

Substrate effects on distribution, biomass allocation, and morphology of forest understory plants

Laura J. Six and Charles B. Halpern

Abstract: Relationships between rooting substrate and the distribution and performance of forest plants are inadequately understood. We tested whether understory species in a dense coniferous forest were associated with coarse woody debris (CWD) or forest floor. In addition, for three species with differing substrate associations (*Vaccinium parvifolium* Smith, *Tiarella trifoliata* L., and *Maianthemum dilatatum* (Wood) Nels. and Macbr.), we excavated individuals rooted in CWD and forest floor, and compared biomass allocation and plant morphological traits. Substrate samples were also tested for moisture content. Of 29 species tested, 18 (62%) showed positive associations with forest floor and 6 (21%) with CWD. Forest floor is a more predictable and stable substrate; in these forests it also supports lower moss cover that can inhibit seedling establishment. As expected, plants rooted in forest floor (which was drier) allocated greater biomass to below-ground structures. Root-system traits, however, did not suggest plasticity in response to resource availability. Instead, the physical structure of logs may constrain root systems in CWD. In addition, total plant biomass did not differ between substrates suggesting that under low light, species may be incapable of responding to differences in belowground resources. Alternatively, substrate associations may develop earlier in the life histories of these plants via differential germination and survival.

Key words: biomass allocation, *Maianthemum dilatatum*, Pacific Northwest, plant morphology, root system, substrate affinity.

Résumé : On comprend mal les relations entre le substrat d'enracinement et la distribution ainsi que la performance des plantes forestières. Les auteurs ont vérifié si les espèces de sous-étage d'une forêt dense de conifères sont associées avec de gros débris ligneux (CWD) ou avec le parterre forestier. Ils ont excavé les racines individuelles enracinées dans les CWD ou le parterre forestier chez trois espèces associées à des substrats différents (*Vaccinium parviflorum* Smith, *Tiarella trifoliata* L. et *Maianthemum dilatatum* (Wood) Nels. and Macbr.), et ils ont comparé l'allocation de la biomasse et les caractères morphologiques des plantes. Ils ont également analysé la teneur en humidité d'échantillons de substrats. Des 29 espèces considérées, 18 (62 %) montrent une association positive avec le parterre forestier et 6 (21 %) avec les CWD. Le parterre forestier constitue un substrat plus prévisible et plus stable; dans ces forêts, il supporte également un couvert de mousse peu élevé qui peut inhiber l'établissement des plantules. Comme prévu, les plantes enracinées dans le parterre forestier (plus sec) allouent une plus grande biomasse aux structures hypogées. Cependant, les caractères racinaires ne suggèrent pas de plasticité en réaction à la disponibilité des ressources. Au contraire, la structure physique des billes peut contraindre les systèmes racinaires, dans les CWD. De plus, la biomasse totale des plantes ne diffère pas selon les substrats suggérant que sous de faibles intensités lumineuses, les espèces pourraient ne pas réagir aux différentes ressources hypogées. En échange, les associations aux substrats pourraient se développer plus tôt dans le cycle vital de ces plantes via une germination et une survie différentielles.

Mots-clés : allocation de biomasse, *Maianthemum dilatatum*, nord-ouest de la Côte du Pacifique, morphologie végétale, système racinaire, affinité aux substrats.

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Introduction

Considerable attention has been devoted to the role of coarse woody debris (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) and forest-floor bryophytes (e.g., Rambo and Muir 1998a, 1998b; Krusys and Jonsson 1999; Turner

and Pharo 2005). For example, in forests of the western Cascade Range, Oregon, Christy and Mack (1984) found that 98% of *Tsuga heterophylla* (Rag.) Sarg. seedlings occurred on decayed logs even though logs typically cover < 10% of the forest floor (Spies et al. 1988). Many mosses and liverworts also display an affinity for CWD (e.g., Rambo and Muir 1998a; Turner and Pharo 2005), and for-

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L.J. Six^{1,2} and C.B. Halpern. College of Forest Resources, Box 352100, University of Washington, Seattle, WA 98195-2100, USA.

¹Corresponding author (e-mail: laura.six@weyerhaeuser.com).

²Present address: Western Timberlands Research, Weyerhaeuser Company, WTC 1A5, Box 9777, Federal Way, WA 98063-9777, USA.

ests with a greater abundance of decayed logs often support richer bryophyte communities (Andersson and Hytteborn 1991; 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 varying patterns of association. In some forests, few understory species are associated with substrates (e.g., McGee 2001). Elsewhere, logs and stumps support a subset of the forest-floor community (Thompson 1980). Finally, woody substrates and the forest floor can support distinctly different communities, although differences can disappear over time as logs decay and are colonized by species from the forest floor (Kennedy and Quinn 2001; Lee and Sturges 2001).

