AN ABSTRACT OF THE THESIS OF

Elizabeth A. St. Pierre for the degree of Doctor of Philosophy in Forest Science was presented on March 15, 2000. Title:

Effects of Canopy Gaps in Douglas-Fir Forests and Resource Gradients on Fecundity and Growth of Understory Herbs

Signature redacted for privacy.

Abstract approved: ______________________________
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Effects of small-scale disturbances on fecundity and growth rates of *Linnaea borealis* L., *Tiarella trifoliata* L. var. *unifoliata*, and *Trillium ovatum* Pursh. were studied in old-growth forests in the *Tsuga heterophylla* Zone on the west slope of the Cascade Mountain Range of Oregon. Performance of each species was compared in experimental gaps of different sizes (created in 1990) and in relation to gradients of light and soil moisture. Effects of plant age and size and rhizome depth were additionally evaluated for *Trillium*. Locations of seedlings were surveyed for all three species relative to positions within and around gap and control treatments.

Growth and fecundity of all three species were higher in or around gaps than under closed canopies. Growth and fecundity of *Linnaea* and *Tiarella* were greater within gaps than in controls and adjacent borders of gaps. Fecundity of *Linnaea* was greater in large gaps than in small gaps and controls. *Tiarella* seedlings were present in gaps and on gap borders but not in controls. Fecundity and leaf area of *Trillium* were greatest in positions north of canopy gaps. *Trillium* seedlings were present on gap borders but no seedlings were found within gaps. Within gaps, *Trillium* also had lower rates of seed production (per m^2 cover), horizontal growth, and relative increases in abundance than did the other two species.

Performance of all three species varied more with gap position and resources than with gap size. Within gaps, fecundity was lowest in central positions for *Linnaea* and in northern positions for *Tiarella*. Unlike *Trillium*, growth rates of these species were greater in southern than in positions north of gaps. Effects of gap position were modified in some cases by debris, shrubs, and topographical structures. Fecundity increased with light (at low soil moisture) for *Linnaea* and soil moisture for *Tiarella;* growth rates increased with soil moisture for both of these species. Fecundity of *Trillium* was a function of plant development and resources and was most directly related to leaf area. Seed production and leaf area of *Trillium* peaked at low light intensity. Canopy heterogeneity therefore influences life cycles of these forest herbs.

Effects of Canopy Gaps in Douglas-Fir Forests and Resource Gradients on Fecundity and Growth of Understory Herbs

by

Elizabeth A. St. Pierre

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Completed March 15, 2000
Commencement June 2000

Doctor of Philosophy thesis of Elizabeth A. St. Pierre presented on March 15, 2000

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ACKNOWLEDGEMENTS

Tom Spies was a tremendous influence in the development of the experimental design and the structure of this dissertation and I very much appreciate his financial support and facilities which enabled me to start work on it. Members of my committee (Bill Ferrell, Don Zobel, and Dan Luoma) also contributed ideas to the design of my study and interpretation of results. I appreciate use of Don Zobel's lab and Morrie Craig's office space. I thank Sue Tornquist for her support as a graduate representative. Logan Norris also provided financial support, facilities in the Forest Science Lab and priceless encouragement. John Tappeiner generously provided resources for work that helped me develop my analytical skills and hypotheses for this dissertation and will always have my graditude for giving me credit for my ideas and work.

Andy Gray not only paved the way for this dissertation by sharing data, ideas and equipment from his gap study but also by simply letting me know I that I am capable of completing this and other scientific work. Al Levno kindly helped my with facilities at H. J. Andrews. Laurel Grove shared the benefits of her many years of experience as an editor by helping me organize and articulate ecological and statistical concepts and data. Lisa Ganio provided statistical advise and Trina Filan assisted with data entry and quality. Rob Pabst shared many references and assisted in field work. Mark Wilson's direct and constructive criticism contributed to the quality and progress of my dissertation and to my enthusiasm for future work in ecology. Many, many friends and neighbors also provided encouragement and support.

Funding was provided by the USFS Pacific Northwest Research Station, NSF/USDA NRLCGP 96-35101-3781 and the 1997-1998 Cathy Bacon Scholarship.

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EFFECTS OF CANOPY GAPS IN DOUGLAS-FIR FORESTS AND RESOURCE GRADIENTS ON FECUNDITY AND GROWTH OF UNDERSTORY HERBS

CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Disturbance initiates succession by changing abiotic, biotic, and spatial factors that influence the probability of establishment and survival of species. Populations that increase in response to light, nutrients, or space available after moderate disturbances may, in contrast, decrease after severe or new types of disturbances or changes in resources during succession. The timing and distance between germination sites and propagule sources also contribute to initial patterns of species abundance (Harper 1977, Matlack 1994).

