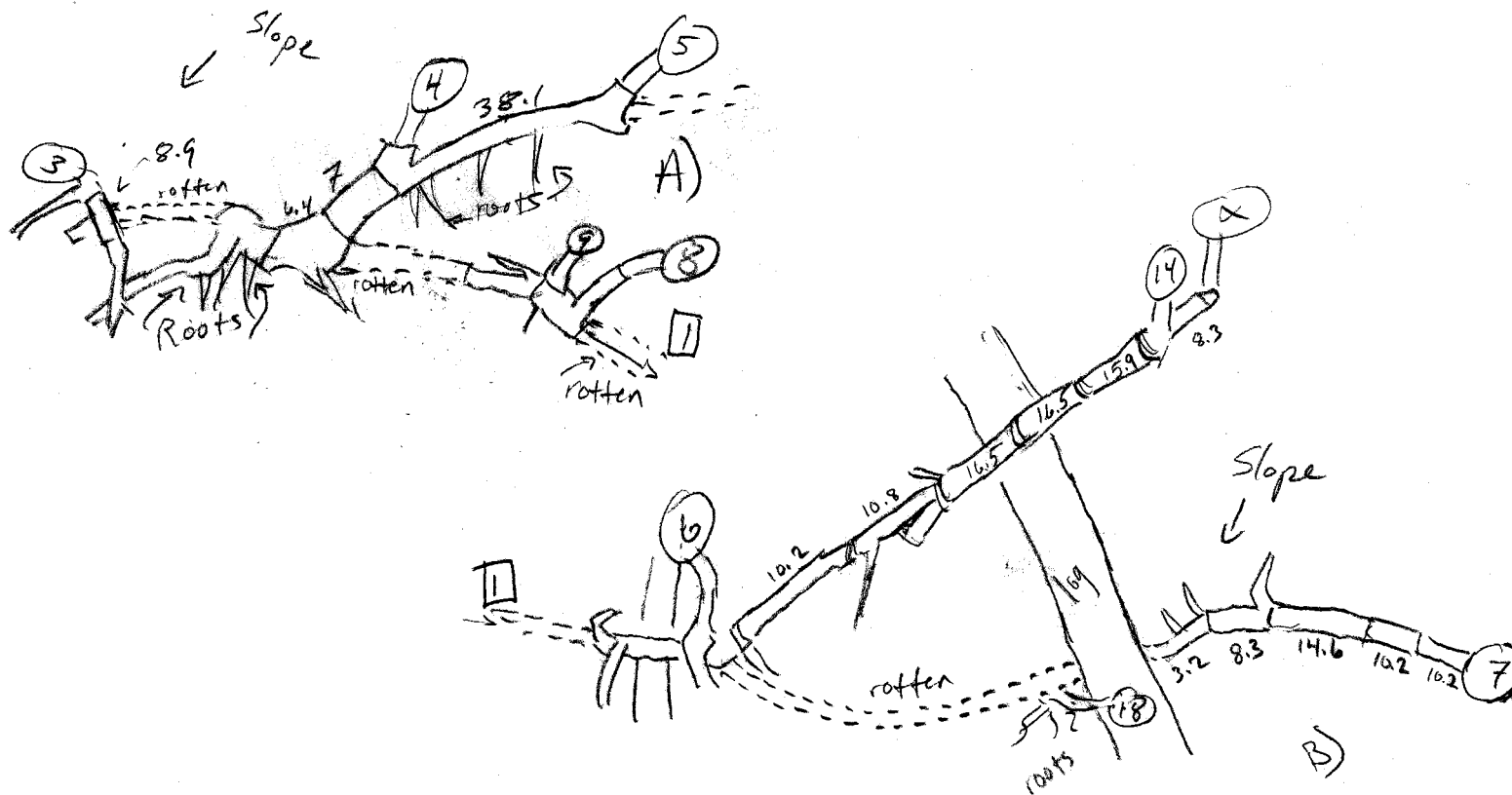


FIGURE C.4 Beaver Creek site. A) Field sketch and notes of stem complex. Increment lengths are in centimeters. Circled numbers and letters are vertical stems. B) Stem complex continued from A).