Several mechanisms may explain species' associations with CWD. By establishing on logs, short-statured species can avoid competition with taller, more vigorous plants (e.g., Harmon and Franklin 1989; Rambo and Muir 1998a; Simard et al. 1998). Thus, the ability to germinate and persist on logs may be advantageous in the forest understory where light is often limiting (Burton and Mueller-Dombois 1984; Tappeiner and Alaback 1989; Rambo and Muir 1998a; Lieffers et al. 1999; Lezberg et al. 2001). Other resources also may be more available in CWD than on the forest floor. For example, decayed wood retains more 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 a more stable source of water. Although the availability of inorganic nitrogen (N) may not differ between woody and nonwoody 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; Aerts and Chapin 2000), leading to a positive association with CWD.

Variation in resource availability among substrates also has 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 is limiting, allocation may shift to below-ground structures (e.g., Paz 2003; Khurana and Singh 2004).

In addition to affecting allocation patterns, substrate-related differences in resource availability may influence the morphological attributes of plants. For example, clonal herbs can vary the density or spacing of ramets by adjusting the length or degree of branching of rhizomes 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, rhizome segments are expected to be shorter and the amount of branching greater (Slade and Hutchings 1987; de Kroon and Schieving 1991). However, resource acquisition also involves tradeoffs. If light is very limiting, the

cost of investing in foraging organs (e.g., rhizomes) is 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 limited lateral spread or branching, and instead maintain long-lived ramets in place through annual releafing (Ashmun and Pitelka 1984; Huffman et al. 1994; Lezberg et al. 2001).

In this study, we investigate the role of substrate 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 understory suggest that both light and belowground resources are limiting. However, CWD is abundant (as in many forests of this region) and could play a critical role in understory development. Our objectives are threefold. First, we quantify the distributions of understory species on two common substrates, fine litter on the forest floor and CWD. Second, we select three species with differing substrate affinities, *Vaccinium parvifolium* Smith (associated with CWD), *Tiarella trifoliata* L. (associated with forest floor), and *Maianthemum dilatatum* (Wood) Nels. and Macbr. (no association with either substrate), and compare biomass allocation, morphological traits, and overall performance (total biomass) between individuals rooted in forest floor and CWD. Third, we measure seasonal trends in substrate moisture to determine whether differences in moisture availability are consistent with patterns of plant performance. We pose two general and several specific hypotheses to guide comparisons of plant performance:

1. Plants rooted in CWD or 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. Plants rooted in CWD will have (i) reduced allocation to belowground structures (i.e., greater ratio of above- to below-ground biomass), (ii) taller shoots, more leaves, and (or) greater leaf area, and (iii) smaller, shallower root systems (i.e., decreased root spread, area, and depth, and shorter rhizomes with greater density of branching and more rhizome tips).
2. Species will show differences in overall performance (total biomass per plant) on CWD and the forest floor consistent with their affinities for these substrates. More specifically, (i) *Vaccinium parvifolium* will exhibit greater plant biomass on CWD, (ii) *Tiarella trifoliata* will exhibit greater plant biomass on the forest floor, and (iii) *Maianthemum dilatatum* will show comparable plant biomass 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 a.s.l. on a gentle (<10%), southwest-facing slope. Soils are classified as Kaleetan sandy loam (websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx). The climate is maritime, with cool, wet winters and warm, dry summers (Franklin and Dyness 1988). The daily mean maximum temperature occurs in Au-

gust (22 °C) and mean minimum in January (−1 °C). Annual precipitation averages 256 cm, with ~50% falling between November and February (climate-station data from nearby Cedar Lake; 475 m a.s.l.; 1931–2005, Western Regional Climate Center, www.wrcc.dri.edu/summary/climsmwa.html).

The study forest is ~60 years old, having regenerated naturally after clearcut logging. Stumps indicate previous dominance by old-growth *Pseudotsuga menziesii* (Mirb.) Franco, *Tsuga heterophylla*, and *Thuja plicata* Donn ex D. Don. The current stand is dense, with 1425 stems/ha (trees ≥ 1.4 m tall) and a basal area of 75 m²/ha (D.G. Sprugel, unpublished data, 2006). *Tsuga heterophylla* is dominant (70% of stems, 58% of basal area), with lesser amounts of *P. menziesii* (21% of stems, 36% of basal area). CWD is abundant on the forest floor, a result of previous timber harvest and recent mortality from self-thinning. Light availability is low, averaging ~5% of above-canopy light (K.A. Grieve, unpublished data, 2006). Understory plant cover is also low, averaging 3% (C.B. Halpern, unpublished data, 2006).

