

Substrate Effects on Distribution, Biomass Allocation, and Morphology of Forest  
Understory Plants

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A thesis  
submitted in partial fulfillment of the  
requirements for the degree of

Master of Science

University of Washington

2007

Program Authorized to Offer Degree:  
College of Forest Resources

University of Washington  
Graduate School

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**Abstract**

Substrate Effects on Distribution, Biomass Allocation, and Morphology of Forest Understory Plants

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Considerable research has been devoted to the role of coarse woody debris (CWD) in forest ecosystems. However, few studies have examined how plant distribution and performance are affected by rooting substrate. I tested whether understory plant species showed an affinity for CWD or the forest floor in a young coniferous forest in western Washington. For three common species with differing substrate affinities, I also tested whether rooting substrate affected allocation to above- and below-ground structures, morphological traits, or overall performance (total biomass and plant nitrogen), consistent with differences in moisture availability between substrates.

I tested whether understory species showed significant associations with CWD or the forest floor using 1200, 1 x 1 m quadrats in which I compared cover of CWD and forest floor (as measures of substrate availability) and the density of shoots of each species emerging from each substrate. To examine relationships between rooting substrate and plant performance, I excavated three common understory species: *Tiarella trifoliata* (preference for forest floor), *Vaccinium parvifolium* (preference for CWD), and *Maianthemum dilatatum* (no preference for either substrate). For each species, the

below-ground structures (rhizomes and roots) and aerial shoots (stems and leaves) of 30 pairs of plants (one rooted in CWD, one in the forest floor) were measured, then dried to determine mass. Replicate samples of each substrate were collected every 3 wk (June through mid-September) to test for differences in volumetric moisture.

Most species (83%) displayed a preference for substrate; of these, 75% preferred the forest floor. Species preferences for CWD or forest floor did not appear to be related to plant stature or any other morphological or life-history trait. Most species may be associated with the forest floor because it is a more predictable and stable substrate. Alternatively, preference for the forest floor may relate to competition with mosses: moss cover was more than twice as high on CWD as on the forest floor (87 vs. 38%). Patterns of biomass allocation in *Maianthemum*, *Tiarella*, and *Vaccinium* were consistent with differences in moisture availability between substrates: plants rooted in the forest floor (which was consistently drier over the growing season) allocated greater biomass to below-ground structures. However, effects of substrate on above-ground traits (e.g., leaf density, leaf area, and shoot height) were non-significant, and effects on below-ground traits were largely inconsistent with differences in moisture availability between substrates.

Depth and lateral spread of rhizome systems may be determined by the physical structure of decaying logs rather than by resource availability. In addition, light may be so limiting in these forests that it masks the potential for species to respond to substrate-related differences in resource availability. Finally, it is possible that associations with substrates are driven not by differences in performance of established plants, but by differences in dispersal, germination, and/or early survival.

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## ACKNOWLEDGEMENTS

Many people contributed to this project, either by direct research assistance, or by enhancing my experience of graduate school. I would first like to thank my advisor, Charlie Halpern, for his guidance. I am grateful for his patience, advice, and sharing of knowledge in forest and plant ecology. My committee members, Bob Bilby and Doug Sprugel, have also offered valuable feedback and support throughout this process.

Several people provided field assistance for this project. I would like to thank Joe Antos for teaching me first-hand how to excavate understory plants, and for showing me the fun in following rhizomes to their live tips. I also owe thanks to Bob Bilby, Jim and Cathy Keeley, and Lauren Mollot for volunteering to spend a day in the field learning about my project and plant excavation. I am grateful for Anna Leon, John Six, and Mike Tjoekler who put in extensive field time excavating understory plants and enriched tedious field work with good attitudes and conversation. Fellow students and post-docs in the Halpern lab offered much advice and feedback throughout various stages in this project, and I am thankful for their help. My research greatly benefited from the statistical prowess of not only Charlie, but also Steve Duke, to whom I am very grateful. I thank Amy LaBarge and Rolf Gersonde of Seattle Public Utilities for encouraging and logistically supporting my research in the Cedar River Watershed..

I thank Weyerhaeuser Western Timberlands Research for providing financial assistance for graduate school, and to the people there for encouraging me to pursue a Master's degree. Many scientists and technicians at the Weyerhaeuser Technology Center in Federal Way, Washington and the George R. Staebler Forest Resources Research Center in Centralia, Washington have overwhelmed me with their support and assistance. They not only provided a large network of support during graduate school, but also facilitated my interest in pursuing a forest ecology career in the first place. Specifically, I thank John Browning, Jim Keeley, Tom Terry, Erin Wallich, and Patty Ward for sharing software, providing workspace, loaning equipment, answering questions, and offering sound advice on various aspects of my project.

My deepest thanks and appreciation go to my family. My parents took the time to come out to my field site and learn about my research, even excavating what turned out to be some of the longest *Maianthemum* rhizome systems recorded for my study. I am grateful for my dad who has proven to be a friendly comrade in the forestry profession, and for my mom and sister who always keep me in touch with the non-ecological parts of life. Most of all, I am grateful to John, whose unwavering support and encouragement has kept me sane throughout this experience. Getting my master's degree was indeed a team effort.

## INTRODUCTION

Coarse woody debris (CWD) plays many important ecological functions in forest ecosystems: creating habitat for wildlife; storing moisture, organic matter, and nutrients; and providing sites for asymbiotic fixation of nitrogen (Harmon et al. 1986, Stevens 1997). Considerable attention has been devoted to the role of CWD as a substrate for tree seedlings (e.g., Christy and Mack 1984, Harmon and Franklin 1989, Simard et al. 1998, Takahashi et al. 2000, Narukawa and Yamamoto 2003, Zielonka 2006) and forest floor bryophytes (e.g., Crites and Dale 1998; Rambo and Muir 1998a, 1998b; Kruys and Jonsson 1999; Turner and Pharo 2005). For example, in the western Cascades of Oregon, Christy and Mack (1984) found that 98% of *Tsuga heterophylla* seedlings regenerated on decayed logs although logs typically cover only 4-11% of the forest floor (Spies et al. 1988). Zielonka (2006) observed a similar association of *Picea abies* seedlings with CWD in subalpine forests in the Carpathian Mountains of Poland. Preferential establishment of tree seedlings on logs has been attributed to the greater moisture-holding capacity of decayed wood and to an escape from competition with understory vegetation on the forest floor (e.g., Harmon and Franklin 1986, Simard et al. 1998). Similarly, mosses and liverworts that are sensitive to desiccation or are easily overgrown by vascular plants display an affinity for CWD (e.g., Rambo and Muir 1998a, Turner and Pharo 2005), and forests with a greater abundance of decayed logs often support richer bryophyte communities (Andersson and Hytteborn 1991, Berg et al. 1994, Rambo and Muir 1998b).

In contrast, limited research has been devoted to the role of CWD in the

distribution of forest herbs or shrubs (but see Lemon 1945, Thompson 1980). Previous studies suggest that different patterns of association are possible. In some forests, few understory species show an affinity for a particular substrate (e.g., McGee 2001). Elsewhere, logs and stumps support only a subset of the forest-floor community (Thompson 1980). Finally, woody substrates and the forest-floor can support distinctly different plant communities (Kennedy and Quinn 2001, Lee and Sturges 2001) although these differences can diminish over time as logs decay and are gradually colonized by species from the forest floor (e.g., Lee and Sturges 2001).

Several mechanisms may explain the associations of some herbaceous or woody species with CWD. By establishing on logs, short-statured species may avoid competition with taller, more vigorous plants. Thus, the ability to germinate and persist on logs may be advantageous in the forest understory where light is often limiting (Tappeiner and Alaback 1989, Lieffers et al. 1999, Lezberg et al. 2001). Other resources may also be more available in CWD than on the forest floor. For example, decayed wood has greater ability to retain water than does fine litter or mineral soil (Harmon et al. 1986). Thus, in forests in which moisture is limiting during the growing season, logs can provide more stable sources of water. Although available mineral N ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) may not differ between woody and non-woody substrates (Bazzaz 1996, Hart 1999, Takahashi et al. 2000), some species — particularly those with ecto- or ericoid mycorrhizae — may capitalize on organic forms of N in wood (Read 1991; Kaye and Hart 1997; Näsholm et al. 1998, 2000; Aerts and Chapin 2000), leading to a positive association with these substrates.

Differences in resource availability among substrates also have the potential to affect plant size and morphology. Low resource availability can limit growth and biomass accumulation in clonal forest herbs (Tappeiner and Alaback 1989, Huffman and Tappeiner 1997, Lezberg et al. 2001). However, plants may also respond to resource limitation by changing allocation to above- or below-ground structures (Reynolds and Thornley 1982, Chapin et al. 1993, Paz 2003, Trubat et al. 2006). For example, at low levels of light, forest herbs may invest in leaves at the expense of below-ground structures (Givnish 1982). Conversely, where soil moisture or nutrients are limiting, allocation may shift to below-ground structures (Paz 2003, Trubat et al. 2006).

In addition to affecting allocation to above- and below-ground structures, differences in resource availability between substrates may influence the morphological attributes of plants. This should be particularly apparent in clonal herbs that are able to vary the density or spacing of ramets by adjusting the length or degree of branching of rhizome segments or stolons (Bell 1984). Where resources are limiting, greater foraging should lead to longer rhizome segments with lower branching density. Where resources are more plentiful, clonal plants should have shorter rhizome segments and greater branching (Slade and Hutchings 1987, de Kroon and Schieving 1991). However, resource acquisition also involves tradeoffs. If light is very limiting, the costs of investing in foraging organs (e.g., rhizomes) are unlikely to be offset by access to additional resources (de Kroon and Schieving 1991, Lezberg et al. 2001). Consequently, under conditions of extreme resource limitation, clonal plants may show very limited lateral spread or

branching, instead maintaining long-lived ramets in place through annual releafing (Ashmun and Pitelka 1984, Huffman et al. 1994, Lezberg et al. 2001).

In this study, I investigate the role of coarse woody debris in the distribution and performance of forest understory plants in a dense, second-growth stand in western Washington. The high density of trees and depauperate nature of the understory suggest that both light and below-ground resources are likely to be limiting. My research has three related components. First, I describe the distributions of understory herbs and shrubs with respect to two common substrates, fine litter on the forest floor and CWD. Second, I select three species with differing substrate affinities, *Tiarella trifoliata* (associated with forest floor), *Vaccinium parvifolium* (associated with CWD), and *Maianthemum dilatatum* (no association with either substrate), and compare biomass allocation, morphological traits, and overall performance (total biomass and plant nitrogen) between individuals rooted on the forest floor and on CWD. Finally, I quantify differences in moisture content and light availability between substrates and interpret patterns of plant performance with respect to these differences.

I pose two general and several specific hypotheses to guide my comparative studies of plant performance:

1. Plants rooted in CWD or in the forest floor will differ in patterns of biomass allocation and in morphological traits in ways that are consistent with the greater moisture-holding capacity of CWD. More specifically, plants rooted in CWD will have:
  - a. reduced allocation to below-ground structures (i.e., greater ratio of above- to

below-ground biomass),

- b. taller shoots, more leaves, and/or greater leaf area, and
  - c. smaller, shallower root systems (i.e., decreased root spread, area, and depth, and shorter rhizomes with greater density of branching and of rhizome tips).
2. Species will show differences in overall performance on CWD and the forest floor consistent with their affinities for these substrates. More specifically,
- a. *Vaccinium* will exhibit greater overall performance (total biomass, plant N) on CWD than on the forest floor,
  - b. *Tiarella* will exhibit greater overall performance on the forest floor, and
  - c. *Maianthemum* will show comparable performance between substrates.

## METHODS

### *Study Site*

The study site is in the Cedar River Municipal Watershed in the western foothills of the central Cascade Mountains of Washington (47°20'N, 121°32'W). It lies at 600 m elevation on a shallow southwest-facing slope (<10%) above Bear Creek. Soils are classified as Kaleetan sandy loam (<http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx>). Climate is maritime, with cool wet winters and warm, relatively dry summers (Franklin and Dyrness 1988). Mean maximum daytime temperatures occur in August (22°C); mean minimum daytime temperatures occur in January (-1°C). Annual precipitation averages 256 cm, with ~50% falling between November and February. Annual snowfall averages 166 cm, concentrated between December and March (climate-station data from nearby Cedar Lake; 475 m elevation; 1931-2005, Western Regional Climate Center, <http://www.wrcc.dri.edu/summary/climsmwa.html>).