Differential performance (e.g., growth and reproduction rates) among established species can change their relative abundance. The relative performance of species varies with availability of resources (e.g., light and soil moisture) and life history patterns (e.g., allocation and reproductive modes). The actual resource levels available to a plant are determined by disturbance regime, site factors such as topography and microclimate, and interactions with other organisms (e.g., competition, herbivory, and allelopathy) that release or deplete resources.

Species composition and abundance vary with the timing, spatial distribution, and type of disturbances (Pickett et al. 1985). However the degree of effects of disturbance vary with the spatial and temporal perspective. For example (Spies et al. 1999) illustrate that while conditions within canopy gaps may rapidly change, the number of gaps remains about the same over time across a stand. In another example, simulation models that incorporate long-term fluctuations in species dominance at a landscape scale predict lower rates of change in species composition and abundance than do brief observations made at smaller scales. In other words, the cumulative area of many small disturbance patches can average out over time. For example, the proportions of five successional stages in a 900-km^2 area of Superior National Forest remained relatively constant during a 10-yr period even though half of the stands changed from one successional stage to another during that time (Perry 1995).

Species composition and abundance can be *relatively* similar among plant communities when disturbance regimes and climate somewhat resemble historic conditions. For example, six major vegetation zones correspond to certain elevations and distances from the coast in the Pacific Northwest (PNW) region because climate and topography determine temperature, precipitation, and seasons, which in turn place limitations on the range of species in these zones (Zobel et al. 1976, Franklin and Dyrness 1988). Performance of dominant tree species in the overstory and sub-canopy and of the herbs and shrubs in the understory that define each zone vary with, for example, their ability to tolerate moisture stress, temperature extremes, and fire (Zobel et al. 1976, Waring and Schlesinger 1985). Forest succession in the mid-elevation zone on the west slope of the central Cascade Mountain Range of Oregon still results in a mix of dense, shade-tolerant western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and intolerant Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Franklin and Dyrness 1988; Stewart 1986). Species such as *Linnaea borealis* L., *Tiarella trifoliata* L. var. *unifoliata*, and *Trillium ovatum* Pursh., though patchy in distribution, thus remain common throughout the understory of the Western Hemlock Zone (Franklin and Dyrness 1988; Zobel et al. 1976).

1.2 Forest gap dynamics

Wind and wildfire in Douglas-fir forests of the PNW produce openings ranging from less than 0.1 to over 100,000 ha. Gap sizes of old-growth forests have a log-normal distribution in which small (85-m^2) gaps are most common and large gaps are rare. Although large gaps in old stands persist up to 100 yr, the smaller (19-m^2) gaps of young stands are more ephemeral, lasting only 25 yr because of rapidly expanding tree canopies (Spies et al. 1990). Gaps created by the death of two or more trees in old stands may be as important to ecosystem function as fire because they cumulatively occurred over comparable acreage (Spies et al. 1989).

According to the gap-phase regeneration paradigm (Hubbell and Foster 1986), above- and belowground resource and microsite availability will be greater in canopy gaps until new trees replace the fallen ones. Canopy gaps increase light intensity and the amount of precipitation that reaches the forest floor (Canham et al. 1990; Gray and Spies 1996, 1997). Soil and air temperatures near the ground may consequently be higher and humidity may be lower in gaps than in surrounding forests (Chen et al. 1993; Runkle 1985; Hubbell and Foster 1986). Soil moisture can also be higher in gaps where root density and transpiration rates are low (Gray 1995; Toumey and Kienholz 1931).

Microclimatic and resource characteristics vary by gap size, shape, and orientation; by slope and height of surrounding vegetation; and by position within gaps (Pickett and White 1985). For example, temperature, light intensity, and soil moisture are higher in large canopy gaps than smaller gaps (Gray and Spies 1996, 1997). In the northern hemisphere, northern positions within gaps receive more direct light and reach higher maximum temperatures than southern positions (Canham et al. 1990; Van Pelt et al. 1996). Soil moisture is greatest in gap centers (Gray and Spies 1996).

Shrubs, fallen trees, and pit and mound topography create additional microsites and resource variations within gaps (Lyford and MacClean 1968, Thompson 1985). Soil moisture and nutrients can be retained where fallen trees provide shade, store water, and trap organic debris. Root upheaval in gaps redistributes nutrients to the ground layer where newly exposed mineral soil provides substrates for root growth and germination of seeds (Harmon et al. 1986, Beatty 1984).