Species' associations with substrates

To test for associations of understory species with substrates, we sampled 1200, 1 m \times 1 m quadrats arrayed continuously along three, 400 m transects spaced 20 m apart, parallel with the slope contour. Within each quadrat we estimated the percentage of ground surface covered by forest floor (mainly conifer needles and fine branches < 10 cm diameter) and 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, we calculated confidence limits for population proportions (Zar 1999). For each species with a frequency $\geq 1\%$ (present in ≥ 12 plots), we calculated the proportion of shoots (or fronds) emerging from CWD and the 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 mean 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.

Comparative analyses of substrate effects on plant performance

Study species

Based on the association analysis, three species were selected for more intensive study: *Vaccinium parvifolium* (Ericaceae), *Tiarella trifoliata* (Saxifragaceae), and *Maianthemum dilatatum* (Liliaceae). These were selected because they were among the most common in the understory, they were present on both CWD and the forest floor, and they showed differing associations with substrates: *V. parviflorum*

with CWD, *T. trifoliata* with forest floor, and *M. dilatatum* with neither substrate.

Vaccinium parvifolium is common in the *Picea sitchensis* (Bong.) Carr., *T. heterophylla*, and *Abies amabilis* (Dougl. ex Loud.) Dougl. ex J. Forbes, forest zones of western Washington and northwestern Oregon (Franklin and Dyness 1988). It is a deciduous shrub that can grow to 4 m tall, but juvenile plants (up to 4–5 years old) maintain a trailing habit (Hitchcock and Cronquist 1973). Leaves are deciduous, alternate, 1–2 cm long, and oval to elliptical in shape (Hitchcock et al. 1969).

Tiarella trifoliata is a perennial herb with short rhizomes and little or no clonal growth (Antos and Zobel 1984). Leaves are 5–12 cm long, cordate, and vary from palmately lobed (var. *unifoliata*) to divided into three separate leaflets, each with shallow (var. *trifoliata*) or nearly divided lobes (var. *laciniata*) (Hitchcock et al. 1969). All three varieties were present.

Maianthemum dilatatum is a perennial, rhizomatous herb that is common in moist temperate forests of the Pacific Northwest (LaFrankie 1986; Henderson et al. 1989). Leaves are cordate to sagittate in shape, usually one per ramet, and 5–11 cm long (Hitchcock et al. 1969). *Maianthemum dilatatum* has a modular growth form: ramets consist of a rhizome segment initiated at the base of a parent shoot and a belowground short shoot that gives rise to a vegetative or sexual shoot (i.e., with a terminal inflorescence). Lezberg et al. (2001) provide detailed descriptions of its growth form and clonal architecture.