The study forest regenerated naturally following clearcut logging ~60 yr ago. Historical data are lacking, but stumps indicate previous dominance by old-growth *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Thuja plicata*. The current stand is dense with 1,425 stems/ha (trees  $\geq 1.4$  m tall) and a basal area of 75 m<sup>2</sup>/ha (D. Sprugel, unpublished data). *Tsuga heterophylla* is the dominant species (70% of stems, 58% of basal area), with lesser amounts of *P. menziesii* (21% of stems, 36% of basal area). Understory light is uniformly low, generally <5% of above-canopy light (K. Grieve, unpublished data). Coarse woody debris is abundant on the forest floor, a result of previous timber harvest and ongoing mortality due to self-thinning. Understory plant

cover is very low, averaging 3% (C. Halpern, unpublished data) (Fig. 1).

### *Species Associations with Substrates*

Data were collected during summer 2005 to assess the abundance and potential associations of plant species with substrates. A total of 1200, 1 x 1 m quadrats were sampled. These were arrayed continuously along three, 400-m transects spaced 20 m apart, parallel with the slope contour. Within each quadrat an estimate was made of the percentage of ground surface covered by the two primary substrates, forest floor (mainly conifer needles and fine branches <10 cm diameter) and coarse woody debris (CWD; fresh or decayed logs >10 cm diameter). For each understory species (including trees <1.4 m tall), the number of shoots that emerged from each substrate was tallied; for fern species, the number of fronds was tallied. Nomenclature follows Hitchcock and Cronquist (1973).

To test whether species showed a significant association with CWD or forest floor, confidence limits for population proportions (Zar 1999) were calculated (Appendix I). For each species with a frequency of occurrence  $\geq 1\%$  (present in  $\geq 12$  plots), I estimated the proportion of stems rooted in CWD and a 95% confidence interval (CI) around the mean using the method of Zar (1999). A species whose lower confidence limit was greater than the mean cover of CWD (20.1%) was inferred to have a positive association with CWD; conversely, a species whose upper confidence limit was less than the cover of CWD was inferred to have a positive association with forest floor (i.e., a negative association with CWD). All other species were assumed to exhibit no substrate preference.





Fig. 1. A portion of the study site at Bear Creek. The stand was logged ~60 years ago and has regenerated naturally. Note the density of *Tsuga heterophylla*, abundance of coarse woody debris on the forest floor, and limited development of understory vegetation.

*Comparative Analyses of Substrate Effects on Plant Performance*

*Study species.* — Based on the results of species-substrate relationships, three species were selected for more intensive study to examine whether rooting substrate influenced plant performance. *Maianthemum dilatatum* (Liliaceae), *Tiarella trifoliata* (Saxifragaceae), and *Vaccinium parvifolium* (Ericaceae), were selected because (1) they were among the most common in the understory, (2) they could be found on both CWD and the forest floor, and (3) they showed differing associations with substrates: *Vaccinium* with CWD, *Tiarella* with the forest floor, and *Maianthemum* with neither substrate.

*Maianthemum dilatatum* (Wood) Nels. and Macbr. is a perennial, rhizomatous herb common in moist temperate forests of the Pacific Northwest where temperatures are relatively cool and moisture is fairly abundant (LaFrankie 1986, Henderson et al. 1989). Leaves are cordate to sagittate in shape, usually singular, and 5-11 cm long (Hitchcock et al. 1969). *Maianthemum* has a modular growth form. Ramets consist of a rhizome segment initiated at the base of a parent shoot and a below-ground short shoot that gives rise to a vegetative (leafy) or sexual shoot (leafy with a terminal inflorescence). Lezberg et al. (2001) provide a detailed description of its growth form and clonal architecture.

*Tiarella trifoliata* L. is a perennial, rhizomatous herb, but non-clonal. Its distribution extends from southeast Alaska to the west coast of California, and includes Washington, Oregon, and Idaho (Soltis et al. 1992). *Tiarella* is usually found in moist woods and near streams (Hitchcock et al. 1969). *Tiarella* has three varieties that overlap in their distributions, vars. *trifoliata*, *unifoliata* (Hook.), and *laciniata* (Hook.); these

differ primarily in the width and relative dissection of leaf blades (Hitchcock and Cronquist 1973). Leaves are generally 5-12 cm long and cordate, and vary from palmately lobed (var. *unifoliata*) to divided into three separate leaflets, each with shallow lobes (var. *trifoliata*) or nearly divided (var. *laciniata*) (Hitchcock et al. 1969). All were present in my study site with varying abundance.

*Vaccinium parvifolium* Smith occurs west of the Sierra Nevada and Cascade Mountains from Washington to California, and in coastal areas of British Columbia and Alaska (Camp 1942). It is common in the *Picea sitchensis*, *Tsuga heterophylla*, and *Abies amabilis* forest zones of western Washington and northwestern Oregon (Franklin and Dyrness 1988). It is a deciduous shrub that can grow to 4 m tall, but juvenile plants (up to 4-5 yr) maintain a trailing habit (Camp 1942, Hitchcock and Cronquist 1973). Branches are green and strongly angled; leaves are deciduous, alternate, 1-2 cm long, and oval to elliptical-in shape (Hitchcock et al. 1969).

*Sample selection and plant excavations.* — From 50 pairs of flagged individuals (focal shoots) of each species, 30 were randomly chosen for excavation and detailed measurement. Each sample pair consisted of a plant rooted on a decayed log (decay class IV; Fogel et al. 1973) and a nearby plant rooted in the forest floor; pairs were generally within 1 m of each other. All plants were selected from within a total area of 1.5 ha. *Vaccinium* was distributed throughout this area, but most *Maianthemum* and *Tiarella* were from a smaller area of ~0.3 ha. In addition, for *Vaccinium*, relatively small plants (generally <15 cm tall) were chosen to facilitate excavation and to ensure that below-ground structures were largely contained within the target substrate.

Beginning at the focal shoot of each plant, all below-ground structures and associated aerial shoots were carefully measured, mapped, and excavated using hand tools (Antos and Zobel 1984, Lezberg et al. 2001) (Appendix II). Excavations of *Maianthemum* included the entire clonal fragment (*sensu* Antos 1988) terminating in live or dead rhizome tips. Below-ground systems, particularly those of *Maianthemum*, often covered large areas and occasionally traveled off the intended substrate. For each sample, I recorded the proportion of the below-ground system present in each substrate. On average, plants rooted in CWD had 96% (*Maianthemum*) to 100% (*Tiarella* and *Vaccinium*) of their below-ground structures in the intended substrate. Corresponding values for plants rooted in the forest floor ranged from 90% (*Maianthemum*) to 95% (*Tiarella*).

*Plant measurements.* — Above-ground structures were quantified in several ways. For each plant, I counted the number of shoots. For each shoot I also measured height (*Maianthemum*, consisting of a single petiole and leaf) or length (*Vaccinium*, with the shoot stretched linearly). Shoot height was not measured for *Tiarella* because some plants had flowering stems while others did not. For all plants, I also counted total number of leaves (leaf density per plant), then separated leaves from stems and estimated total leaf area from a scanned image. Leaf area calculations were made using ImageJ 1.36b software (Wayne Rasband, National Institute of Health, Bethesda, Maryland). From total leaf area I then calculated the average area of a leaf (mean leaf area).

Detailed measurements of below-ground structures were also made, either directly during excavation or subsequently from maps constructed during excavation (see Antos

and Zobel 1984) (Fig. 2). Length and width of root system spread were expressed as the greatest longitudinal length and the perpendicular width of the root system, respectively. Rooting depth was estimated as the maximum depth of the root system measured from the top of the litter layer on mineral soil or on CWD. Rooting area was calculated as the product of length and width of root spread. Rooting volume was calculated as the product of rooting area and rooting depth. To determine whether log shape influenced rooting habit, root system shape was calculated as the ratio of length and width of the root system (with the expectation that plants on logs would have larger ratios).

Because of its modular, clonal habit, I measured several additional characteristics of the below-ground systems of *Maianthemum*. Each clonal fragment possessed multiple rhizome tips as a result of branching. I recorded the number of rhizome tips that were live (white and growing) and dead (brown and often fragmented) and expressed these relative to total rhizome length (i.e., density of live and dead tips; Fig. 2; see also Lezberg et al. 2001); density of total tips was then calculated by summation. Total rhizome length was calculated as the sum of the lengths of all rhizome segments. Density of rhizome branching was expressed as number of intersections (branching points) divided by total rhizome length.

After plants were excavated, they were transported to the lab, carefully rinsed to remove soil, and separated into above- and below-ground parts. These were dried at 70°C for 48 hr and weighed to the nearest 0.01 g. Above- and below-ground biomass was recorded; total biomass was then calculated by summation. For each species, two composite samples from each substrate were created from the 30 original plants to

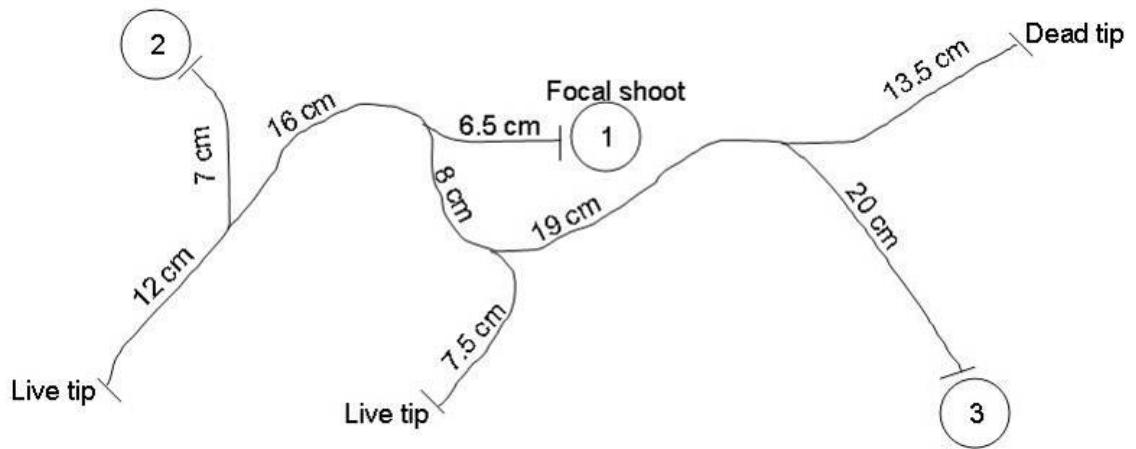


Fig. 2. Example of an excavation map for a clonal fragment of *Maianthemum dilatatum*. All rhizome segments (lengths between branches or aerial shoots) were measured. Circled numbers (used only during excavation) represent aerial shoots (petiole and leaf); rhizome tips were classified as live or dead (as labeled).

achieve enough mass for analysis of total plant N (using the automated combustion method; Gavlack et al. 2003). Although foliar N may be a better indicator of nutrient availability, whole plants were processed because of insufficient mass in leaves. Nevertheless, total plant N and foliar N are typically correlated (Kerkhoff et al. 2006). Analyses were performed by A and L Western Agricultural Laboratories, Inc. (Medford, Oregon).

*Additional measurements of the local environment.* — I took several additional measurements to test whether there were consistent differences in other attributes of the local environment that might explain, or contribute to, differences in plant performance between substrates. These included cover (%) of mosses and vascular plants (herbs, shrubs, and tree seedlings), and depth of litter. Cover estimates were made with a 0.2 x 0.5 m quadrat centered on the focal shoot; litter depth was measured near the base of the focal shoot. A rectangular quadrat was chosen because it closely resembled the shape of the log, and therefore measurements taken within the quadrat accurately reflected the local environment.

*Differences in moisture and light availability.* — To test for differences in moisture availability between substrates, I collected samples of CWD and forest floor soil. Samples were paired as a decay-class IV log and adjacent forest floor (typically <50 cm away), but were not associated with excavated plants. To quantify volumetric moisture, 20 samples of each substrate were collected every 3 wk from late June to mid-September 2005 (a total of five measurement times) using a Model 0200 Soil Core Sampler (Soilmoisture Equipment Corp., Goleta, California). Moss and larger organic

material (including fine branches and conifer needles) were first manually removed from the log or forest floor. A sample of 76.5 cm<sup>3</sup> (5.7 cm diameter) was extracted from the substrate between a depth of 2 and 5 cm, the region within which plants roots were most dense. Samples were weighed wet, dried at 35°C for 48 hr, and weighed again.