1.3 Significance of forest canopy gaps to herbs

Effects of canopy gaps on trees and tree seedlings are better understood than the effects of canopy on herbs. Gaps in the forest canopy may increase fitness of forest herbs by increasing availability of resources necessary for growth and seed production (McConnaughay and Bazzaz 1990). Direct light in canopy gaps provides opportunities for production of photosynthates used for construction and maintenance of plants (Waring and Schlesinger 1985). Even at low light, survival and growth rates can increase when sufficient soil moisture is available to roots (Atzet et al 1972; Fisher et al. 1991). Growth rates of forest herbs may be greater where direct light in sunflecks alternates with shade than in sites with continuous direct light because of the moisture stress and evaporative loads caused by long-wave (heat) radiation (Chadzon and Pearcy 1991, Knapp et al. 1989, Pfistch and Pearcy 1992, Shultz and Adams 1995).

Heat in gaps can induce flowering and sustain seed production (Larcher 1995) for plants that have grown to reproductive size (Wesselingh et al. 1997); however, after nutrients are allocated to reproduction, growth rates may decrease for some species (Pitelka et al. 1985). Elevated temperatures near the ground and lower humidity in gaps during the day (Chen et al. 1993; Runkle 1985; Hubbell and Foster 1986) also contribute to increased transpiration rates and moisture stress of herbs in gaps, especially for species with wide leaves (Waring and Schlesinger 1985).

Gaps may also be places of relatively high soil moisture because of lower root density, higher precipitation, and lower evapotranspiration. Herbs may benefit from this increase in available water. For example, seedlings and young (but not old) ramets of *Tiarella trifoliata* L. and *Linnaea borealis* L. are rooted near the soil surface (Antos and Zobel 1984a), where low soil moisture (Gray, pers.comm. 1999) may expose the plants to moisture stress. Growth rates of tree seedlings (Gray and Spies 1996) increase with soil moisture, and moisture will allow survival of seedlings that would otherwise die in low light (Atzet et al. 1972; Fisher et al. 1991). Presence of herbs with shallow rhizomes, such as *Streptopus roseus*, may depend on moisture retained by accumulations of decayed logs, litter, and humus (Antos 1988), especially where live tree roots do not deplete soil moisture (Toumey and Kienholz 1931).

1.4 Gap partitioning hypothesis

Gaps have been hypothesized as a mechanism for niche differentiation in forests (Bazazz and Pickett 1980, Denslow 1980), where differences in species performance (fecundity and growth) along light gradients lead to the coexistence of species in forests. An alternative hypothesis is that complex resource gradients under forest canopies where resource availability is not related to canopy gaps may be more important to species fitness (Lieberman et al. 1989). The hypothesis that species coexist because of vertical, horizontal, or temporal partitioning of space has been rejected for canopy trees both in western coniferous forests (Lertzman 1992) and in the tropics (Denslow 1987, Hubbell et al. 1999) because of the lack of short-lived, fast-growing "ruderal" trees in these regions. However, gap partitioning may occur among early- and late-successional species of maples in the Midwest (Bazazz 1996).

Differences in invasibility of gaps and partitioning of species among gap size, gap position, and time since gap creation may, however, occur among herbs that vary in (1) rates of response (e.g., growth and seed production) and (2) types of response (e.g., seeds vs. vegetative growth) to habitats and disturbance regimes (Bazazz 1996; Antos and Zobel 1984b). Detailed examples of variations among herbs that may result in gap partitioning are described in the literature review (section 1.4).

Several studies suggest that herbs differ in their response to resources patterns which are, in turn, functions of gap size, gap position and disturbance intensity. Some studies document variations in plant response as disturbance regimes vary over space and time. For example, *Erythronium americanum* increased flowering rates in single- but not multiple-tree gaps (Collins et al. 1988). Kotanen (1997) found that grassland species that reproduce largely by clonal growth were first to occupy gap edges but were subsequently crowded out by species with slow but dense growth. Recently disturbed sites are colonized by species with rapid vegetative spread such as *Linnaea*, but not by species with persistent buds buried to 2-3 cm (geophytes) (Sobey and Barkhouse 1977, McIntyre et al. 1995, Denslow 1985). Intense logging and burning may prevent establishment of *Linnaea, Tiarella* and other forest herbs for at least 20 yr (Clark 1990; Halpern and Spies 1994).