Sample selection and plant excavations

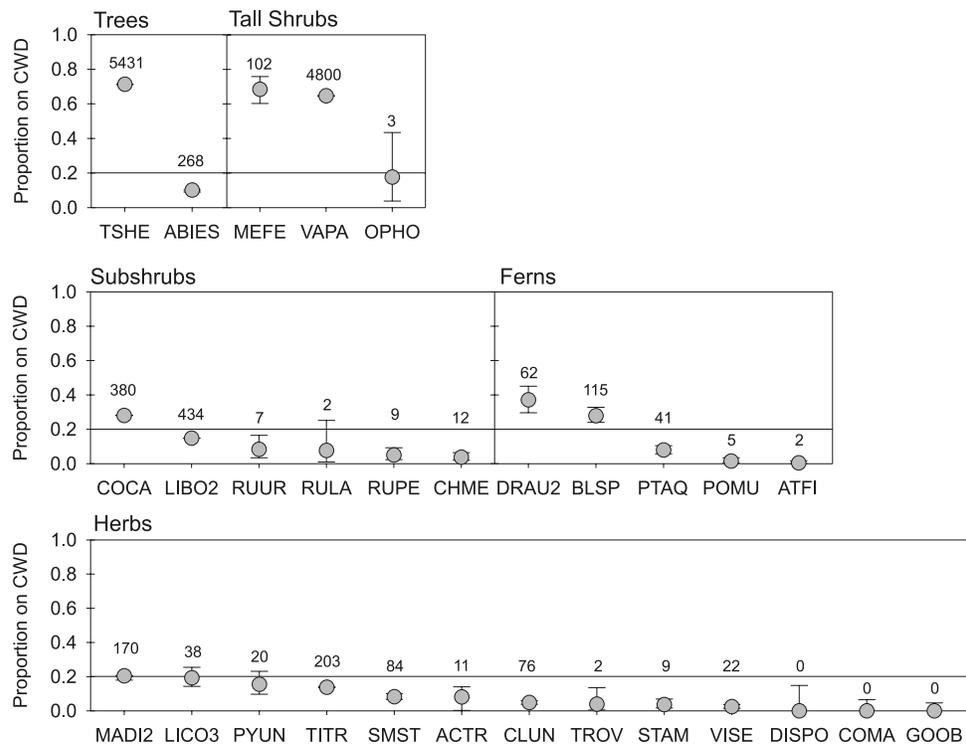
From 50 pairs of flagged individuals (focal shoots) of each species, 30 were randomly chosen for excavation and detailed measurement. Each pair consisted of a plant rooted on a decayed log and a nearby plant rooted in the forest floor; pairs were generally within 1 m of each other. For *V. parvifolium*, small plants (generally < 15 cm tall) were chosen to facilitate excavation and to ensure that belowground structures were largely contained within the target substrate.

Beginning at the focal shoot of each plant, all belowground structures and associated aerial shoots were carefully measured, mapped, and excavated using hand tools (Antos and Zobel 1984; Lezberg et al. 2001). Excavations of *M. dilatatum* included the entire clonal fragment (sensu Antos 1988) terminating in live or dead rhizome tips. Belowground systems, particularly those of *M. dilatatum*, often covered large areas and occasionally traveled off the intended substrate. Thus, for each sample, we recorded the proportion of the belowground system present in each substrate. On average, plants rooted in CWD had 96% (*M. dilatatum*) to 100% (*T. trifoliata* and *V. parvifolium*) of belowground structures in the intended substrate. Corresponding values for plants rooted in the forest floor ranged from 90% (*M. dilatatum*) to 95% (*T. trifoliata*).

Plant measurements

Aboveground structures were quantified in several ways. For each plant, we counted the number of shoots. For each shoot we also measured height (*M. dilatatum*, consisting of a single petiole and leaf) or length (*V. parvifolium*, with the

Fig. 1. Population proportions for understory species with > 1% frequency (by growth form, arranged in descending order of preference for CWD). Trees were < 1.4 m tall. Points represent mean proportions of shoots on CWD; bars are 95% confidence intervals. Numbers above points are numbers of shoots (or fronds) on CWD. 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 forest floor. All other species display no substrate association. *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*; COMA, *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*.



shoot stretched linearly); shoot height was not measured for *Tiarella* because not all plants had flowering stems. For all plants, we also counted total number of leaves (leaf density per plant), then separated leaves from stems and estimated total leaf area from a scanned image (ImageJ 1.36b software, Wayne Rasband, National Institute of Health, Bethesda, Md.).

Detailed measurements of belowground structures were also made, either directly during excavation or from maps constructed during excavation (see Antos and Zobel 1984). Length and width of spread of the root system (rhizomes and roots) were expressed as the greatest longitudinal length and perpendicular width, respectively. Rooting depth was estimated as the maximum depth of the root system measured from the top of the litter layer (for both forest floor and CWD substrates). Rooting area was calculated as the product of root-system length and width. Rooting volume was calculated as the product of rooting area and rooting depth. We expected root systems to be more linear on logs than on the forest floor, thus we also calculated the length to width ratio (root-system shape).

Because of its modular, clonal habit, we measured several additional belowground traits in *M. dilatatum*. Each clonal

fragment possessed multiple rhizome tips as a result of branching. We recorded the number of live rhizome tips (white and growing) and dead tips (brown and often fragmented) and expressed these relative to total rhizome length (i.e., density of live and dead tips; see Lezberg et al. 2001). 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 h and weighed to the nearest 0.01 g to obtain above-ground, below-ground, and total biomass.