Volumetric moisture was computed as the difference between wet and dry weights divided by the sample volume.

I also tested whether light availability (photosynthetic photon flux density, PPFD) differed above plants rooted on CWD and the forest floor. PPFD ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) was measured with an AccuPAR LP-80 ceptometer (Decagon Devices Inc., Pullman, Washington). Measurements were taken after excavations were completed, at a height of 1 m above each sample location ( $n = 30$  samples per species per substrate). Readings were made between 10:50 and 12:00 hr (when the sun was most directly overhead) on 17 October 2006, a uniformly overcast day.

*Analyses.* — To test whether biomass allocation or morphology differed between plants rooted on CWD and forest floor (hypothesis 1), I conducted two-way analysis of variance (ANOVA) on each measure of plant performance. Sources of variation included substrate ( $df = 1$ ), species ( $df = 2$ ), and a substrate x species interaction ( $df = 2$ ). If the interaction was significant, a paired  $t$ -test was conducted to identify the species for which there was a significant effect of substrate. For below-ground characteristics measured only for *Maianthemum*, I used paired  $t$ -tests to assess differences between substrates.

A series of paired  $t$ -tests was also used to determine whether individual species showed differences in overall performance (total biomass) between substrates consistent



with their affinities for these substrates (hypothesis 2). Because there was sufficient plant material for only two composite samples of plant N per species by substrate, differences in plant N were not tested statistically.

To test whether additional, measured attributes of the local environment differed for plants rooted on CWD and forest floor (and thus, might explain differences between substrates), I conducted two-way ANOVA on total cover of mosses and vascular plants, and on litter depth. Sources of variation included substrate ( $df = 1$ ), species ( $df = 2$ ), and a substrate x species interaction ( $df = 2$ ). If the interaction was significant, a paired  $t$ -test was conducted to identify the species for which there was a significant effect indirectly associated with substrate.

Two-way ANOVA was also used to test for differences in moisture and light availability between substrates. For volumetric moisture, sources of variation included substrate ( $df = 1$ ), sampling date ( $df = 4$ ), and their interaction ( $df = 4$ ). (Because measurements were taken from different locations on each sampling date, repeated measures ANOVA could not be employed). For light availability, sources of variation included substrate ( $df = 1$ ), species ( $df = 2$ ), and their interaction ( $df = 2$ ).

Statistical analyses were conducted using the mixed model procedure in Statistical Analysis System (SAS) version 9.1 (SAS Institute, Inc. 1999). An alpha level of 0.05 was used to determine statistical significance. All data met the assumptions of normality and homogeneity of variance (based on Levene's test), thus transformations were not necessary.

## RESULTS

### *Species Associations with Substrates*

A total of 48 species was recorded in the 1200 quadrats (Table 1). The vast majority (97%) of quadrats contained stems of at least one species. Average and median stem densities were  $26.3/\text{m}^2$  (SE = 33.3) and  $15.0/\text{m}^2$ , respectively. Understory trees (<1.4 m tall but mostly first- and second-year seedlings) occurred in 87% of quadrats with a combined average density of  $8.6/\text{m}^2$ . Among the five tree species, *Tsuga heterophylla* comprised 74% of stems, and conifers 99.98% of stems. Tall shrubs occurred in 62% of quadrats with an average density of 6.4 stems/ $\text{m}^2$ ; most (97%) were *Vaccinium parvifolium*. Sub-shrubs (woody species, either short-statured or with a creeping or trailing habit) were present in 31% of quadrats with an average density of 4.1 stems/ $\text{m}^2$ . Ferns (five species) occupied 28% of quadrats with an average frond density of 1.6/ $\text{m}^2$ . Herbs occupied 48% of quadrats with an average stem density of 5.7/ $\text{m}^2$ . Of 25 herb species, four occurred in >10% of quadrats (*Clintonia uniflora*, *Tiarella trifoliata*, *Smilacina stellata*, and *Maianthemum dilatatum*).

CWD covered an average of 20.1% of the ground surface. Of the 29 understory species tested (those with  $\geq 1$  % frequency), six showed positive associations with CWD (one tree, two tall shrubs, one sub-shrub, and two ferns) and 18 showed positive associations with forest floor (one tree, four sub-shrubs, three ferns, and ten herbs) (Fig. 3).

Table 1. Frequency and density of understory species at Bear Creek. Frequency is the proportion of quadrats in which a species occurred ( $n = 1200$ ). Values  $<0.01$  are listed as “t” (trace).

Growth form	Species	Frequency (%)	Mean density (no./m <sup>2</sup> )	SE
Trees	<i>Tsuga heterophylla</i>	68.58	6.35	0.36
	<i>Abies</i> spp. ( <i>A. amabilis</i> / <i>A. procera</i> )	61.17	2.20	0.11
	<i>Acer macrophyllum</i>	0.08	t	t
	<i>Thuja plicata</i>	0.17	t	t
	<i>Alnus rubra</i>	0.08	t	t
	Total trees	86.33	8.56	0.39
Tall shrubs	<i>Vaccinium parvifolium</i>	60.08	6.19	0.27
	<i>Menziesia ferruginea</i>	5.08	0.12	0.02
	<i>Oplopanax horridus</i>	1.17	0.01	t
	<i>Acer circinatum</i>	0.83	0.02	0.01
	<i>Gaultheria shallon</i>	0.50	0.01	0.01
	<i>Sorbus sitchensis</i>	0.08	t	t
	Total tall shrubs	61.58	6.36	0.27
Sub-shrubs	<i>Cornus canadensis</i>	16.25	1.13	0.02
	<i>Linnaea borealis</i>	9.33	2.44	0.42
	<i>Chimaphila menziesii</i>	9.33	0.27	0.03
	<i>Rubus ursinus</i>	3.42	0.07	0.01
	<i>Rubus pedatus</i>	1.67	0.15	0.04
	<i>Rubus lasiococcus</i>	1.25	0.02	0.01
	Total sub-shrubs	30.83	4.08	0.46
Ferns	<i>Pteridium aquilinum</i>	21.25	0.43	0.03
	<i>Dryopteris austriaca</i>	3.83	0.14	0.02
	<i>Athyrium filix-femina</i>	4.08	0.37	0.07
	<i>Blechnum spicant</i>	2.92	0.34	0.08
	<i>Polystichum munitum</i>	3.00	0.28	0.07
	Total ferns	27.75	1.57	0.16
Herbs	<i>Clintonia uniflora</i>	29.33	1.31	0.09
	<i>Tiarella trifoliata</i>	15.17	1.23	0.14
	<i>Smilacina stellata</i>	15.08	0.85	0.09
	<i>Maianthemum dilatatum</i>	12.00	0.69	0.07
	<i>Viola sempervirens</i>	6.83	0.76	0.14
	<i>Streptopus amplexifolius</i>	5.92	0.21	0.04
	<i>Listera cordata</i>	4.08	0.16	0.04
	<i>Goodyera oblongifolia</i>	3.42	0.07	0.01
	<i>Trillium ovatum</i>	3.08	0.04	0.01
	<i>Achlys triphylla</i>	2.83	0.11	0.03
	<i>Pyrola uniflora</i>	2.25	0.11	0.03
	<i>Disporum</i> spp.	1.50	0.02	0.01
	<i>Corallorhiza maculata</i>	1.33	0.05	0.11

Table 1. Continued.

Growth form	Species	Frequency (%)	Mean density (no./m <sup>2</sup> )	SE
Herbs (cont.)	<i>Galium triflorum</i>	0.92	0.05	0.02
	<i>Viola glabella</i>	0.75	0.02	0.01
	Graminoid sp.	0.58	0.01	t
	<i>Pyrola chlorantha</i>	0.42	0.02	0.01
	<i>Asarum caudatum</i>	0.33	0.02	0.01
	<i>Aruncus sylvester</i>	0.17	t	t
	<i>Hypopitys monotropa</i>	0.17	t	t
	<i>Listera caurina</i>	0.17	t	t
	<i>Lilium columbianum</i>	0.08	t	t
	<i>Osmorhiza chilensis</i>	0.08	t	t
	<i>Stenanthium occidentale</i>	0.08	t	t
	<i>Trautvetteria caroliniensis</i>	0.08	t	t
	<i>Trientalis latifolia</i>	0.08	t	t
Total herbs		48.08	5.73	0.41

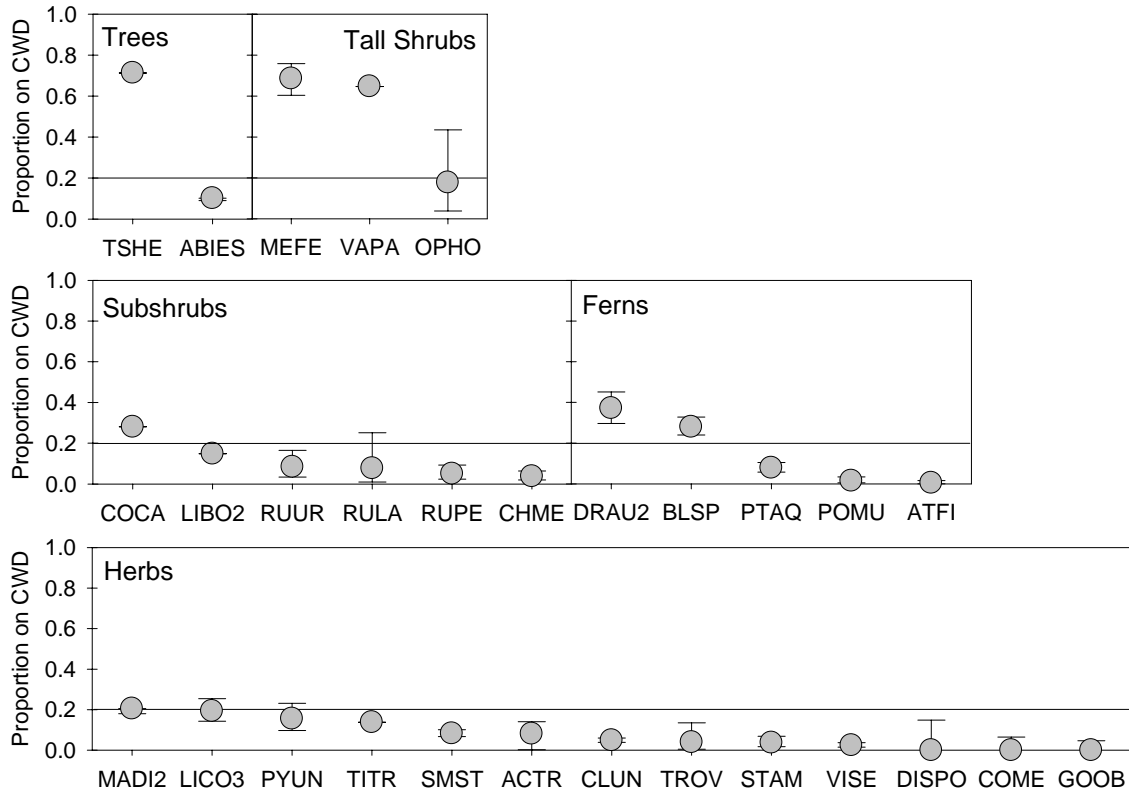


Fig. 3. Population proportions for understory species with >1% frequency (by growth form, arranged in descending order of preference for CWD). Trees were  $\leq 1.4$ m tall. Points represent mean proportions of shoots on CWD; bars are 95% confidence intervals. A species whose lower confidence limit is greater than the proportion of ground surface covered by CWD (solid horizontal line, 0.20) has a positive association with CWD; a species whose upper confidence limit is lower than this value has a positive association with the forest floor. All other species display no substrate association. Codes are: Abies = *Abies* spp. (*A. procera* / *A. amabilis*), ACTR = *Achlys triphylla*, ATFI = *Athyrium filix-femina*, BLSP = *Blechnum spicant*, CHME = *Chimaphila menziesii*, CLUN = *Clintonia uniflora*, COCA = *Cornus canadensis*, COME = *Corallorhiza maculata*, DISPO = *Disporum* spp., DRAU2 = *Dryopteris austriaca*, GOOB = *Goodyera oblongifolia*, LIBO2 = *Linnaea borealis*, LICO3 = *Listera cordata*, MADI2 = *Maianthemum dilatatum*, MEFE = *Menziesia ferruginea*, OPHO = *Oplopanax horridus*, POMU = *Polystichum munitum*, PTAQ = *Pteridium aquilinum*, PYUN = *Pyrola uniflora*, RULA = *Rubus lasiococcus*, RUPE = *Rubus pedatus*, RUUR = *Rubus ursinus*, SMST = *Smilacina stellata*, STAM = *Streptopus amplexifolius*, TITR = *Tiarella trifoliata*, TROV = *Trillium ovatum*, TSHE = *Tsuga heterophylla*, VAPA = *Vaccinium parvifolium*, VISE = *Viola sempervirens*.

