Responses of herbs and shrubs to reduced root competition under canopies and in gaps: a trenching experiment in old-growth Douglas-fir forests

Briana C. Lindh, Andrew N. Gray, and Thomas A. Spies

Abstract: We tested the effect of root trenching on vegetation in closed-canopy and gap locations in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests. Based on theory, we expected belowground competition to be intense in a region with low summer rainfall, and trench responses were expected to be greater in the high light environment of the gaps. We installed 1 m deep trenches around study plots and lined the trenches to prevent reinvasion by tree roots. Soil moisture was measured monthly during the growing season for the first 3 years after trench installation. Vegetation in these trenched plots was compared with control plots 10 years after installation of the plots. Trenched plots with no vegetation manipulation averaged 92% total understory cover, while untrenched plots averaged 47% cover. Contrary to our expectation, both vegetation and soil moisture responses to trenching were greater in areas of high tree canopy cover than in gaps. Trenched plots under closed canopies were moister than control plots throughout the growing season. We conclude that understory plants at these sites were limited at least as much by belowground competition as by above-ground competition.

Résumé : Nous avons testé, sous couvert et dans des ouvertures, l'effet sur la végétation du creusement d'une tranchée dans la zone racinaire dans des forêts de douglas (*Pseudostuga menziesii* (Mirb.) Franco). Sur une base théorique, nous anticipions que la compétition souterraine serait forte dans une région où la précipitation estivale est faible et que la réaction au traitement serait plus forte dans les ouvertures où il y a plus de lumière. Nous avons creusé des tranchées de 1 m de profondeur autour des parcelles expérimentales et recouvert les parois pour empêcher la réinstallation des racines des arbres. L'humidité du sol a été mesurée à tous les mois pendant la saison de croissance durant les trois premières années après le creusement des tranchées. La végétation dans les parcelles expérimentales où la végétation n'avait pas été perturbée avaient en moyenne un couvert total de 92 % en sous-étage comparativement à 47 % pour les parcelles témoins. Contrairement à nos attentes, tant la végétation que l'humidité du sol ont davantage réagi au traitement dans les zones avec un fort couvert arborescent que dans les ouvertures. Les parcelles traitées sous un couvert fermé étaient plus humides que les parcelles témoins pendant toute la saison de croissance tandis que l'effet du traitement dans les ouvertures globalement plus humides s'est fait sentir seulement à la fin de la saison de croissance. Nous concluons que dans ces sites, la végétation en sous-étage est limitée au moins autant par la compétition souterraine que par la compétition épigée.

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B.C. Lindh.¹ 2082 Cordley Hall, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331, U.S.A.

A.N. Gray and T.A. Spies. USDA Forest Service, Pacific Northwest Research Station. 3200 SW Jefferson Way, Corvallis, OR 97331, U.S.A.

¹Corresponding author (e-mail: blindh@willamette.edu).

Introduction

The relative importance of aboveground and belowground controls on understory responses to disturbances of the tree canopy is not well understood. While the response of vegetation to canopy gaps has largely been discussed in terms of light (Whigham et al. 1993; Pascarella and Horvitz 1998), the death of canopy trees also influences soil moisture (Gray et al. 2002) and nutrient availability (Matson and Boone 1984). Root trenching studies have frequently demonstrated that growth and establishment of herbs, shrubs, and tree

seedlings is strongly influenced by belowground competition for moisture and nutrients. In a recent review of root trenching studies, Coomes and Grubb (2000) cite situations in which understory response to gaps was controlled more by light than by water or nutrients and other situations in which the reverse was true. They propose a conceptual framework that predicts the relative importance of root competition as a function of summer rainfall, soil fertility, and the density of shade cast by the dominant tree species. Where soils are nutrient rich and moist throughout the year, vegetation responses to gaps will be controlled more by aboveground competition than by belowground competition. Where soils are nutrient poor and dry in summer, they predict a large response to root trenching (release from belowground competition). Coomes and Grubb (2000) further propose that trenching effects should be larger in gaps than under dense. closed canopies; they argue that the lack of light under the closed canopy should prevent a large response to an increase in belowground resource availability.