Additional measurements of local environment

For each plant excavated, we measured several aspects of local environment that had the potential to mask or confound differences in performance between substrates. These included cover (%) of mosses and vascular plants (herbs, shrubs, and tree seedlings), depth of litter, and light availability. Cover estimates were made with a 0.2 m × 0.5 m quadrat centered on the focal shoot with its long axis ori-

ented parallel to the log. Litter depth was measured near the base of the focal shoot. Light availability (photosynthetic photon flux density [PPFD], $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was measured with an AccuPAR LP-80 ceptometer (Decagon Devices Inc., Pullman, Wash.). Light measurements were taken after excavations were completed at 1 m above each sample location. Readings were made between 1050 and 1200 h (when the sun was most directly overhead) on 17 October 2006, a uniformly overcast day.

Differences in moisture availability between substrates

To test for differences in moisture availability between substrates, we collected samples of CWD and forest floor soil. Samples were paired as a decayed log and adjacent forest floor (<50 cm apart), but were not associated with excavated plants. To quantify volumetric moisture content, 20 samples of each substrate were collected every 3 weeks from late June to mid-September 2005 using a soil core sampler (Model 0200, Soilmoisture Equipment Corp., Goleta, Calif.). A sample of 76.5 cm³ (5.7 cm diameter) was extracted from the substrate between a depth of 2 and 5 cm, the region of highest root density. Samples were weighed wet, dried at 35 °C for 48 h, and weighed again. Volumetric moisture was computed as the difference between wet and dry weights divided by sample volume.

Analyses

To test whether biomass allocation or morphology differed between plants rooted in CWD and forest floor (hypothesis 1), we 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 × species interaction (df = 2). To test whether attributes of the local environment differed for plants rooted in CWD and forest floor, similar tests were run on moss cover, vascular plant cover, litter depth, and light availability. If an interaction term was significant, a paired *t*-test was conducted to identify the species for which there was a significant effect of substrate.

For belowground traits measured only for *M. dilatatum*, we used paired *t*-tests to assess differences between substrates. Paired *t*-tests were 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).

Finally, two-way ANOVA was used to test for differences in moisture availability between CWD and forest floor. Sources of variation included substrate (df = 1), sampling date (df = 4), and their interaction (df = 4).

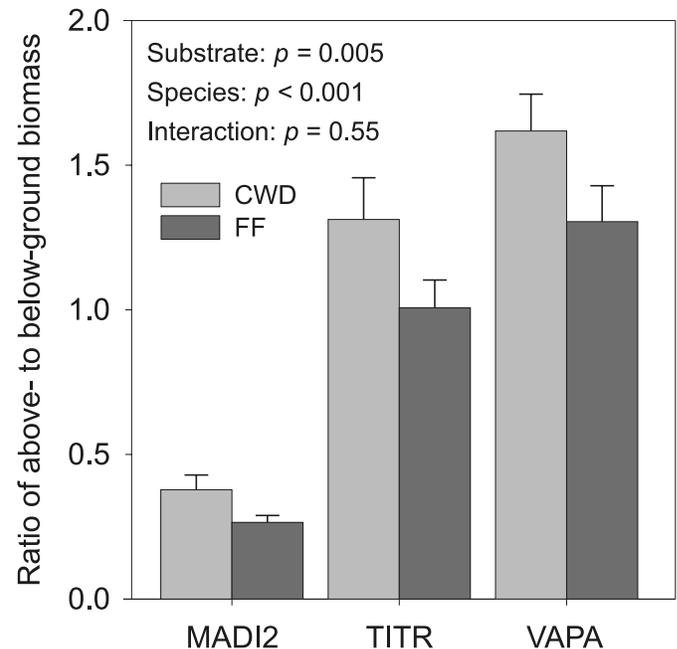
Statistical analyses were conducted using the mixed-model procedure in SAS version 9.1 (SAS Institute Inc. 2003). An alpha level of 0.05 was used to determine statistical significance. All data met the assumptions of normality and homogeneity of variance (based on Levene's test).

Results

Species' associations with substrates

In total, 48 species were recorded in the 1200 quadrats (Six 2007). CWD covered an average of 20.1% of the ground surface. Of 29 species tested (those with ≥1% fre-

Fig. 2. Ratio of above- to below-ground biomass for *Maianthemum dilatatum* (MADI2), *Tiarella trifoliata* (TITR), and *Vaccinium parvifolium* (VAPA) rooted in coarse woody debris (CWD) and the forest floor (FF) Values are means + 1 SE; *p* values are from two-way analysis of variance.



quency), 6 (21%) showed positive associations with CWD (1 tree, 2 tall shrubs, 1 subshrub, and 2 ferns) and 18 (62%) showed positive associations with forest floor (1 tree, 4 subshrubs, 3 ferns, and 10 herbs) (Fig. 1).