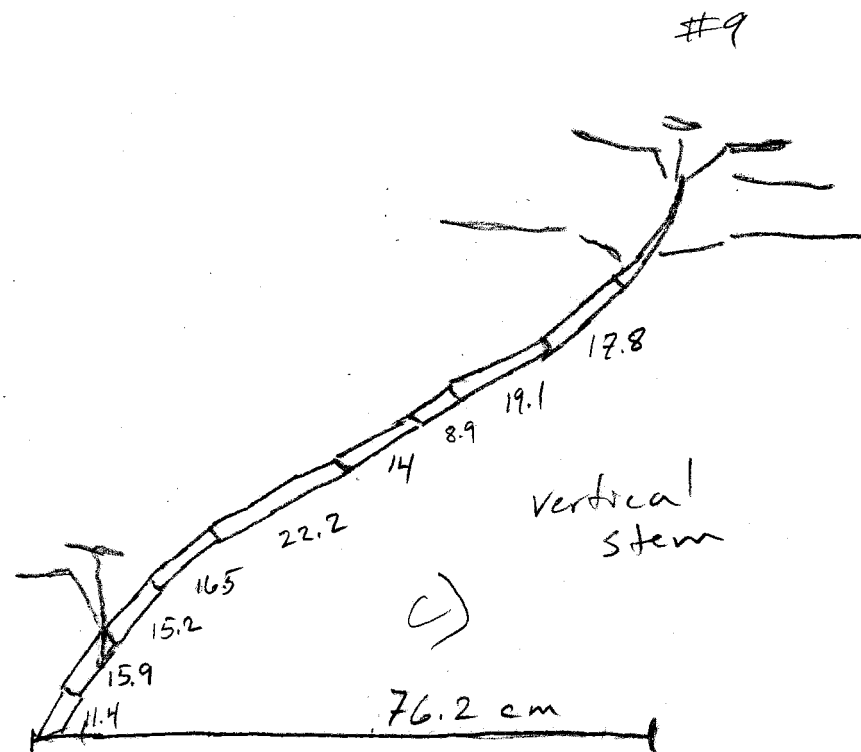


FIGURE C.4 (continued)

Beaver Creek site. C) Side view illustration of selected vertical stem.