Few studies have examined responses of understory vegetation to reduced root competition and canopy openness in the dense Pseudotsuga menziesii forests of the Pacific Northwest. The climate in this region is characterized by abundant winter precipitation with summer drought and soils that are relatively nutrient poor. According to the conceptual framework of Coomes and Grubb (2000), we should expect root trenching in this region to increase vegetation establishment and growth via an increase in soil moisture and nutrient levels. The dense shade of the tree canopies would be expected to prevent large trench responses under closed canopies, while canopy gaps should show large trench responses. Only two studies have evaluated root competition in Douglas-fir forests (Christy 1986; Simard et al. 1997), and their results are only partly consistent with each other and with the predictions of Coomes and Grubb (2000). In Oregon, Christy (1986) found that trenching to reduce root competition had a greater effect on growth of juvenile Tsuga heterophylla (Raf.) Sarg. than did the creation of canopy gaps. However, Simard et al. (1997) did not find any effects of trenching on growth of P. menziesii seedlings in British Columbia. Neither study found that growing season soil moisture increased in the trench plots as would be predicted by Coomes and Grubb (2000). Simard et al. (1997), along with Hart and Sollins (1998), found increases in soil moisture in trench plots in relation to controls only in early fall, after plant growth had ceased. The failure of these studies to find a soil moisture response is surprising given the summer drought that is characteristic of P. menziesii forests. In contrast. Gray et al. (2002) did find that growing season soil moisture was higher in gaps and in trench plots than in controls for conifer forests in Washington and Oregon. None of these studies reported how differences in soil moisture between trench and control plots varied over the growing season or between years. Given the variation observed in vegetative and soil moisture responses to release from root competition and canopy shading in this region and the inconsistency of some of the results with predictive models, it is clear that our understanding of these processes is incomplete.

No studies have examined the response of the herb and shrub layer to reduced root competition in Pacific Northwest

P. menziesii forests. In contrast with tropical forest understories, Pacific Northwest forest understories have relatively few tree seedlings; herbs and shrubs make up most of the diversity and biomass. McCune (1986), in a grand fir (Abies grandis (Dougl. Ex D. Don) Lindl.) forest in Montana, showed striking increases in herb cover (a jump from 7% to 55%) as a result of trenching. In a white pine (Pinus strobus L.) forest in New Hampshire, Tuomey and Keinholz (1931) found an eightfold increase in the number of understory herb and shrub individuals 8 years after trenching. Differences persisted 20 years after establishment, with particularly striking establishment and growth of eastern hemlock (Tsuga canadensis (L.) Carrière) individuals in the trenched plot (Lutz 1945). Walter and Breckle (1985) reviewed the results of several studies published in Russia and Germany. Trenching in boreal spruce (Picea spp.) or Siberian fir (Abies sibirica Ledeb.) forest transformed sparse understories into lush carpets dominated by Oxalis acetosella L. (see citations in Walter and Breckle 1985). Trenching studies generally examine vegetative rather than reproductive responses, perhaps because it is widely held that light is the primary resource that limits flowering of understory vegetation (Chazdon 1991; Niesenbaum 1993; Cunningham 1997). The one study that has examined the effect of killing tree roots on flowering in an understory herb found no treatment effect (Hughes et al. 1988). Using observational data, however, St. Pierre (2000) found that soil moisture and light levels helped explain flowering of two understory herb species in experimental canopy gaps.

In this study, we extend research into root competition and gap effects by examining the response of cover and flowering of forest herbs and shrubs to trenching in oldgrowth *P. menziesii* forests in the Pacific Northwest. Our objectives are (i) to compare the cover of herbs and shrubs in trenched and untrenched plots in canopy gaps and beneath closed canopies; (ii) to compare the number of flowering ramets in these treatments; and (iii) to evaluate changes in soil moisture over the growing season and among years in relation to the treatments.