Comparative analyses of substrate effects on plant performance

Consistent with hypothesis 1a, plants rooted in CWD and forest floor differed in their patterns of biomass allocation. For all three species, biomass allocated to aboveground structures was significantly higher for plants rooted in CWD than in the forest floor (Fig. 2).

In contrast to patterns of biomass allocation, there were no significant effects of substrate for any aboveground trait, including leaf density, shoot height, and total or average leaf area (hypothesis 1b; Fig. 3).

Patterns of variation in belowground traits (hypothesis 1c) were more complex, but largely inconsistent with our expectations (Fig. 4). Length of root-system spread and root-system shape (length to width ratio) were significantly greater in CWD than in forest floor. Rooting depth differed between substrates for *T. trifoliata* and *M. dilatatum*, but only *T. trifoliata* differed in the direction predicted by hypothesis 1c: root systems were half as deep in CWD as in forest floor. In contrast, *M. dilatatum* had deeper root systems in CWD. Width of root-system spread, rooting area, and rooting volume differed among species, but showed no response to substrate (Fig. 4).

Of the five belowground traits measured only in *M. dilatatum*, three showed significant differences between substrates, but in a direction inconsistent with hypothesis 1c: density of dead rhizome tips, total rhizome tips, and rhi-

Fig. 3. Aboveground morphological traits of *Maianthemum dilatatum* (MADI2), *Tiarella trifoliata* (TITR), and *Vaccinium parvifolium* (VAPA) (means + 1 SE) rooted in coarse woody debris (CWD) and the forest floor (FF); *p* values are from two-way analysis of variance. Shoot height was not measured for *Tiarella* because not all plants had flowering stems.

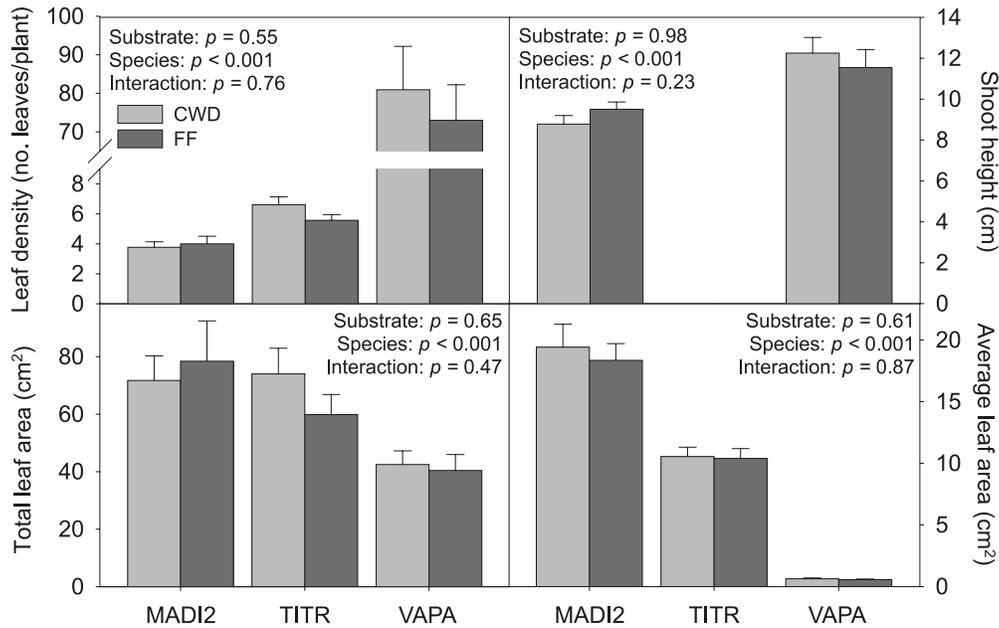


Fig. 4. Belowground morphological traits of *Maianthemum dilatatum* (MADI2), *Tiarella trifoliata* (TITR), and *Vaccinium parvifolium* (VAPA) (means + 1 SE) rooted in coarse woody debris (CWD) and the forest floor (FF); *p* values are from two-way analysis of variance. Where a substrate × species interaction was significant, separate *t*-tests were conducted by species, with asterisks denoting a significant substrate effect ($p \leq 0.05$).