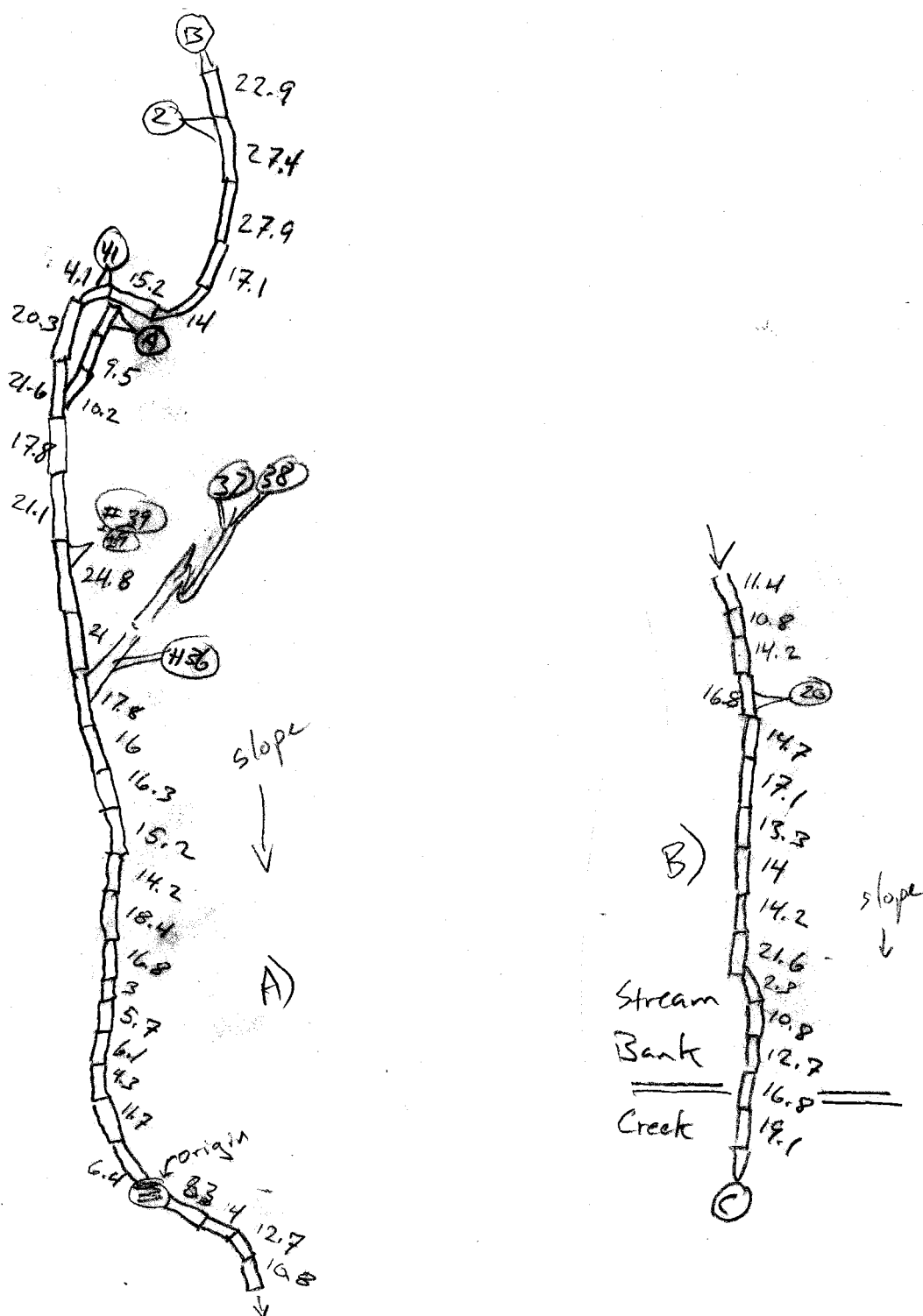


FIGURE C.5 Rock Creek site. A) Field sketch and notes of stem complex. Increment lengths are in centimeters. Circled numbers and letters are vertical stems. B) Stem complex continued from A).