Materials and methods

Our two study sites were in mid-elevation old-growth forests on the west side of the Cascade Mountains in northern Oregon and southern Washington. Both were mixed-species stands with a dominant canopy of *P. menziesii* and a subcanopy of *T. heterophylla*. Recent (last 25 years) average annual precipitation at the H.J. Andrews Experimental Forest site (44°15′N, 122°15′W) and at the Wind River Experimental Forest (45°50′N, 122°00′W) is about 220 cm, with less than 10% of that falling during the months June– September.

Trenched plots (belowground gaps) were installed to complement an experimental canopy gap study at the H.J. Andrews and Wind River sites (Gray and Spies 1996). These plots were installed in 1990 and monitored for 4 years for soil moisture response (Gray et al. 2002). Vegetation in the plots had never been quantified until the present study.

Our experimental design was a split-plot, with two whole plots (closed-canopy or naturally occurring gap) at each of

the two sites (H.J. Andrews and Wind River). Within each whole plot, four factorial combinations of trenching (trenched or control) and clipping (clipped or not) were assigned randomly to four adjacent (separated by 2-5 m) subplots. While we did not measure initial plant cover, subplots were selected to be visually homogeneous. Treatment effects could potentially be confounded with differences in initial cover; however, random assignment of treatments to plots sought to avoid this problem. Trenched plots were created by severing tree roots to a depth of 1 m around the perimeter of a 3 m \times 3 m area. Plots did not include sapling or adult trees but did include occasional tree seedlings less than 30 cm tall. The trenches were lined with 0.5 mm stainless steel mesh on up- and down-slope sides and black plastic on other sides to prevent the reinvasion of tree roots. The clipping treatment was applied during the first 3 years of the experiment and then discontinued; the objective of the treatment was to estimate understory vegetation effects on soil moisture. All plants (herbs, shrubs, and tree seedlings) were clipped to ground level. After clipping was discontinued, some existing plants recovered and many new plants seeded in. Although the clipping treatment per se is not the focus of this paper, clipped plots were included in this analysis to increase the sample size over which trench effects could be estimated.

We sampled the plant communities in these plots in the summer of 2000, 10 years after installation. Sampling was carried out in a 2 m \times 2 m plot set within the 3 m \times 3 m treatment plot to avoid edge effects. Cover of each plant species was estimated visually and added to yield a total cover value, which for some plots exceeded 100%. We also counted the number of flowering ramets for each species; because different species flowered in each plot, numbers for each species were added to give the total number of flowering ramets. Growing season soil moisture in the plots was sampled monthly in May-October of 1991, 1992, and 1993. Volumetric soil moisture was determined using time domain reflectometry (model 1502C, Tektronix Inc., Beaverton, Ore., U.S.A.; Gray and Spies 1995; Gray et al. 2002). Two parallel probes extended vertically 45 cm into the soil in each plot; the value reported for each plot is the average from two sets of probes. In this paper, we present the monthly trends in soil moisture and the relationship between vegetation and soil moisture response; a previous analysis provided a test of significance of the effect of trenching on soil moisture (Gray et al. 2002).

Cover and flowering response variables were analyzed in a split plot ANOVA with canopy cover as the whole plot factor and trenching and clipping as subplot factors. The analysis was carried out using PROC MIXED in SAS (version 8, SAS Institute Inc. 1999) with trenching, clipping, and canopy openness as fixed effects and site as a random block effect. The approximate normality of the cover data supported a parametric analysis. The number of flowering ramets was log-transformed to improve normality.