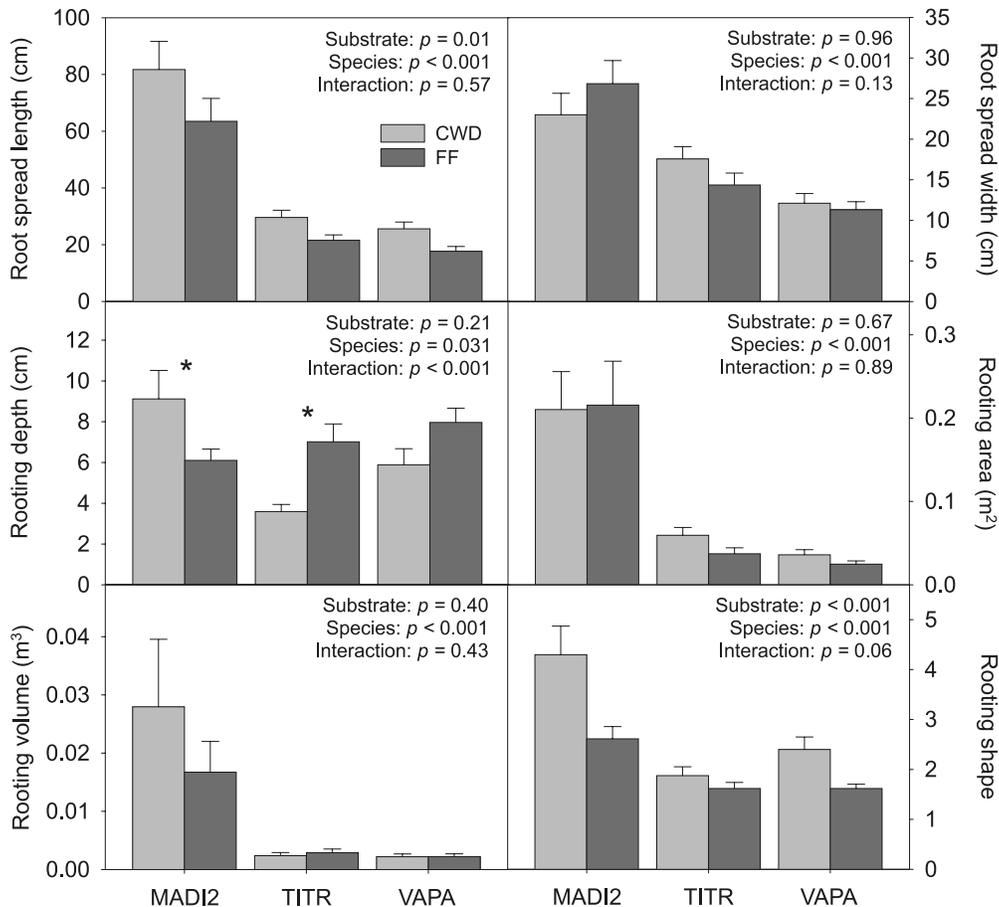
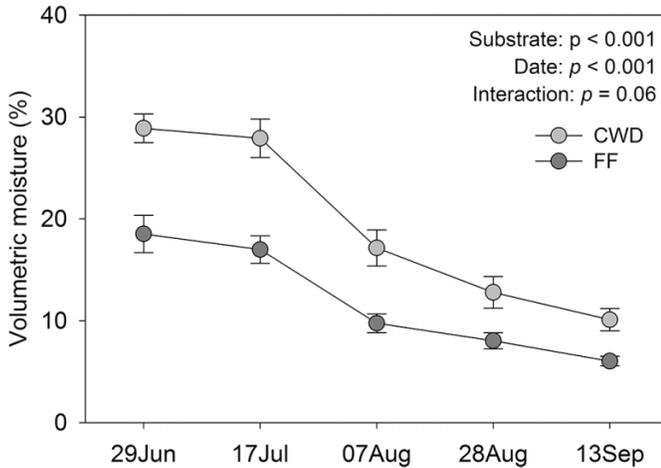


Fig. 5. Trends in volumetric moisture in coarse woody debris (CWD) and forest floor (FF) substrates during the 2006 growing season. Values are means \pm 1 SE ($n = 20$, Jun–Aug; $n = 10$, Sep); p values are from two-way analysis of variance.



zome branching were significantly lower for plants rooted in CWD ($p = 0.009$, 0.036 , and 0.038 , respectively, from paired t -tests). Density of live rhizome tips and total rhizome length were similar between substrates.

Among attributes of the local environment (cover of mosses and vascular plants, depth of litter, and light availability), only moss cover showed a significant difference between substrates (50%–300% greater on CWD; $p < 0.001$ for main effect of substrate).