*Comparative Analyses of Substrate Effects on Plant Performance*

*Substrate effects on biomass allocation and morphology.* — Consistent with hypothesis 1a, plants rooted in CWD and forest floor differed in their patterns of biomass allocation. Plants rooted in CWD allocated significantly more biomass to above-ground structures (Fig. 4). This pattern was consistent for *Maianthemum*, which invested more in below-ground structures (ratio  $<1$ ), as well as *Tiarella* and *Vaccinium*, which invested more in above-ground structures (ratios  $>1$ ).

In contrast to patterns of biomass allocation, I was unable to detect a significant effect of substrate on any above-ground trait, including leaf density, shoot height, total leaf area, and mean leaf area (hypothesis 1b; Fig. 5).

Patterns of variation in below-ground traits (hypothesis 1c) were more complex, but largely inconsistent with my expectations (Fig. 6). Length of root spread and root system shape (ratio of length to width of root system) were significantly greater in CWD than in the forest floor. Although rooting depth differed between substrates for *Tiarella* and *Maianthemum*, for only *Tiarella* were trends consistent with hypothesis 1c: root systems were half as deep in CWD as in the forest floor. In contrast, *Maianthemum* exhibited deeper root systems in CWD. Width of root spread, rooting area, and rooting volume differed among species, but showed no response to substrate (Fig. 6).

Three of five of the additional below-ground traits measured for *Maianthemum* showed patterns inconsistent with hypothesis 1c: density of dead rhizome tips, total density of rhizome tips, and rhizome branching density were significantly lower for plants

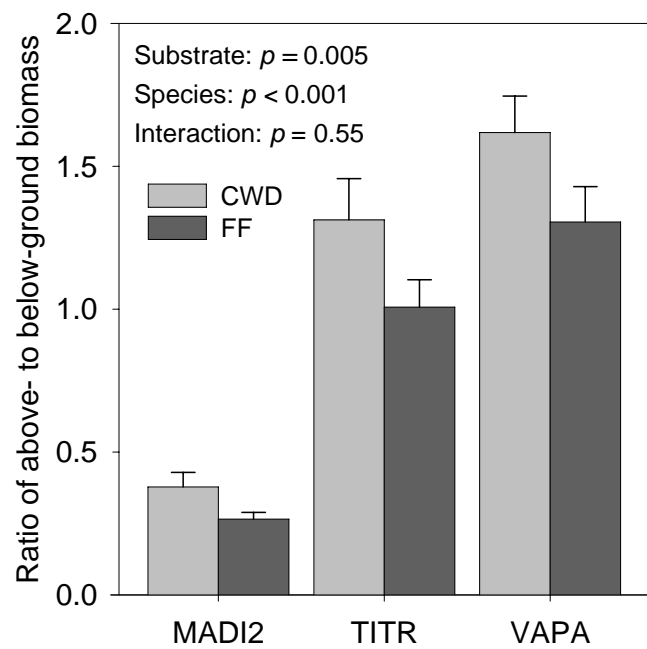


Fig. 4. Ratio of above- to below-ground biomass for *Maianthemum dilatatum*, *Tiarella trifoliata*, and *Vaccinium parvifolium* rooted in CWD and the forest floor. Values are means  $\pm$  1 SE.  $P$  values are from two-way analysis of variance.

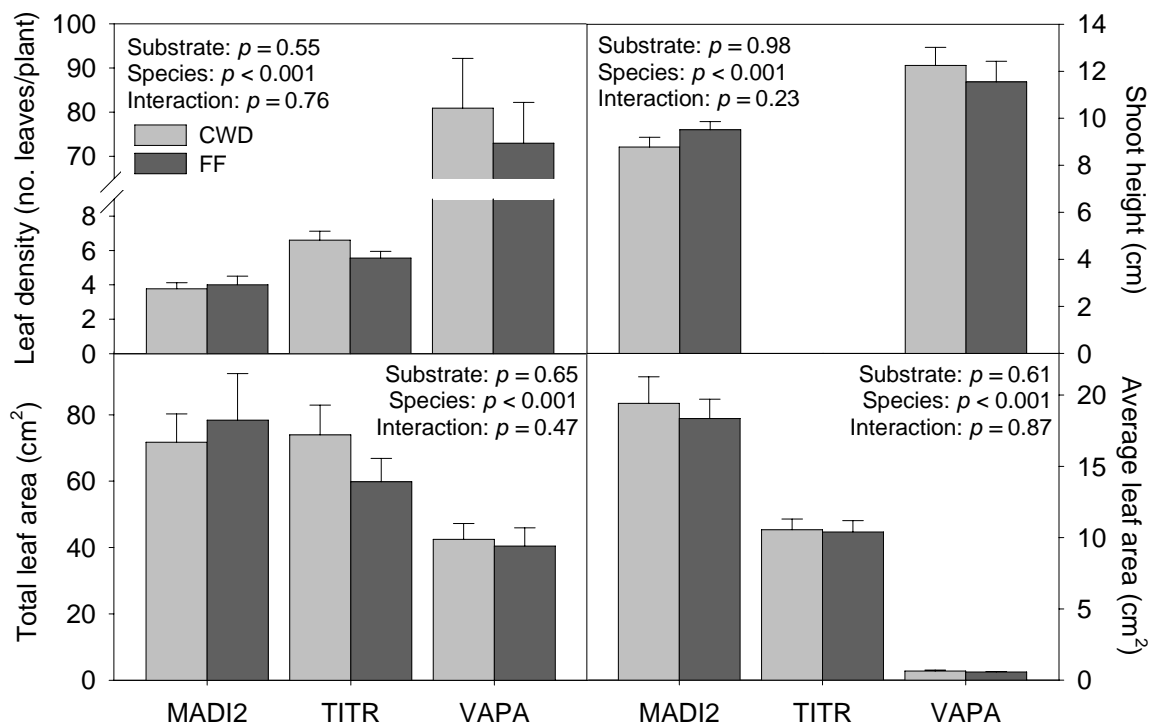


Fig. 5. Above-ground morphological traits of *Maianthemum dilatatum*, *Tiarella trifoliata*, and *Vaccinium parvifolium* (means  $\pm$  1 SE) rooted in CWD and the forest floor.  $P$  values are from two-way analysis of variance. Shoot height was not measured for *Tiarella* (see Methods).



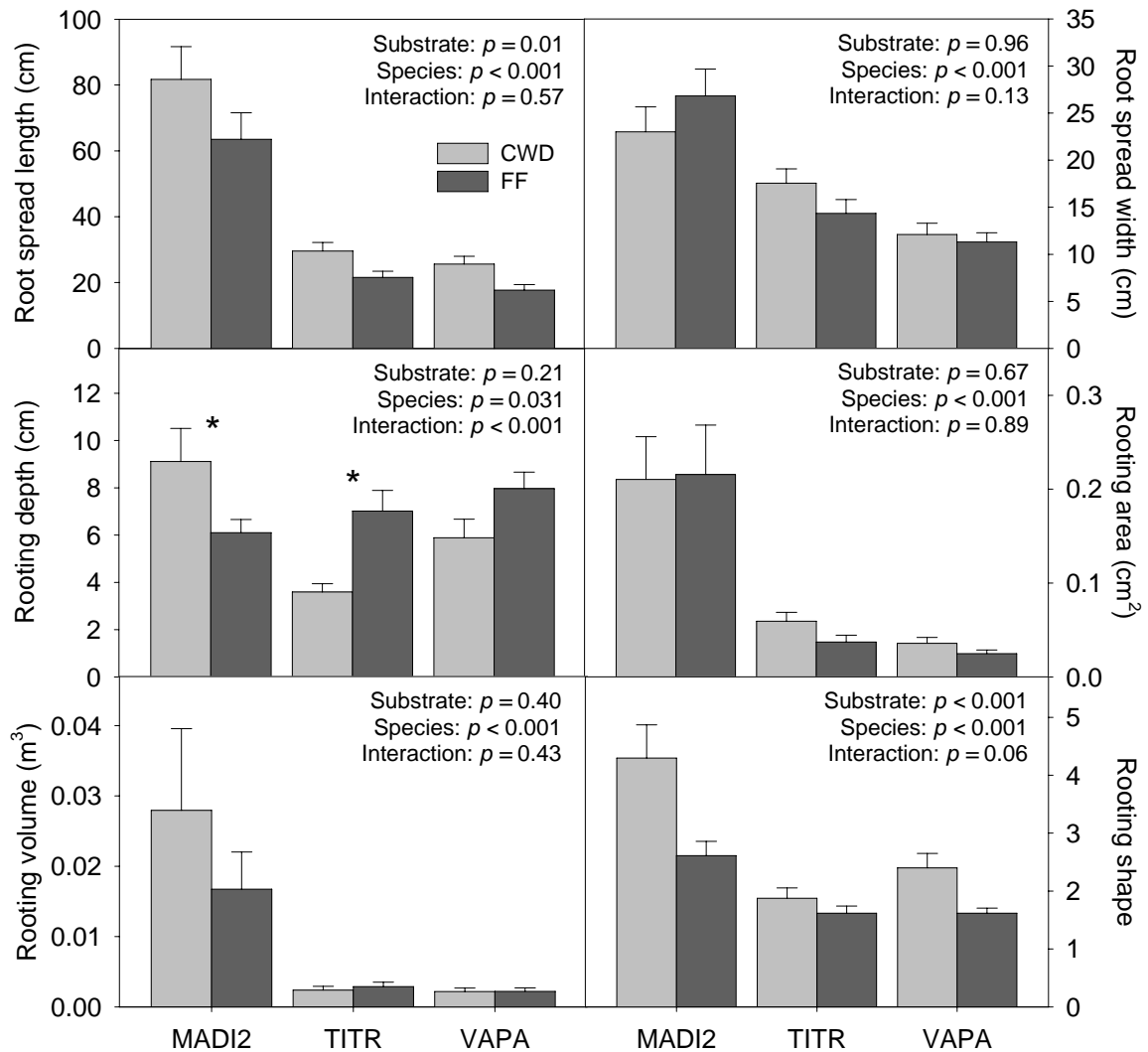


Fig. 6. Below-ground morphological traits of *Maianthemum dilatatum*, *Tiarella trifoliata*, and *Vaccinium parvifolium* (means +1 SE) rooted in CWD and the forest floor.  $P$  values are from two-way analysis of variance. Where a substrate  $\times$  species interaction was significant, separate  $t$ -tests were conducted by species. Asterisks indicate a significant substrate effect ( $p \leq 0.05$ ).

rooted in CWD (Fig. 7). Density of live rhizome tips and total rhizome length were similar between substrates (Fig. 7).

Of the additional attributes of local environment measured in association with substrates (i.e., cover of mosses and vascular plants, depth of litter), only moss cover showed significant variation (Fig. 8). Cover was ~50% greater on CWD supporting *Vaccinium* and ~300% greater on CWD supporting *Tiarella*.

*Individual species responses to substrate.* — In contrast to hypothesis 2, there were no differences in overall performance (total biomass or plant N) between substrates for any of the species (Fig. 9). Plant N ranged from 1.00% in *Vaccinium* to 1.44% in *Tiarella* (Fig. 10).

*Differences in moisture and light availability.* — Volumetric moisture declined significantly over the growing season in both substrates. However, as expected, moisture content was consistently greater in CWD than in the forest floor soil (Fig. 11a). This difference was large (56-76% greater) through much of the summer. Light availability differed significantly above plants representing each species (highest for *Tiarella*), but it did not differ between substrates (Fig. 11b). In absolute terms, light levels at the forest floor averaged ~5% of above-canopy light (K. Grieve, unpublished data).