Results

Plots were dominated by herbs and low shrubs, with occasional tall shrubs and tree seedlings present. Trenched plots had higher vegetation cover than controls in both the intact Fig. 1. Response of understory vegetation to trenching and clipping (averaged over canopy openness). Sample size for each bar is four (an open- and closed-canopy plot at each of two sites). Error bars are one standard error.



vegetation (unclipped plots) and recovering vegetation (clipped plots) (Fig. 1, $F_{[1,6]} = 64.74$, p = 0.0002). Trenched plots (unclipped) had 92% cover, while control plots had 47% cover. Trench plots in gaps had about 30 percentage points higher plant cover than trenched plots under closed canopy, providing an estimate of response to aboveground gaps.

Cover in the trenched plots was composed of the fern *Polystichum munitum* (Kaulf.) K. Presl (Polypodiaceae) and the low shrub *Berberis nervosa* Pursh (Berberidaceae) at the H.J. Andrews gap area, the herb *Coptis laciniata* A. Gray (Ranunculaceae) at the Andrews closed-canopy area, and the herb *Achlys triphylla* (Sm.) DC. (Berberidaceae) at both canopy densities at Wind River. These species were also present in the control plots, but at lower abundance. The total number of flowering ramets (of all species) tended to be higher in trenched than in control plots (26 vs. 16; $F_{[1,6]} = 4.40$, p = 0.08). At the H.J. Andrews site, most flowering ramets belonged to the herb *Tiarella trifoliata* L. (Saxifragaceae), and at Wind River, to the herb *Achlys triphylla*.

The effect of trenching on soil moisture was evident throughout the growing season and in all 3 years (Fig. 2). Each year varied in the initial soil moisture measurement, but the pattern of drying over the summer and the relative position of the treatments were the same in all years. The trenched plots exhibited the highest soil moisture; trenched plots had high and similar soil moisture regardless of canopy density. In the gap areas, the control plots started at the same soil moisture as the trenched, but dried faster to end the season four percentage points drier. In the closed canopy areas, the control plots were much drier than the trenched plots (eight percentage points), and that difference was already present in May at the time of the first measurement. Statistical evidence for an effect of clipping on soil moisture was weak but suggestive ($F_{[1,1]} = 5.32$, p = 0.06). Considering only untrenched plots, clipped plots had four percentage points higher soil moisture than unclipped; however, in trenched plots, clipping had no effect.

Fig. 2. Soil moisture measured throughout the growing season in unclipped plots. Each point is the average of two values (one from each site). Circles (\bigcirc) are closed-canopy control plots, triangles (\triangle) are gap control plots, pluses (+) are closed-canopy trench plots, and crossed lines (×) are gap trenched plots.



Like soil moisture, the vegetation responded much more to trenching in the closed canopy area. The average difference in plant cover between trenched and control plots was much greater in closed-canopy than gap areas (64 percentage points versus 27 percentage points, considering only those plots with unclipped vegetation; see Fig. 3). The plot pairs that show the largest difference in plant cover associated with trenching also show the largest differences in soil moisture (Fig. 3).

Discussion

Our data show clear differences in understory vegetation cover, flowering, and growing season soil moisture associated with the removal of competition by tree roots. This finding matches our expectation that belowground competition should be important in summer-dry regions. Our results clarify that even in a closed-canopy old-growth coniferous forest, belowground competition may be more important than light limitation. At our sites, the difference in plant cover moving from control to trench under a closed canopy (45 percentage points) was larger than that associated with moving from closed-canopy to gap areas, where light levels Fig. 3. Vegetation cover and soil moisture in control and trenched plots. Each point is the value from one sample plot; open symbols correspond to control plots, filled symbols to trenched plots, and lines connect adjacent pairs of control and trenched plots. Soil moisture values are from October 1991, the driest month in the first year following trenching.



should be optimal for understory plants (30 percentage points).