The availability of resources and microsites in persistent canopy gaps may explain why Spies (1991) and Habeck (1968) found a greater abundance of understory herbs such as *Linnaea* and *Tiarella* in old stands than in young stands. *Linnaea*'s stolons grow rapidly in disturbed forests (Sobey and Barkhouse 1977; Antos and Zobel 1984a) with relatively low light (Eriksson 1988). *Tiarella* produces more biomass (Hanley et al. 1997), germinates and survives at greater rates (Tappeiner et al. 1989) in old forests with windthrow gaps that increase availability of soil moisture and light.

1.5 Goals, objectives, hypotheses and significance of this dissertation

The overall goals of this study were to evaluate how small-scale disturbances affect forest herbs and to determine whether herbs differ in their response to gaps and resource gradients in gaps. The first objective was to determine whether rates of fecundity, growth, and recruitment of *Tiarella*, *Linnaea* (both in Chapter 2), and *Trillium* (Chapter 3) increase in response to canopy gaps and, if so, to determine whether such performance varies among gap size and position. The second objective was to compare fecundity and growth of the three species along gradients of resources (e.g., soil moisture content and light intensity). A third objective (for *Trillium* only) was to evaluate how age and plant development affect herb response to canopy gaps. This information is important for understanding mechanisms that determine diversity of herbs in PNW forests.

I hypothesized that (1) performance of *Linnaea* and *Tiarella* would be greater within gaps than in the control treatments (dense stands that were not experimentally logged in 1990), (2) response levels for both species would vary among positions of large gaps and (3) both seed production and growth would increase with light and soil moisture. All three of these hypotheses are based on the general autecology (relationships of phenological, physiological, morphological, behavioral, and genetic traits that are important to continued success in a given habitat) and habitats of these herbs.

In contrast, I hypothesized that seed production, growth, and recruitment of *Trillium* would be greatest in positions bordering canopy gaps and other sites with intermediate light and in sites with relatively high levels of soil moisture. I also hypothesized rates of seed production for *Trillium* would vary with age and size of various plant parts.

This study is significant because most field studies of understory herbs compare their abundance among disturbance regimes or forest types or sites and do not evaluate the underlying biological causes (such as rates of seed production and growth) of those patterns. Although the averages and extremes of growth rates and fecundity have been measured for some species of herbs (e.g., Antos and Zobel 1984a), these measurements have rarely been taken in conjunction with measurements of resources (but see Eriksson 1988, Shultz and Adams 1995, Pitelka et al. 1980, Pfitch and Pearcy 1992) or gaps (Collins et al. 1985, 1988), let alone both resources and gaps (Hanley et al. 1997). Consequently, this study is the first to examine fecundity and growth of herbs relative to resources in forest gaps in an experimental setting.

1.6 Literature review

To understand how understory species might respond to small-scale disturbances in PNW forests, I will first review how plants generally allocate biomass to various plant parts along gradients of resource availability and environmental conditions. Next, I will review the possible effects of environmental factors (e.g., light, soil moisture, and temperature) that may occur in gaps and under a canopy on the resource-absorbing structures of the three herbaceous species studied. Specifically, I will discuss how seed production and growth rates may vary with the morphology and physiology of the leaves, stems, and roots of each species in the conditions that may occur in gaps. Finally, I will discuss how seedling density of each species may vary with dispersal mode and germination rates along gradients of resources under gaps and canopy.

1.6.1 General life history strategies

Because all resources are limited, a plant with a successful life history strategy allocates resources to modules that ensure growth, survival, and/or reproduction in its environment. Additional biomass allocated to structures that absorb resources (e.g., leaves and roots) may be supported in some but not all habitats or disturbance regimes. Therefore, tradeoffs between investments in vegetative and reproductive structures determine species fitness. Three classification schemes for plant life history patterns will be described.

Grime (1979) identified strategies selected in three types of habitats. In habitats where resources such as light, water and nitrogen are scarce and in extreme conditions such as heat, plants generally experience stress (e.g., they limit the rate of dry-matter production). "Stress tolerators"can persist in such environments by limiting allocations of photosynthates to roots and shoots, seed production, relative growth rates, and leaf and root surface areas even after conditions improve. In environments with abundant resources, "competitors" are species which rapidly increase and maintain high relative growth rates but cannot support this increased biomass if the availability of resources decreases. Environments that become resource-rich as a result of disturbance can be rapidly, but temporarily colonized by "ruderal" species with early and profuse seed production and short lifespans.