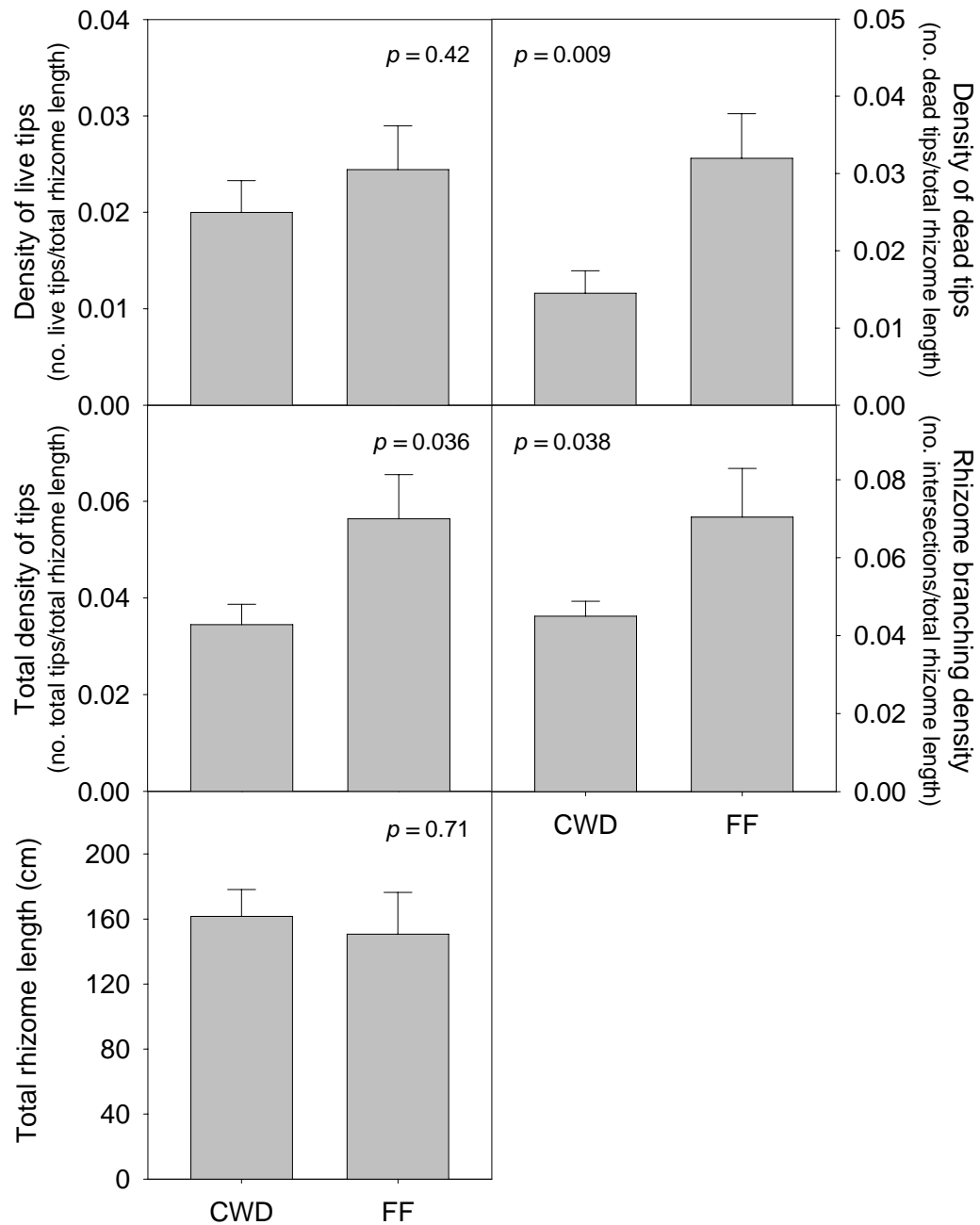


Fig. 7. Additional below-ground morphological traits for *Maianthemum dilatatum* (means  $\pm$  1 SE) rooted in CWD and the forest floor.  $P$  values are from paired  $t$ -test for means.

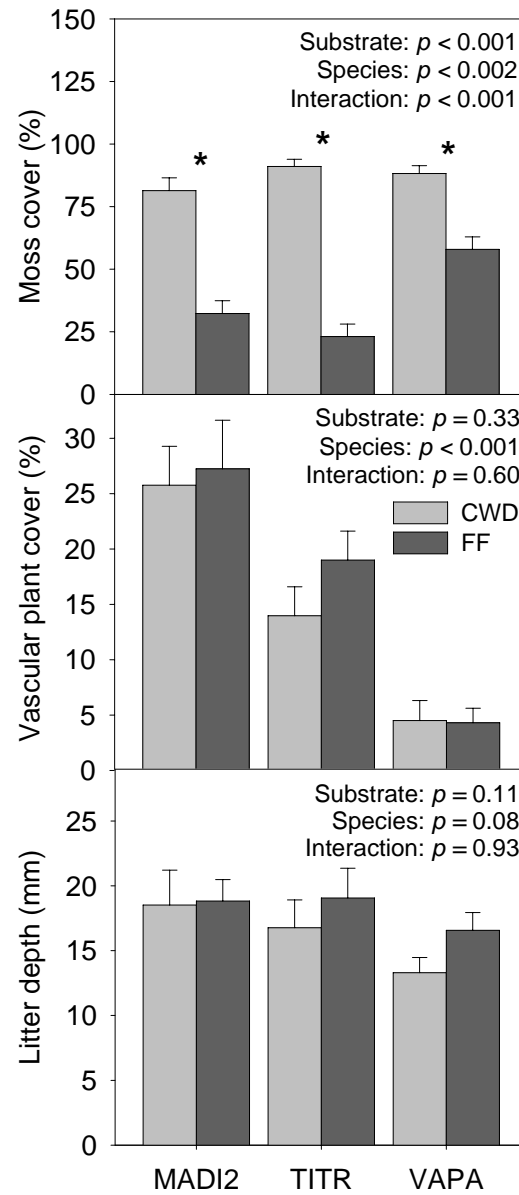


Fig. 8. Additional attributes of the local environment (means +1 SE) associated with CWD and the forest floor.  $P$  values are from two-way analysis of variance. Where a substrate x species interaction was significant, separate  $t$ -tests were conducted by species; asterisks indicate a significant substrate effect ( $p \leq 0.05$ ).

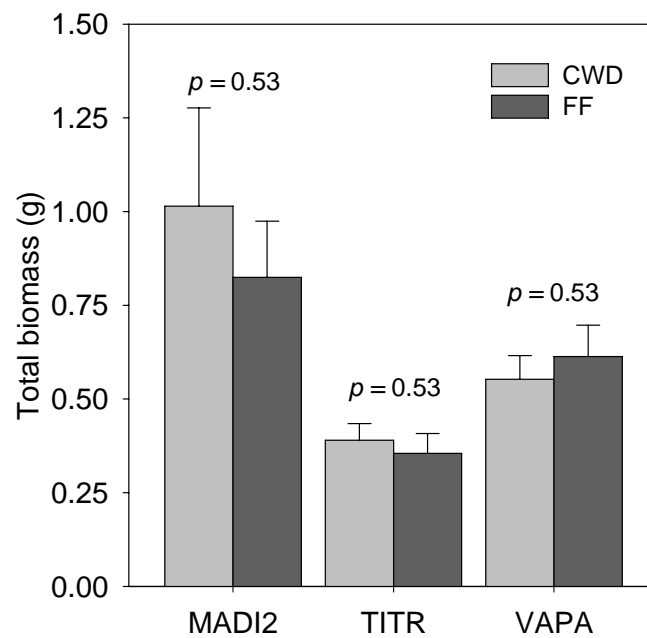


Fig. 9. Total plant biomass for *Maianthemum dilatatum*, *Tiarella trifoliata*, and *Vaccinium parvifolium* (means +1 SE) rooted in CWD and the forest floor. *P* values are from paired *t*-tests.

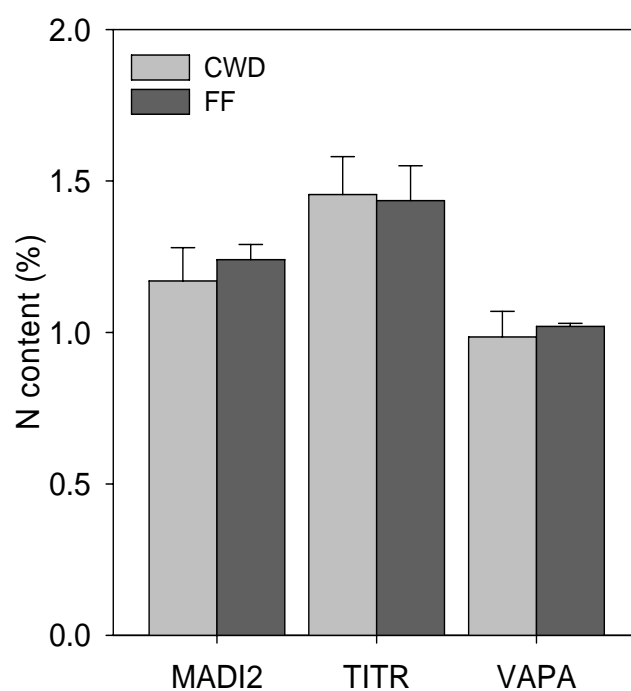


Fig. 10. Plant nitrogen (N) content for *Maianthemum dilatatum*, *Tiarella trifoliata*, and *Vaccinium parvifolium* (means +1 SE) rooted in CWD and the forest floor. Effects of substrate and species were not tested due to limited replication ( $n = 2$  composite samples per species per substrate).

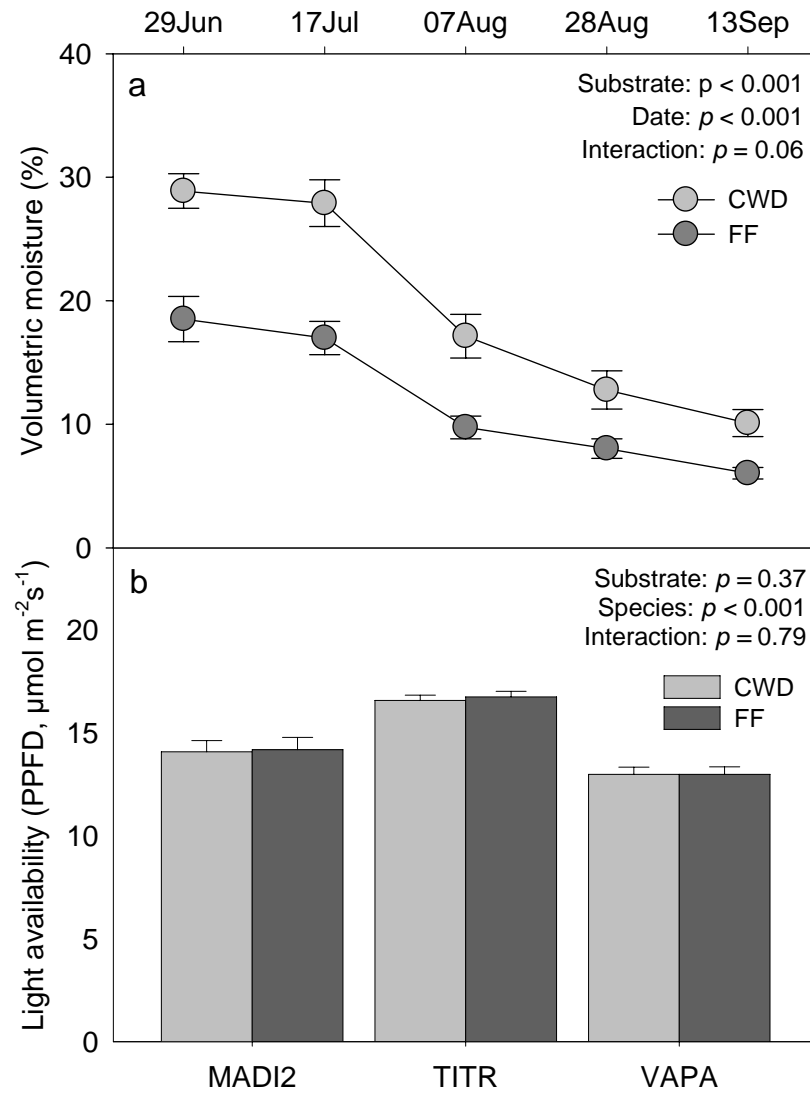


Fig. 11. Differences in (a) volumetric moisture and (b) light availability for CWD and forest floor substrates. Values are means  $\pm 1$  SE ( $n = 20$ , Jun-Aug;  $n = 10$ , Sep).  $P$  values are from two-way analysis of variance.