Both vegetation and soil moisture responses to trenching were much higher in the closed-canopy areas than in the gaps. Our finding contrasts with the prediction of Coomes and Grubb (2000) that trench responses would be greater in gaps. In our sites, the gaps probably had lower root densities than the closed canopy sites. Experimental gaps nearby had much lower fine root densities in mineral soil than did control plots (Vogt et al. 1995). Severing the less numerous roots in our gap areas would have had less effect on belowground resources than severing the dense carpet of roots in the closed-canopy area. Further evidence for lower root densities in the gap is provided by the fact that the difference in soil moisture between control and trenched plots was already present in May in the closed-canopy area, while it developed gradually over the summer in the gaps. The dependence of the trenching effect on canopy environment (and by extension, root density) may explain why other researchers found trenching effects on soil moisture only at the end of the growing season (Simard et al. 1997; Hart and Sollins 1998) if their sites had lower root densities than ours.

The magnitude of vegetation response that we observed correlated well with the magnitude of effect that trenching has on soil moisture (see Fig. 3). Our vegetation response may be due to soil moisture alone or to a concomitant increase in the availability of nutrients, which we did not measure. However, in a nearby site, Hart and Sollins (1998) found that trenched plots had total nitrogen amounts indistinguishable from control plots, although trenched plots did have higher rates of nitrogen mineralization. Since increased water availability can increase both the supply of available nitrogen and the ability of the plant to take it up (Chapin et al. 1987; Riegel et al. 1992), it is not easy to separate the effects of water and nutrients.

Findings from trench studies carried out in temperate and tropical regions suggest responses to both soil moisture and nutrients (Coomes and Grubb 2000). Studies from wet coni-

fer forests in Europe have suggested that nutrients mediate the trenching response (reviewed in Walter and Breckle 1985). Walter and Breckle (1985) suggest that at the aridity limit of European tree species, understories tend to be depauperate because on these sites the trees are using all the available water and leaving none for the understory. In the open, dry Pinus ponderosa Dougl. ex P. & C. Laws. forests of eastern Oregon. Riegel and coworkers (1992) showed that understories were limited by belowground resources rather than light. They found increases in both water and nitrogen levels as a result of trenching and concluded that plants were responding to both. In fact, we should expect plants in forest understories to be simultaneously limited by water, nutrients, and light and to be able to respond to increased abundance of any of these resources (Chapin et al. 1987). Studies in tropical forests have produced comparable results, with trenching having zero or negative effects on plant performance in nutrient-rich wet sites (Denslow 1991; Ostertag 1998) and positive effects in nutrient-poor (Coomes and Grubb 1998) or dry sites (Gerhardt 1996).

Understory plants in summer-dry coniferous forests face limiting levels of several resources because the trees whose canopies shade the understory also bear roots that deplete levels of water and nutrients in the soil. Smith and Huston (1989) hypothesized that plants cannot develop strategies to simultaneously and efficiently use low levels of water and light. Shade-tolerant plants should develop large thin leaves at the expense of a limited root system, while droughttolerant plants should have large belowground allocation and thick evaporation-resistant leaves. Coomes and Grubb (2000) suggested that plants that do tolerate both stresses have the small leaves of a drought-adapted plant and grow extremely slowly as a result of their very limited light capture. Of the herbs that responded most vigorously to trenching in the closed-canopy sites in our study, one appears tolerant of both drought and shade, while the other is a shade tolerator that evades drought through early senescence in the summer. Coptis laciniata, the dominant species in the shade plots at the H.J. Andrews site, exhibits small, thick, evergreen leaves that probably resist evaporation well. It is highly clonal, slow growing, and able to occupy even the densest forest. Achlys triphylla, which dominated the trenched plots at Wind River, has large, thin leaves more typical of a shadeadapted plant. Perhaps as a result, it appears very vulnerable to drought. It occupies the wettest sites within coniferous forests and uses a "spring ephemeral" strategy, otherwise rare in western coniferous forests, to evade the dry late summer period.

We found suggestive evidence that the number of flowering ramets was higher in trenched plots than in controls; this effect was stronger in the closed-canopy areas than in gaps. This result suggests that for the species flowering in our plots (primarily *Tiarella trifoliata* L. and *Achlys triphylla*), not only vegetative growth but sexual reproduction is limited by belowground resources. This experimental result supports the observational work of St. Pierre (2000), who found that *Tiarella trifoliata* fecundity was explained better by soil moisture than by light levels in gaps.