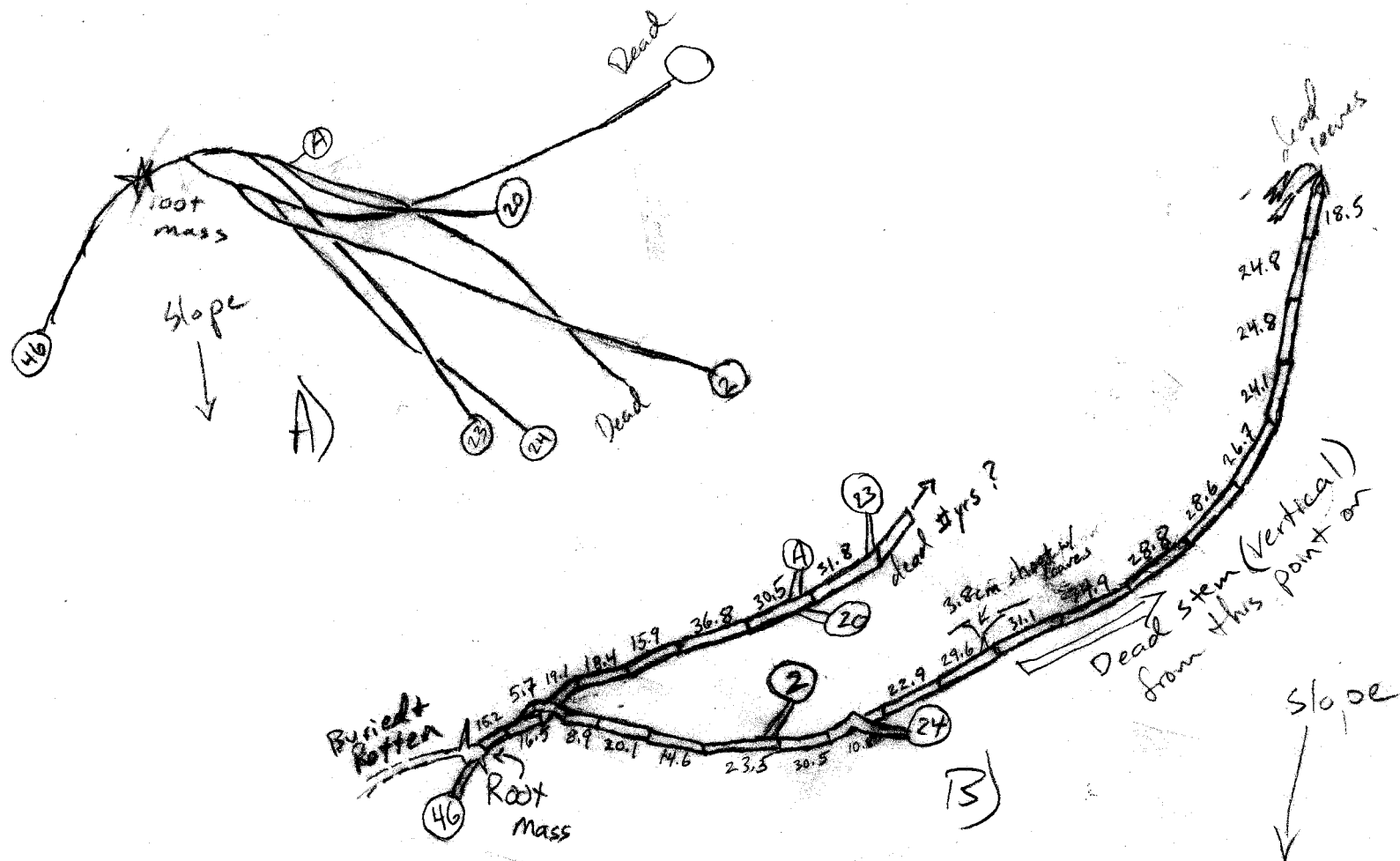


FIGURE C.6 Bummer Creek site. A) Diagram of stem complex. B) Field sketch and notes of stem complex. Increment lengths are in centimeters. Circled numbers and letters are vertical stems.