## DISCUSSION

### *Substrate Affinities of Understory Plants*

Most understory species (83%) displayed a substrate association, and many more species preferred forest floor to CWD. These associations are consistent with those observed in northeastern hardwood forests (McGee 2001): of the herbaceous plant species that displayed a substrate preference, six of seven were associated with the forest floor. Rooting on the forest floor may be advantageous for several reasons. First, the forest floor is a more predictable substrate than CWD; the latter becomes available only when a tree falls. In addition, the forest floor provides a more physically stable substrate. In contrast, as logs decay, bark sloughing and wood fragmentation can lead to plant mortality or exposure of root systems (Harmon et al. 1986, Harmon and Franklin 1989). Release of nitrogen may also be more rapid from the forest floor than from CWD (Sollins et al. 1987, Harmon and Hua 1991; but see Hart 1999). Finally, in these dense young forests, germination and early survival may be greater on the forest floor because competition from mosses is lower: moss cover was more than twice as high on CWD (87% vs. 38% on the forest floor). Because moss mats can dry out before roots of germinants reach the substrate, they can act as barriers to seedling establishment (Harmon and Franklin 1989).

In contrast, many fewer species showed an association with CWD. For smaller growth forms, CWD may provide an escape from competition with taller plants on the forest floor (Messier 1992, Huffman et al. 1994). However, differences in stature cannot be used to explain substrate associations in these forests: three of six species associated



with CWD were among the tallest growth forms (trees and tall shrubs). No other simple morphological or life-history trait (e.g., leaf longevity, clonality, mode of dispersal, or seral status) can be invoked to explain the substrate preferences of most species.

It is possible that species associated with CWD are limited by moisture availability at some point in their life histories and thus benefit from the greater retention of water by logs. *Tsuga heterophylla* seedlings, for example, are particularly sensitive to moisture stress (Williamson 1976, Christy and Mack 1984) and exhibit a very strong association with CWD. It is also possible that some species are associated with CWD because they possess ecto- or ericoid mycorrhizal associations that allow them to efficiently access organic forms of nitrogen (see review in Kaye and Hart 1997). However, evidence of significant or preferential uptake of organic N remains equivocal (e.g., Bending and Read 1996, Näsholm et al. 1998, Persson et al. 2003, Bennett and Prescott 2004). Moreover, for species compared in this study, N concentrations were comparable between individuals rooted in CWD and the forest floor, suggesting little difference in N availability between substrates or in the abilities of species to acquire N.

Despite the prevalence of species-substrate associations in this forest, relatively few constituted obligate (or nearly obligate) relationships (see Appendix I, Table 2). One likely explanation is that resource availability or quality may not have been sufficiently different between substrates to restrict the distributions of species. Decayed logs were covered to varying depths by fine litter, and highly decayed wood was present in the forest floor. Species may thus encounter characteristics of both substrates, regardless of rooting location. Contrasts in substrate quality may have been stronger had I sampled

fresh logs; however, these were relatively uncommon and supported fewer vascular plants. Finally, many herbaceous and semi-woody species in these forests are clonal (Hitchcock et al. 1969, Antos and Zobel 1984, Lezberg et al. 1999) with an ability to place roots and rhizomes in multiple substrates. From a functional perspective, distinguishing a primary rooting substrate may be difficult.

### *Substrate Effects on Understory Plant Performance*

I hypothesized that plants rooted in CWD and the forest floor would show differences in biomass allocation and morphology in a manner consistent with differences in moisture availability between substrates. Patterns of biomass allocation were consistent with this expectation: plants rooted in the forest floor (characterized by lower volumetric moisture throughout the growing season) allocated greater biomass to below-ground structures. Similar patterns of allocation along resource gradients have been observed in other forest plants. For example, in Neotropical forests, Paz (2003) observed that woody seedlings showed the greatest allocation to roots in forests with the longest dry season. Similarly, in a transplant experiment, bamboo from a subtropical evergreen forest showed the greatest allocation to below-ground structures under the lowest levels of mean summer moisture (Qing et al. 2004).

In contrast to patterns of biomass allocation, differences in plant morphology were less consistent with my expectations. Root-system length and shape (ratio of length to width) differed between substrates, reflecting the tendency for root systems to develop linearly along logs. Differences in rooting depth between substrates, varied, however, among species. Roots of *Tiarella* grew significantly deeper in the forest floor, but

counter to expectation, roots of *Maianthemum* were deeper in CWD. This contrast may reflect an interaction between the physical structure of logs and differences in the root systems of species. Wood may limit depth of rooting in non-rhizomatous species that possess finer roots (*Tiarella*). In contrast, vigorous rhizomes of clonal species such as *Maianthemum* can follow the grain of decay in logs, resulting in deeper penetration of root systems.

Plant foraging theory and empirical studies suggest that clonal herbs should develop more compact, highly branched rhizome systems in environments with greater resource availability (Slade and Hutchings 1987, de Kroon and Schieving 1991, D'Hertefeldt and Jónsdóttir 1994) and more diffuse, less branched rhizome systems where resources are more limiting or more heterogeneous in space. Interestingly for *Maianthemum*, branching of rhizome systems and densities of dead and total rhizome tips were lower in CWD where resource availability, in this case moisture, was greater. This counterintuitive result could be explained if foraging were driven by differences in N availability, rather than moisture. On the other hand, plant N was comparable for individuals rooted in CWD and the forest floor, suggesting minimal differences in resource availability between substrates. Alternatively, morphological plasticity in *Maianthemum* may be constrained by the physical properties of CWD. Rhizome systems in CWD tended to be linear, following the grain of decay; this resulted in fewer opportunities for branching compared to the forest floor.

I also hypothesized that individuals of *Vaccinium*, *Tiarella*, and *Maianthemum* would differ in overall performance (total biomass and plant N) between substrates in a

manner consistent with their affinities for these substrates. However, all three species showed similar performance between substrates. There are several plausible explanations for this result. First, it is likely that light, rather than moisture or nutrient availability, is the resource that most limits plant growth in these dense, young forests (e.g., Ashmun and Pitelka 1984, Messier 1992, Canham et al. 1996). Light transmission to the forest floor was extremely low, averaging ~5% of that available above the canopy. Under these conditions, plants may be incapable of responding to differences in below-ground resources (Messier 1992, Canham et al. 1996). It is also possible that the associations of *Vaccinium* with CWD, or *Tiarella* with the forest floor, do not reflect differences in the performance of established plants, but rather differential dispersal to, or germination or early survival on, these substrates (Christy and Mack 1984, Tappeiner and Alaback 1989, Caspersen and Sapruncoff 2005). Once plants are established, substrate differences may have little effect on plant growth or survival (Lemon 1945). These alternative explanations clearly point to the need for studies of plant distribution and performance in forests in which light is less limiting, and for experiments that test whether substrate associations can be explained by differences in seed dispersal, germination, and/or early plant survival.

## REFERENCES

- Aerts R. and Chapin, F.S., III. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research* 30:1–67.
- Andersson, L.I. and Hytteborn, H. 1991. Bryophytes and decaying wood – a comparison between managed and natural forest. *Holarctic Biology* 14: 121-130.
- Antos., J.A. 1988. Underground morphology and habitat relationships of three pairs of forest herbs. *American Journal of Botany* 75: 106-113.
- Antos, J.A. and Zobel, D.B. 1984. Ecological implications of belowground morphology of nine coniferous forest herbs. *Botanical Gazette* 145: 508-517.
- Ashmun, J.W. and Pitelka, L.F. 1984. Light-induced variation in the growth and dynamics of transplanted ramets of the understory herb, *Aster acuminatus*. *Oecologia* 64: 255-262.
- Bazzaz, F.A. 1996. Plants in changing environments: linking physiological, population, and community ecology. Cambridge University Press, New York, NY.
- Bell, A.D. 1984. Dynamic morphology: a contribution to plant population ecology. Pages 48-65 in R. Dirzon and J. Sarukhan, editors. *Perspectives in plant population ecology*. Sinauer, Sunderland, Massachusetts, USA.
- Bending, G.D. and Read, D.J. 1996. Nitrogen mobilization from protein-polyphenol complex by ericoid and ectomycorrhizal fungi. *Soil Biology and Biochemistry* 28: 1603-1612.
- Bennett, J.N. and Prescott, C.E. 2004. Organic and inorganic nitrogen nutrition of western red cedar, western hemlock and salal in mineral N-limited cedar-hemlock forests. *Oecologia* 141: 468-476.
- Berg, A., Ehnström, B., Gustafsson, L, Hallingbäck, T., Jonsell, M., and Weslien, J. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conservation Biology* 8: 718-731.
- Camp, W.H. 1942. A survey of the American species of *Vaccinium* subgenus *Euvaccinium*. *Brittonia* 4: 205-247.
- Canham, C.D., Berkowitz, A.R., Kelly, V.R., Lovett, G.M., Ollinger, S.V., and Schnurr, J. 1996. Biomass allocation and multiple resource limitation in tree seedlings. *Canadian Journal of Forest Research* 26: 1521-1530.

- Caspersen, J.P. and Saprundoff, M. 2005. Seedling recruitment in a northern temperate forest: the relative importance of supply and establishment limitation. *Canadian Journal of Forest Research* 35: 978-989.
- Chapin, F.S., III, Autumn, K., and Pugnaire, F. 1993. Evolution of suites of traits in response to environmental stress. *The American Naturalist* 142: S78-S92.
- Christy, E.J. and Mack, R.N. 1984. Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. *Journal of Ecology* 72: 75-91.
- Crites, S. and Dale, M.R.T. 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. *Canadian Journal of Botany* 76: 641-651.
- de Kroon, H. and Schieving, F. 1991. Resource allocation patterns as a function of clonal morphology – a general model applied to a foraging clonal plant. *Journal of Ecology* 79: 519-530.
- D'Hertefeldt, T. and Jónsdóttir, I.S. 1994. Effects of resource availability on integration and clonal growth in *Maianthemum bifolium*. *Folia Geobotanica and Phytotaxonomica* 29: 167-179.
- Fogel, R.M., Ogawa, M., and Trappe, J.M., 1973. Terrestrial decomposition: A synopsis. U.S. I.B.P. Coniferous Forest Biome Report 135. Coniferous Forest Biome, College of Forest Resources, University of Washington, Seattle, WA, p. 12.
- Franklin, J.F. and Dyrness, C.T. 1988. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR, US.
- Gavlack, R.G., Horneck, D.A., Miller, R.O., and Kotuby-Amacher, J. 2003. Plant, Soil, and Water Reference Methods for the Western Region. Western Regional Extension Publication 125.
- Givnish, T.J. 1982. On the adaptive significance of leaf height in forest herbs. *The American Naturalist* 120: 353-381.
- Harmon, M.E. and Franklin, J.F. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. *Ecology* 70: 48-59.
- Harmon, M.E. and Hua, C. 1991. Coarse woody debris dynamics in two old-growth ecosystems. *BioScience* 41: 604-610.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Leinkaemper, G.W.,

- Cromack, Jr., K., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15: 133-302.
- Hart, S.C. 1999. Nitrogen transformations in fallen tree boles and mineral soil of an old-growth forest. *Ecology* 80: 1385-1394.
- Henderson, J.A., Peter, D.H., Leshner, R.D., and Shaw, D.C. 1989. Forested plant associations of the Olympic National Forest. USDA Forest Service Pacific Northwest Region, R6-Ecol-TP-001-88.
- Hitchcock, C.L. and Cronquist, A. 1973. *Flora of the Pacific Northwest*. University of Washington, Seattle, WA, US.
- Hitchcock, C.L., Cronquist, A., Ownbey, M., and Thompson, J.W. 1969. *Vascular Plants of the Pacific Northwest*. Volumes 1-5. University of Washington Press, Seattle, WA, US.
- Huffman, D.W. and Tappeiner, J.C., II. 1997. Clonal expansion and seedling recruitment of Oregon grape (*Berberis nervosa*) in Douglas-fir (*Pseudotsuga menziesii*) forests: comparisons with salal (*Gaultheria shallon*). *Canadian Journal of Forest Research* 27: 1788-1793.
- Huffman, D.W., Tappeiner, J.C., II, and Zasada, J.C. 1994. Regeneration of salal (*Gaultheria shallon*) in the central Coast Range forests of Oregon. *Canadian Journal of Botany* 72: 39-51.
- Kaye, J.P. and Hart, S.C. 1997. Competition for nitrogen between plants and soil microorganisms. *Tree* 12: 139-143.
- Kennedy, P.G. and Quinn, T. 2001. Understory plant establishment on old-growth stumps and the forest floor in western Washington. *Forest Ecology and Management* 154: 193-200.
- Kerkhoff, A.J., Fagan, W.F., Elser, J.J., and Enquist, B.J. 2006. Phylogenetic and growth form variation in the scaling of nitrogen and phosphorus in the seed plants. *The American Naturalist* 168: E103-E122.
- Kruys, N. and Jonsson, B.G. 1999. Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. *Canadian Journal of Forest Research* 29:1295-1299.
- LaFrankie, J.V. 1986. Morphology and taxonomy of the new world species of *Maianthemum* (Liliaceae). *Journal of the Arnold Arboretum*.67: 371-439.