Huston and Smith (1987) and Tilman (1988) predict that species in rapidly changing, resource-rich habitats will have suites of traits that are inversely related to those of species in more stable sites. Tilman (1988) hypothesized that "competitors" would persist at low resource levels while depleting light, water, and nutrients from neighbors. Thus, species that allocate greater ratios of biomass to roots vs. shoots compete best in recently disturbed, nutrient-poor sites. In late-successional habitats, allocations to shoots (vs. roots) that can intercept and use low light confer competitive superiority.

Bazzaz (1996) defines response flexibility as the ability of a particular genotype to function in a variety of environments either because of the "plasticity" (variety) of phenotypes that can be expressed in different environments or because of its ability to acclimate previously established modules to new conditions. (A module is a product of a meristem that extends from the beginning of the shoot to the apical meristem and is composed of one or more metamers that consist of a bud, leaf and spacer tissue). Bazazz generalizes that early-successional species respond flexibly and rapidly to changes in resources. Late-successional species, on the other hand, respond to different levels of environmental factors with relatively similar allocational flexibilty, acclimation potential, and resource acquisition rates. Late successional species can persist in low light as seedlings or at negative growth rates as mature individuals but are sensitive to decreases in soil moisture at any light intensity and to high light. This study will focus on how three species that occur in various habitats within late successional forests differ in their response to similar disturbance regimes.

To best categorize the life history strategy for any species, the response of more than one species must be compared for the same conditions at the same time. The flexibility of seed production, growth rates, and size among resource levels may be more comparable among species than their response to stress, because conditions that induce stress for one species may not affect species with other morphologies and physiologies. Flexibility of performance may also be more measurable than the depletion of resources from neighboring plants. In addition, the full range of resource levels also include conditions that induce stress, thus the two processes are not mutually exclusive. Therefore, flexibility of seed production and growth rates will be compared for the three species in this study.

1.6.2 Partitioning of space in gaps among species of trees and herbs

Patterns of allocation, modular construction and physiology may explain why (in contrast to trees) rates of performance for herbs and species presence may differ by several orders of magnitude along gradients of light. Differences in potential size may explain correlations of growth with direct light for trees but not for forest herbs (Pfitsch and Pearcy 1992). Although shade leaves on lower branches of some tree species capture diffuse light, vertical growth of all trees can increase in direct light, regardless of gap size, after branches project new modules with sun leaves above canopies. In addition, roots of trees reach depths where soil moisture remains greater than near the surface, regardless of the size of current gaps in the canopy or roots (unpub. data collectd by A.N. Gray).

On the other hand, because of their limited canopy height and root depth, resource regimes of herbs are determined by the size of gaps in the canopy and roots of surrounding and taller vegetation as well as by the timing and their position in such openings. The lack of trunks on herbs constrains their vertical growth to heights below the canopy of shrubs and trees. In spite of some increase in depth over time, roots of herbs also remain nearer to the soil surface (Antos and Zobel 1986) than do roots of trees. As a result, low soil moisture at the soil surface may expose the herbs to moisture stress unless they are in the moist part of the gap, in a microsite such as moist wood, or in a site with groundwater.

The light regime determines the rates and types of growth and reproductive responses of herbs. For example, in young gaps with bright light, flexible leaf and stem architecture (e.g., variable width, orientation, and size of leaves; numbers, angle, and lengths of stems) confer rapid rates of growth and reproduction. However, as sites with intense light become shaded by other plants, species with such traits will etiolate, retain photosynthate in shoots at the expense of roots, and produce thinner leaves and less dry matter (Grime 1979). Low seed weight may further increase rates of seedling mortality (Grime 1979) and low tissue density may decrease the lifespan of such species (Ryser 1996)

On the other hand, in sites where light, water and other resources are less available but more stable, herbs persist at lower rates of performance (fecundity, growth, dispersal, germination) than herbs adapted to more abundant resources. Persistence is accomplished by limiting biomass that would enable the plant to change the size and growth rates of its parts (Gadgil and Solbrig 1972; Grime 1979). Allocation of limited photosynthates to a few but large and heavy seeds provides resources for germination and growth in nutrient-depleted, shady sites and for penetrating leaf litter that tends to accumulate under the forest canopy (Tilman 1988, Sydes and Grime 1982). Resource allocations to non-photosynthetic mechanical tissues that support large, horizontally oriented, wide leaf blades confer persistence in shade (Givinish 1982). Allocations to dense stems may confer longevity (Ryser 1996). Continuation of low growth rates in spite of resource fluctuations prevents development of large structures that cannot be sustained if conditions deteriorate (Bazazz 1996; Grime 1979). These tradeoffs, however, contribute to the lower abundance of forest herbs compared to early-successional species, especially in frequently disturbed sites (Primack and Miao 1992, Bierzychudek 1982).