As mentioned above, previous work on effects of trenching in *P. menziesii* forests has focused on understory trees

rather than shrubs and herbs (Christy 1986; Simard et al.1997) and has found mixed results. Working only a few kilometres away from one of our study sites. Christy (1986) found that root trenching around suppressed Tsuga heterophylla juveniles increased their growth. Simard et al. (1997) transplanted P. menziesii seedlings into trenched and control plots and found that trenching had no significant effect on total growth; stunting of height (vs. stem diameter) growth in the trenched seedlings suggested a negative effect of root trenching. Simard et al. (1997) attributed this lack of positive response to two factors: (i) soil moisture may not have been limiting in her system because of significant summer rainfall and (ii) trenching lowered mycorrhizal diversity on the roots of the seedlings and precluded mycorrhizal connections between the seedlings and overstory trees. Since the understory herbs and shrubs that responded to trenching in our study are probably mostly vesicular-arbuscular mycorrhizal (Brundrett and Kendrick 1988), they are unlikely to share mycorrhizal species or direct hyphal connections with the overstory; trenching would thus not have any deleterious effect. Interestingly, tree seedlings established and grew fairly well in our trenches, suggesting either that these species (primarily Abies spp. and Tsuga heterophylla) do not rely on mycorrhizal innoculum or hyphal connections from the canopy trees or that the benefit provided by trenching outweighed the loss of mycorrhizae.

Our results suggest that in the summer-dry P. menziesii forests that we studied, belowground competition may play a large role in explaining the patterns of understory-overstory interactions. Even under dense shade, root trenching produced dramatic increases in understory plant cover. Densely stocked young coniferous forests, referred to as closed canopy or "dark". often have depauperate herb layers. Although light limitation probably plays a role, young forests have the highest root densities of any stand age (Vogt et al. 1983), and the even spacing of these forests will result in few belowground gaps. The characteristic patchiness of oldgrowth forest understories (Franklin et al. 1981) may be better explained by patchiness of belowground rather than aboveground resources. Above- and below-ground gaps will be correlated but not necessarily totally overlapping in space or time; this lack of overlap may help explain observed disjunctions between canopy cover and understory vegetation response.

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References

Brundrett, M.C., and Kendrick, B. 1988. The mycorrhizal status, root anatomy, and phenology of plants in a sugar maple forest. Can. J. Bot. 66: 1153–1173.

- Chapin, F.S.I., Bloom, A.J., Field, C.B., and Waring, R.H. 1987. Plant responses to multiple environmental factors. BioScience, **37**: 49–56.
- Chazdon, R.L. 1991. Effects of leaf and ramet removal on growth and reproduction of *Geonoma congesta*, a clonal understory palm. J. Ecol. **79**: 1137–1146.
- Christy, E.J. 1986. Effects of root competition and shading on growth of suppressed western hemlock (*Tsuga heterophylla*). Vegetatio, 65: 21–28.
- Coomes, D.A., and Grubb, P.J. 1998. Responses of juveniles to above- and belowground competition in nutrient-starved Amazonian rainforest. Ecology, **79**: 768–782.
- Coomes, D.A., and Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecol. Monogr. 70: 171–207.
- Cunningham, S.A. 1997. The effect of light environment, leaf area, and stored carbohydrates on inflorescence production by a rain forest understory palm. Oecologia, **111**: 36–44.
- Denslow, J.S. 1991. The effect of understory palms and cyclanths on the growth and survival of *Inga* seedlings. Biotropica, 23: 225–234.
- Franklin, J.F., Cromack, K., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, F., and Juday, G. 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-118.
- Gerhardt, K. 1996. Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. For. Ecol. Manage. 82: 33–48.
- Gray, A.N., and Spies, T.A. 1995. Water content measurement in forest soils and decayed wood using time domain reflectometry. Can. J. For. Res. 25: 376–385.
- Gray, A.N., and Spies, T.A. 1996. Gap size, within-gap position, and canopy structure effects on conifer seedling establishment. J. Ecol. 84: 635–645.
- Gray, A.N., Spies, T.A., and Easter, M.J. 2002. Microclimatic and soil moisture responses to gap formation in coniferous forests. Can. J. For. Res. 32: 332–343.
- Hart, S.C., and Sollins, P. 1998. Soil carbon and nitrogen pools and processes in an old-growth conifer forest 13 years after trenching. Can. J. For. Res. 28: 1261–1265.
- Hughes, J.W., Fahey, T.J., and Bormann, F.H. 1988. Populations persistence and reproductive ecology of a forest herb: Aster acuminatus, Am. J. Bot. 75: 1057–1064.
- Lutz, H.J. 1945. Vegetation on a trenched plot twenty-one years after establishment. Ecology, 26: 200–202.