- Lee, P. and Sturges, K. 2001. The effects of logs, stumps, and root throws on understory communities within 28-year-old aspen-dominated boreal forests. *Canadian Journal of Botany* 79: 905-916.
- Lemon, P.C. 1945. Wood as a substratum for perennial plants in the Southeast. *The American Midland Naturalist* 34: 744-749.
- Lezberg, A.L., Antos, J.A., and Halpern, C.B. 1999. Belowground traits of herbaceous species in young coniferous forests of the Olympic Peninsula, Washington. *Canadian Journal of Botany* 77: 936-943.
- Lezberg, A.L., Halpern, C.B., and Antos, J.A. 2001. Clonal development of *Maianthemum dilatatum* in forests of differing age and structure. *Canadian Journal of Botany* 79: 1028-1038.
- Lieffers, V.J., Messier, C., Stadt, K.J., Gendron, F., and Comeau, P.G. 1999. Predicting and managing light in the understory of boreal forests. *Canadian Journal of Forest Research* 29: 796-811.
- McGee, G.G. 2001. Stand-level effects on the role of decaying logs as vascular plant habitat in Adirondack northern hardwood forests. *Journal of the Torrey Botanical Society* 128: 370-380.
- Messier, C. 1992. Effects of neutral shade and growing media on growth, biomass allocation, and competitive ability of *Gaultheria shallon*. *Canadian Journal of Botany* 70: 2271-2276.
- Narukawa, Y. and Yamamoto, S. 2003. Development of conifer seedlings roots on soil and fallen logs in boreal and subalpine coniferous forests of Japan. *Forest Ecology and Management* 175: 131-139.
- Näsholm, T., Ekblad, A., Nordin, A., Giesler, R., Höglberg, M., and Höglberg, P. 1998. Boreal forest plants take up organic nitrogen. *Nature* 392: 914-916.
- Näsholm, T., Huss-Danell, L.K., and Höglberg, P. 2000. Uptake of organic nitrogen in the field by four agriculturally important plant species. *Ecology* 81: 1155-1161.
- Paz, H. 2003. Root/shoot allocation and root architecture in seedlings: variation among forest sites, microhabitats, and ecological groups. *Biotropica* 35: 318-332.
- Persson, J., Höglberg, P., Ekblad, A., Höglberg, M.N., Nordgren, A., and Näsholm, T. 2003. Nitrogen acquisition from inorganic and organic sources by boreal forest plants in the field. *Oecologia* 137: 252-257.



- Qing, L., Yunxiang, L., and Zhangcheng, Z. 2004. Effects of moisture availability on clonal growth in bamboo *Pleioblastus maculata*. *Plant Ecology* 173: 107-113.
- Rambo, T.R., and Muir, P.S. 1998a. Forest floor bryophytes of *Pseudotsuga menziesii*-*Tsuga heterophylla* stands in Oregon: influences of substrate and overstory. *Bryologist* 101: 116-130.
- Rambo, T.R., and Muir, P.S. 1998b. Bryophyte species associations with coarse woody debris and stand ages in Oregon. *Bryologist* 101: 366-376.
- Read, D.J. 1991. Mycorrhizas in ecosystems. *Experimentia* 47: 376-391.
- Reynolds, J.F. and Thornley, J.H.M. 1982. A shoot:root partitioning model. *Annals of Botany* 49: 585-597.
- SAS Institute, Inc. 2003. SAS/STAT user's guide, version 9.1. SAS Institute, Inc., Cary, NC, US.
- Simard, M.-J., Bergeron, Y., and Sirois, L. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. *Journal of Vegetation Science* 9: 575-582.
- Slade, A.J. and Hutchings, M.J. 1987. The effects of nutrient availability on foraging in the clonal herb *Glechoma hederacea*. *Journal of Ecology* 75: 95-112.
- Sollins, P., Cline, S.P., Verhoeven, T., Sachs, D., and Spycher, G. 1987. Patterns of log decay in old-growth Douglas-fir forests. *Canadian Journal of Forest Research* 17: 1585-1595.
- Soltis, D.E., Soltis, P.S., Kuzoff, R.K., and Tucker, T.L. 1992. Geographic structuring of chloroplast DNA genotypes in *Tiarella trifoliata* (Saxifragaceae). *Plant Systematics and Evolution* 181: 203-216.
- Spies, T.A., Franklin, J.F., and Thomas, T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69: 1689-1702.
- Stevens, V. 1997. The ecological role of coarse woody debris: an overview of the ecological importance of CWD in B.C. forests. Research Branch, B.C. Ministry of Forests, Victoria, B.C. Working Paper 30.
- Takahashi, M., Sakai, Y., Ootomo, R., and Shiozaki, M. 2000. Establishment of tree seedlings and water-soluble nutrients in coarse woody debris in an old-growth *Picea-Abies* forest in Hokkaido, northern Japan. *Canadian Journal of Forest Research* 30: 1148-1155.

- Tappeiner, J.C., II and Alaback, P.B. 1989. Early establishment and vegetative growth of understory species in the western hemlock – Sitka spruce forests of southeast Alaska. *Canadian Journal of Botany* 67: 318-326.
- Thompson, J.N. 1980. Treefalls and colonization patterns of temperate forest herbs. *The American Midland Naturalist* 104: 176-184.
- Trubat, R., Cortina, J., and Vilagrosa, A. 2006. Plant morphology and root hydraulics are altered by nutrient deficiency in *Pistacia lentiscus* (L.). *Trees* 20: 334-339.
- Turner, P.A.M. and Pharo, E.J. 2005. Influence of substrate type and forest age on bryophyte species distribution in Tasmanian mixed forest. *Bryologist* 108: 67-85.
- Williamson, R.L. 1976. Natural regeneration of western hemlock. Pages 166-169 in W.A. Atkinson and R.J. Zasoski, editors. *Western Hemlock Management*. College of Forest Resources, University of Washington, Seattle, Washington, USA.
- Zar, J.H. 1999. *Biostatistical Analysis* (4<sup>th</sup> ed). Prentice-Hall, Upper Saddle River, NJ, US.
- Zielonka, T. 2006. When does dead wood turn into a substrate for spruce replacement. *Journal of Vegetation Science* 17: 739-746.
- Zielonka, T. and Piatek G. 2004. The herb and dwarf shrubs colonization of decaying logs in subalpine forest in the Polish Tatra Mountains. *Plant Ecology* 172: 63-72.

# APPENDIX I: METHODS FOR CALCULATING POPULATION PROPORTIONS

Calculations of population proportions followed the methods of Zar (1999). For each plant species present in at least 1% of quadrats, the estimated population proportion ( $p$ ) was calculated as follows:

$$p = X/n$$

where  $X$  = number of shoots (or fronds) occurring on CWD

and  $n$  = total number of shoots (or fronds).

For each population proportion, the upper and lower limits of a 95% confidence interval were calculated as a function of the  $F$  distribution and binomial distribution:

$$\text{Lower limit: } \frac{X}{X + (n - X + 1) * F_{\alpha(2), v_1, v_2}}$$

where  $v_1 = 2 * (n - X + 1)$

and  $v_2 = 2X$

$$\text{Upper limit: } \frac{(X + 1) * F_{\alpha(2), v'_1, v'_2}}{n - X + (X + 1) * F_{\alpha(2), v'_1, v'_2}}$$

where  $v'_1 = 2 * (X + 1)$

and  $v'_2 = 2 * (n - X)$

Species-specific values for these calculations are presented in Table 2.

Table 2. Values used to estimate confidence limits for population proportions for species present in  $\geq 1\%$  of quadrats.  $X$  = number of shoots on CWD;  $n$  = total number of shoots;  $v_1$  = numerator degrees of freedom, lower confidence limit;  $v_2$  = denominator degrees of freedom, lower confidence limit;  $v'_1$  = numerator degrees of freedom, upper confidence limit;  $v'_2$  = denominator degrees of freedom, upper confidence limit;  $p$  = proportion of total plant population on CWD; Lower Limit = lower limit of a 95% confidence interval; Upper Limit = upper limit of a 95% confidence interval. Numerator and denominator degrees of freedom and  $\alpha = 0.05(2)$  were used to determine the critical value of the  $F$  distribution.

Species	$X$	$n$	$v_1$	$v_2$	$v'_1$	$v'_2$	$p$	Lower Limit	Upper Limit
<i>Abies</i> spp.	268	2643	4752	536	538	4750	0.10	0.09	0.10
<i>Achlys triphylla</i>	11	136	252	22	24	250	0.08	0.00	0.14
<i>Athyrium filix-femina</i>	2	446	890	4	6	888	0.00	0.00	0.02
<i>Blechnum spicant</i>	115	412	596	230	232	594	0.28	0.24	0.33
<i>Chimaphila menziesii</i>	12	322	622	24	26	620	0.04	0.02	0.06
<i>Clintonia uniflora</i>	76	1574	2998	152	154	2996	0.05	0.04	0.06
<i>Cornus canadensis</i>	380	1356	1954	760	762	1952	0.28	0.28	0.28
<i>Corallorhiza maculata</i>	0	55	112	0	2	110	0.00	0.00	0.06
<i>Disporum</i> spp.	0	23	48	0	2	46	0.00	0.00	0.15
<i>Dryopteris austriaca</i>	62	167	212	124	126	210	0.37	0.30	0.45
<i>Goodyera oblongifolia</i>	0	78	158	0	2	156	0.00	0.00	0.05
<i>Linnaea borealis</i>	434	2930	4994	868	870	4992	0.15	0.15	0.15
<i>Listera cordata</i>	38	197	320	76	78	318	0.19	0.14	0.25
<i>Maianthemum dilatatum</i>	170	832	1326	340	342	1324	0.20	0.18	0.21
<i>Menziesia ferruginea</i>	102	149	96	204	206	94	0.68	0.60	0.76
<i>Oplopanax horridus</i>	3	17	30	6	8	28	0.18	0.04	0.43
<i>Polystichum munitum</i>	5	337	666	10	12	664	0.01	0.00	0.03
<i>Pteridium aquilinum</i>	41	519	958	82	84	956	0.08	0.06	0.10
<i>Pyrola uniflora</i>	20	129	220	40	42	218	0.16	0.10	0.23
<i>Rubus lasiococcus</i>	2	26	50	4	6	48	0.08	0.01	0.25
<i>Rubus pedatus</i>	9	180	344	18	20	342	0.05	0.02	0.09
<i>Rubus ursinus</i>	7	84	156	14	16	154	0.08	0.03	0.16
<i>Smilacina stellata</i>	84	1021	1876	168	170	1874	0.08	0.07	0.10
<i>Streptopus amplexifolius</i>	9	246	476	18	20	474	0.04	0.02	0.07
<i>Tiarella trifoliata</i>	203	1475	2546	406	408	2544	0.14	0.14	0.14
<i>Trillium ovatum</i>	2	51	100	4	6	98	0.04	0.00	0.14
<i>Tsuga heterophylla</i>	5431	7621	4382	10862	10864	4380	0.71	0.71	0.71
<i>Vaccinium parvifolium</i>	4800	7422	5246	9600	9602	5244	0.65	0.65	0.65
<i>Viola sempervirens</i>	22	908	1774	44	46	1772	0.02	0.02	0.04

## APPENDIX II: PHOTOGRAPHIC RECORDS OF PLANT EXCAVATIONS

All plants were photographed after excavation. The photographs provided here serve as examples of typical excavated pairs (plant rooted in CWD and a nearby plant rooted in the forest floor) of *Maianthemum dilatatum*, *Tiarella trifoliata*, and *Vaccinium parvifolium*. All photographs are by the author.