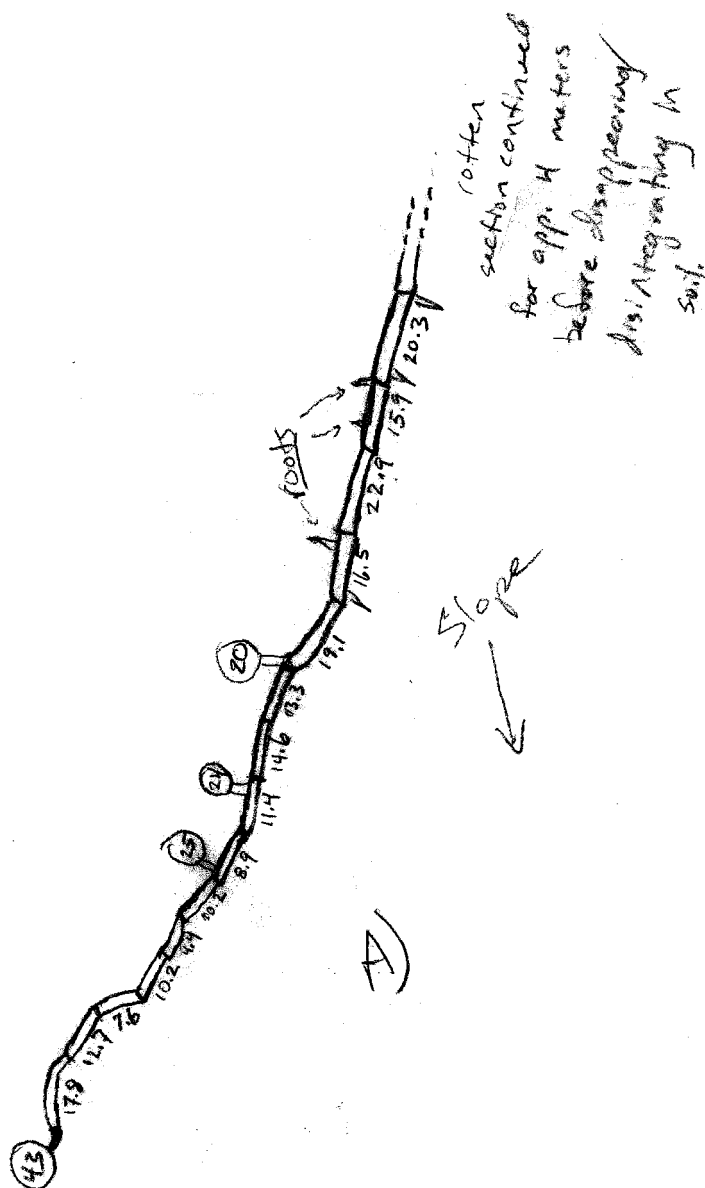


FIGURE C.7 Tobe Creek site. A) Field sketch and notes of stem complex. Increment lengths are in centimeters. Circled numbers and letters are vertical stems.