In contrast to hypothesis 2, there were no differences in overall performance (total biomass per plant) between substrates for any of the species (data not shown).

Volumetric moisture declined significantly over the growing season in both substrates, but was consistently greater in CWD than in the forest floor (Fig. 5). This difference was large (56%–76% greater) through much of the summer.

Discussion

Substrate affinities of understory plants

Most understory species (62% of species tested) were associated with the forest floor and 21% with CWD. These patterns are consistent with those observed in hardwood forests of the northeastern US, where of seven herbaceous species displaying a substrate preference, six were associated with the forest floor (McGee 2001). Rooting on the forest floor may be advantageous for several reasons. First, forest floor is a more predictable substrate than CWD; the latter becomes available only when a tree falls. In addition, 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). Finally, in our dense young forests, germination and survival may be greater on the forest floor because competition from mosses is lower: moss cover averaged more than twice as high on CWD (87%) as on the forest floor (38%). Moss mats that desiccate before roots reach the substrate can be barriers to seedling establishment (Harmon and Franklin 1989).

In contrast, few species showed a positive 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, in our system, differences in plant stature do not explain associations with substrates: three of six species associated with CWD were among the tallest growth forms present (i.e., trees and shrubs).

Species associated with CWD may be limited by moisture availability at some point in their life histories and thus benefit from greater water retention by logs. *Tsuga heterophylla* seedlings, for example, are particularly sensitive to moisture stress (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).

Despite the prevalence of species–substrate associations in this forest, relatively few constituted obligate (or nearly obligate) relationships (Six 2007). 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. Thus, species may encounter elements of both substrates, regardless of rooting location. Furthermore, many herbaceous species in these forests are clonal (Hitchcock et al. 1969; Antos and Zobel 1984; Lezberg et al. 1999) and are able to place roots and rhizomes in multiple substrates.

Substrate effects on understory plant performance

We hypothesized that plants rooted in CWD and the forest floor would show differences in biomass allocation and morphology in ways consistent with the greater moisture-holding capacity of CWD. Patterns of biomass allocation were consistent with this expectation: plants rooted in the forest floor (which was drier throughout the growing season) allocated greater biomass belowground. Similar patterns of allocation along resource gradients have been observed in other forest plants (Paz 2003; Qing et al. 2004).

In contrast to patterns of biomass allocation, differences in plant morphology were less consistent with our expectations. Root-system length and shape differed between substrates, reflecting the tendency to develop linearly along logs. However, differences in rooting depth between substrates were inconsistent among species. Roots of *T. trifoliata* were deeper in the forest floor, but counter to expectation, roots of *M. dilatatum* were deeper in CWD. This contrast may reflect an interaction between the physical structure of logs and differences root-system traits. Wood may limit rooting depth in nonrhizomatous species with finer roots (*T. trifoliata*). In contrast, vigorous rhizomes of clonal species such as *M. dilatatum* 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 systems where resources are

more limiting or heterogeneous in space. However, for *M. dilatatum*, 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 by unmeasured differences in nutrient availability, if foraging was primarily for nutrients (Caldwell 1994) rather than moisture. Alternatively, morphological plasticity in *M. dilatatum* may be constrained by the physical properties of CWD. Rhizome systems in logs tended to be linear, following the grain of decay; this resulted in fewer opportunities for branching than in the forest floor.

We also hypothesized that individuals of *V. parvifolium*, *T. trifoliata*, and *M. dilatatum* would differ in overall performance (total biomass) 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, light rather than moisture or nutrient availability may be 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 at forest floor was consistently very low, averaging ~5% of that above the canopy (K.A. Grieve, unpublished data, 2006). Under these conditions, plants may be incapable of responding to differences in belowground resources (Messier 1992; Canham et al. 1996). It is also possible that associations of *V. parvifolium* with CWD, or *T. trifoliata* with the forest floor do not reflect differences in the performance of established plants, but rather, differences in the success of earlier life stages. Seeds of some species may be preferentially dispersed to (Pearson and Theimer 2004) or retained by particular substrates (see review in Nathan and Muller-Landau 2000). Rates of germination and seedling survival may also differ (e.g., Christy and Mack 1984; Caspersen and Saprunoff 2005). Once established, however, differences in resource availability may have little effect on survival or growth (Lemon 1945). These alternative explanations clearly point to the need for additional studies of species–substrate relationships, including those that consider a wider range of light conditions, other resource constraints, and earlier stages in the life histories of plants.

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