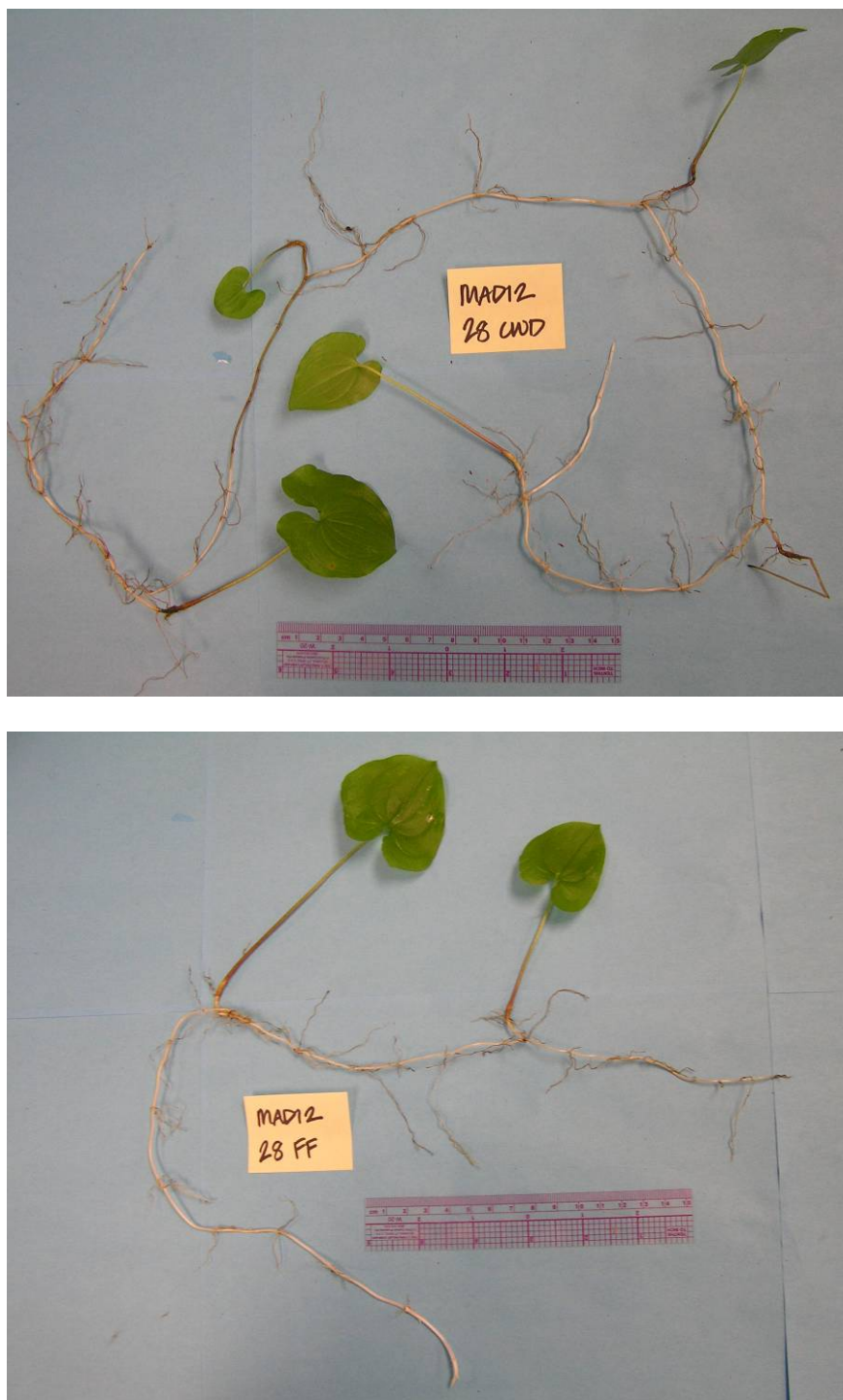


Fig. 12. *Maianthemum dilatatum* excavated from CWD (above) and the forest floor (below).

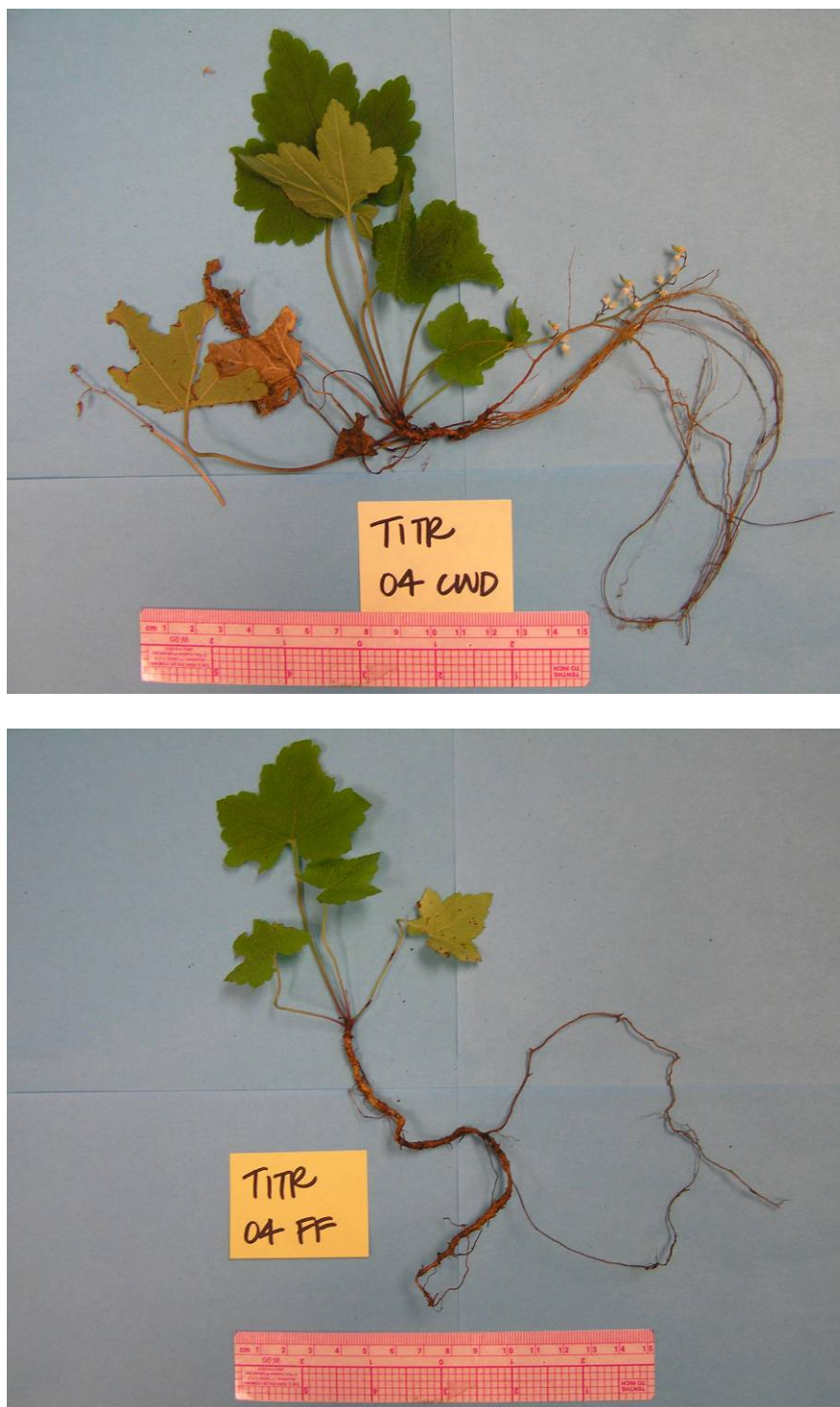


Fig. 13. *Tiarella trifoliata* excavated from CWD (above) and the forest floor (below).

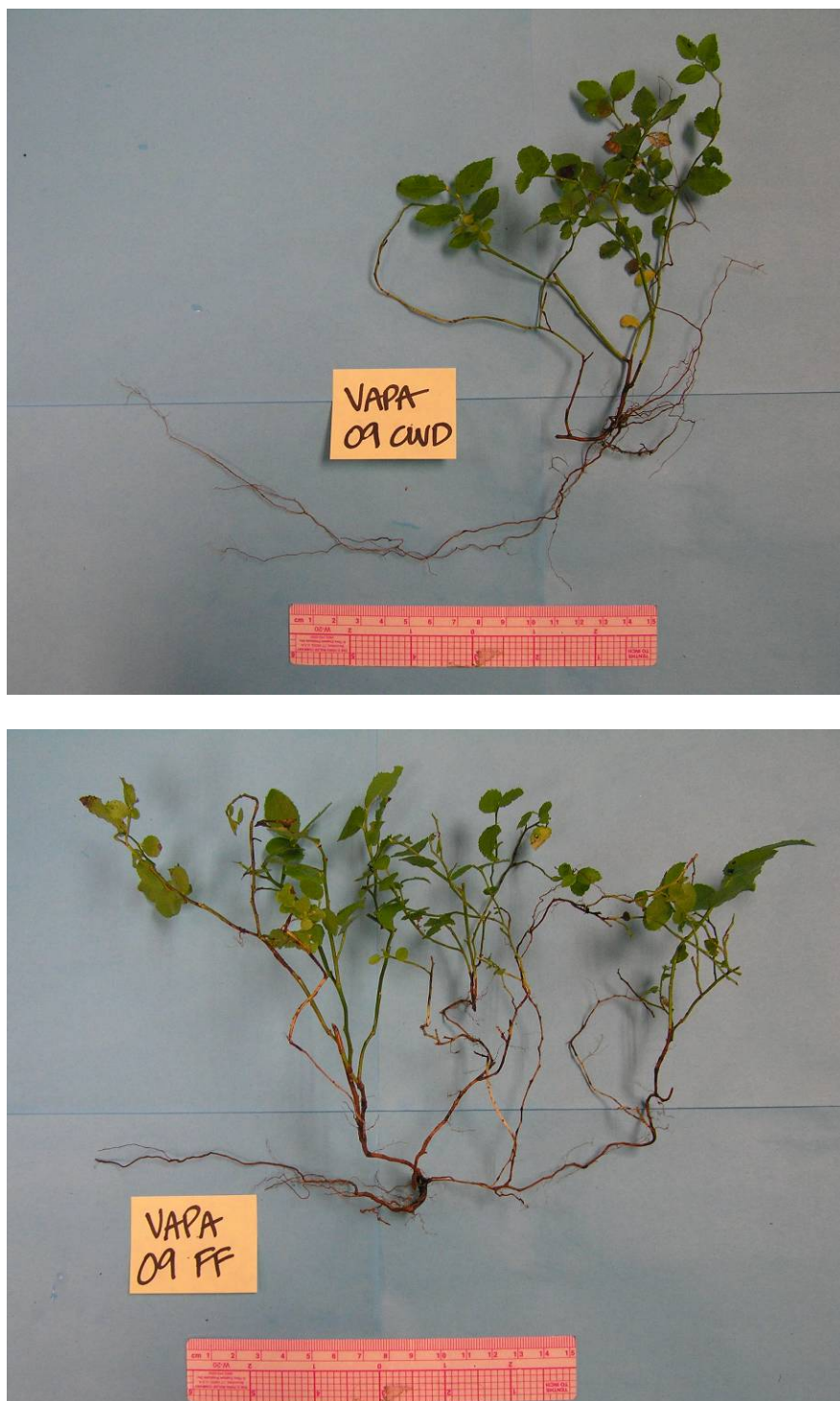


Fig. 14. *Vaccinium parvifolium* excavated from CWD (above) and the forest floor (below).