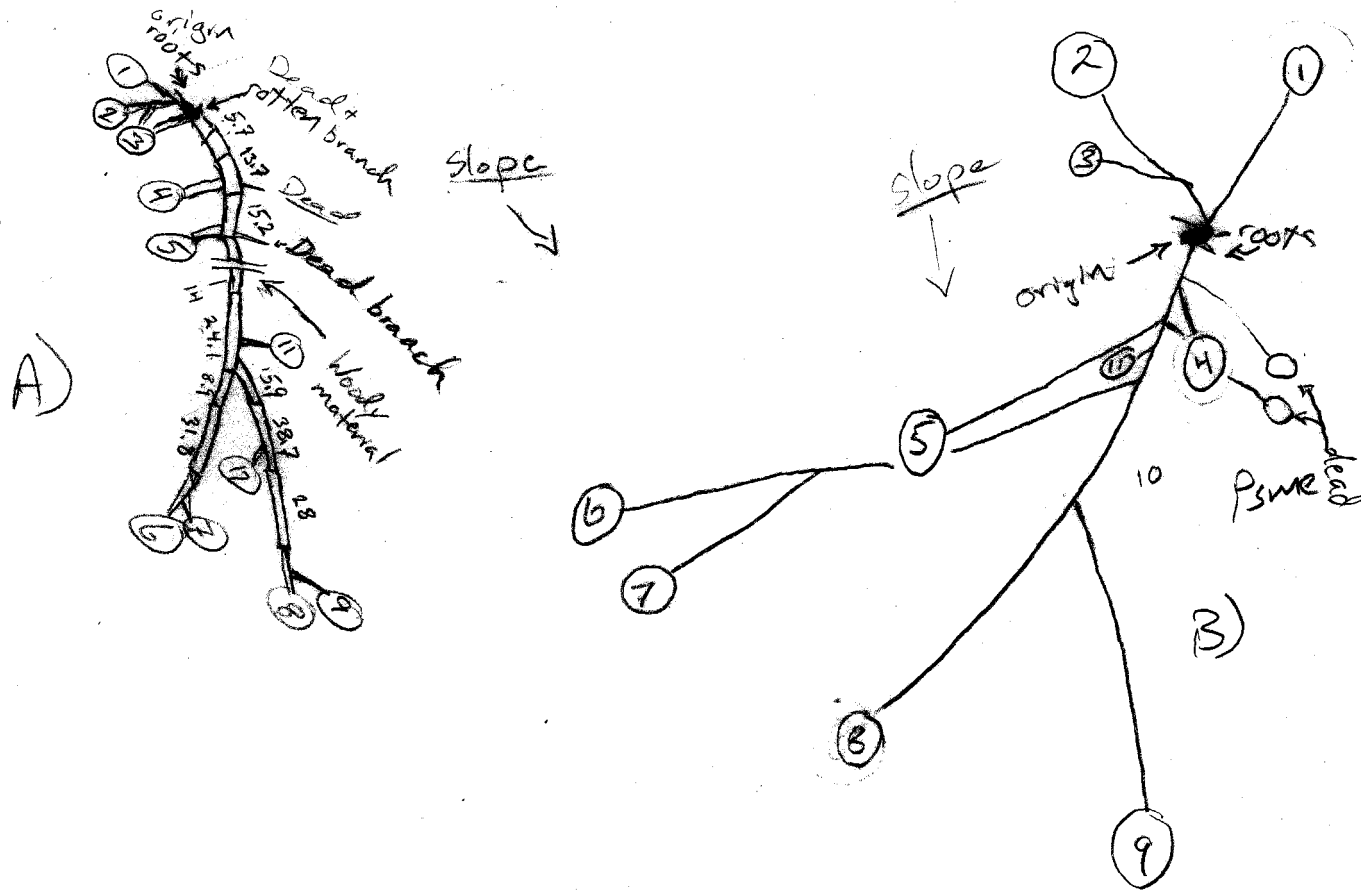


FIGURE C.8 Prairie Mtn. 1 site. A) Field sketch and notes of stem complex. Increment lengths are in centimeters. Circled numbers and letters are Devil's club crowns. B) Diagram of stem complex

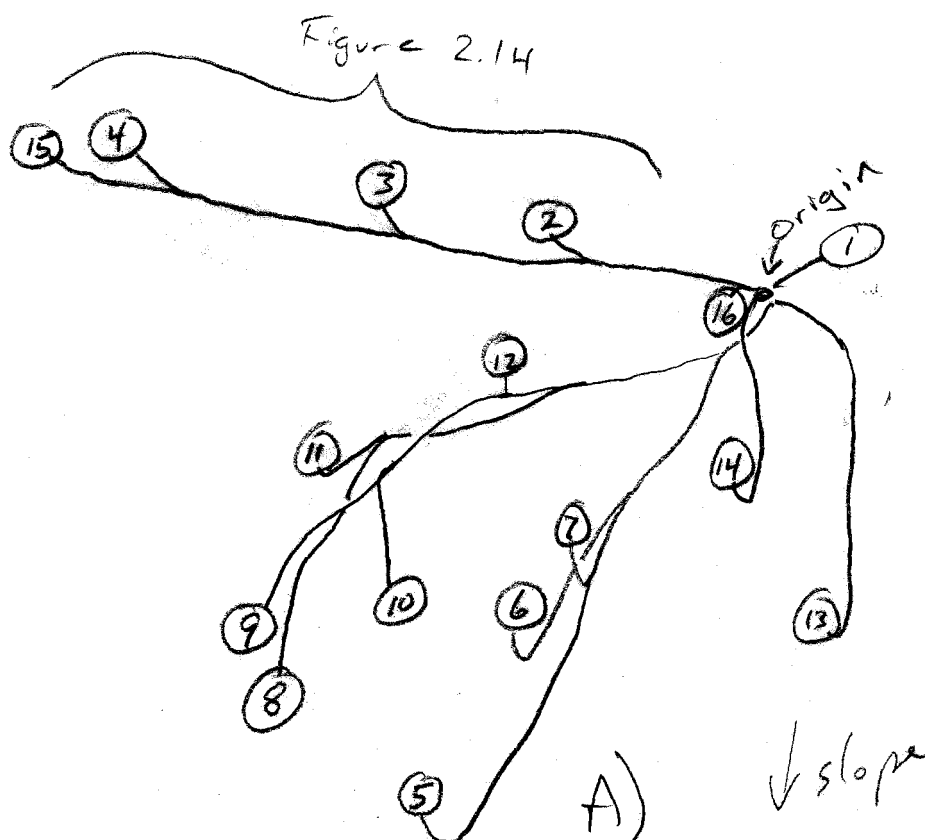


FIGURE C.9 Prairie Mtn. 2 site. A) Diagram of stem complex. Circled numbers are vertical stems. Crowns 2, 3, 4 and 15 are also presented in Figure 2.14.