- Matson, P.A., and Boone, R.D. 1984. Natural disturbance and nitrogen mineralization: wave-form dieback of mountain hemlock in the Oregon Cascades. Ecology, 65: 1511–1516.
- McCune, B. 1986. Root competition in a low-elevation grand fir forest in Montana — a trenching experiment. Northwest Sci. 60: 52–54.
- Niesenbaum, R.A. 1993. Light or pollen seasonal limitations on female reproductive success in the understory shrub *Lindera benzoin*. J. Ecol. 81: 315–323.
- Ostertag, R. 1998. Belowground effects of canopy gaps in a tropical wet forest. Ecology, **79**: 1294–1304.
- Pascarella, J.B., and Horvitz, C.C. 1998. Hurricane disturbance and the population dynamics of a tropical understory shrub: megamatrix elasticity analysis. Ecology, 79: 547–563.
- Riegel, G.M., Miller, R.N., and Krueger, W.C. 1992. Competition for resources between understory vegetation and overstory *Pinus ponderosa* in northeastern Oregon. Ecol. Appl. 2: 71–85.
- SAS Institute Inc. 1999. SAS/STAT guide for personal computers, version 8 ed. SAS Institute Inc., Cary, N.C.
- Simard, S.W., Perry, D.A., Smith, J.E., and Molina, R.A. 1997. Effects of soil trenching on occurrence of ectomycorrhizas on *Pseudotsuga menziesii* seedlings grown in mature forests of *Betula papyrifera* and *Pseudotsuga menziesii*. New Phytol. 136: 327–340.
- Smith, T., and Huston, M. 1989. A theory of the spatial and temporal dynamics of plant communities. Vegetatio, 83: 49–70.
- St. Pierre, E. 2000. Effects of canopy gaps in Douglas-fir forests and resource gradients on fecundity and growth of understory herbs. Ph.D. dissertation, Oregon State University, Corvallis, Ore.
- Tuomey, J.W., and Keinholz, R. 1931. Trenched plots under forest canopies. Yale University School of Forestry Bulletin 30.
- Vogt, K.A., Moore, E.E., Vogt, D.J., Redlin, M., and Edmonds, R.L. 1983. Conifer fine root biomass within the forest floors of Douglas-fir stands of different ages and site productivities. Can. J. For. Res. 13: 429–437.
- Vogt, K.A., Vogt, D.J., Asbjornsen, H., and Dahlgren, R. 1995. Roots, nutrients and their relationship to spatial pattern. Plant Soil, 168–169: 113–123.
- Walter, H., and Breckle, S.W. 1985. Ecological systems of the geobiosphere. I. Ecological principles in global perspective. Springer-Verlag GmbH & Co. KG, Berlin, Germany.
- Whigham, D.F., O'Neill, J., and Cipollini, M. 1993. The role of tree gaps in maintaining the population structure of a woodland herb: *Cynoglossum virginianum* L. Plant Species Biol. 8: 107–115.