1.6.3 Habitats and characteristics of three species of Pacific Northwest herbs

Linnaea borealis L., *Tiarella trifoliata* L. var. *unifoliata*, and *Trillium ovatum* Pursh. are herbs that contrast in morphology and physiology but coexist in PNW forests. *Linnaea* occurs in warm sites at various moisture stress levels in Douglas-fir forests of the Cascade Mountains (Zobel et al. 1976). It inhabits elevated microsites within in wet habitats and grows on decaying coniferous wood in nutrient-rich sites (Klinka et al. 1989). *Tiarella* occurs in cooler sites with lower moisture stress on fresh to very moist, water-receiving, nitrogen-rich soils (Klinka et al. 1989). *Trillium* occurs frequently but at much lower cover than *Linnaea* or *Tiarella* at low to middle elevations of the *Tsuga heterophylla* Zone of the western Cascades (Franklin and Dyrness 1988). *Trillium* and other ant-dispersed herbs, can account for 50% of the sparse herb layer in some old redwood forests (Mesler and Lu 1983). *Trillium* occurs in shaded areas on stream banks and in moist to wet woods that become "boggy" in spring (Klinka et al. 1989; Hitchcock and Cronquist 1973).

Table 1.1 summarizes basic characteristics of the three species of this study. *Linnaea* is a low-growing sub-shrub with shiny, cuticle-laden "evergreen" leaves that persist in winter. *Tiarella*'s broad basal leaves are also long-lived. On the other hand, *Tiarella*'s upper palmate- and cordate-shaped leaves and *Trillium*'s cordate-shaped leaves are deciduous. *Tiarella*'s foliage is thus taller than *Linnaea*'s in the summer. *Trillium*'s leaves emerge in spring and maintain a relatively more horizontal orientation than *Tiarella*'s leaves. Although *Linnaea*'s fecundity can be high (Eriksson 1988), seedlings are rare (Zobel and Antos 1986) and germination rates are low (Clark 1990). Germination rates are also low for *Trillium* (Hanzawa et al. 1993; Deno 1993). *Tiarella*'s seedlings are more frequent than seedlings of the other two species (Zobel and Antos 1986). *Tiarella*'s rhizomes grow more slowly than *Linnaea*'s stolons (Antos and Zobel 1984a) but faster than *Trillium*'s rhizomes (Jules 1996). All three species increase root depth with time and can live over a decade (Antos and Zobel 1984a; pers. obs. 1999).

1.6.4 Possible effects of traits on performance of each species in gaps

1.6.4.1 Leaf architecture and physiology

Trade-offs between benefits of carbon gain and costs of water loss determine leaf size, orientation, shape, longevity, palatability, absorbency, and stomatal conductance of leaves (Givnish 1987). While each of these leaf characteristics may individually vary along gradients of light, soil moisture, and surface temperatures of gaps, leaf architecture that determines placement of leaves can override physiological processes such as photosynthetic rates (Bazazz 1996).

Leaf physiology varies widely among plant species (Larcher 1995). Species with high rates of stomatal conductance are more abundant in areas of high humidity (e.g., the forest understory) or soil moisture (e.g. root gaps) (Givinish 1987). Species of herbs that cannot increase concentration of carboxylating enzymes show signs of photolability in bright light (Boardman 1977).

Plant height among species generally increases with regional precipitation and humidity. Plant height allows interception of light from shorter individuals. However, growth to taller sizes can only occur in sites with sufficient soil moisture (Givinish 1987). The low stature of *Linnaea* may allow photosynthesis during the winter in dry, exposed sites at ground level where temperatures are warm in but not in moist sites where taller deciduous herbs (e.g., *Tiarella*) may intercept light during the growing season. *Linnaea* can also climb up on substrates where other species cannot root (e.g., on logs, stumps, and rootwads) (Antos and Zobel 1984 a, b).

Leaf width among species generally decreases with irradiance because the thicker boundary layer of wide leaves impedes heat loss (Waring and Schlesinger 1985). Leaf width increases with effective precipitation and humidity (Givinish 1987). Leaves tend to be oriented away from the horizontal in sunny, arid sites (Givinish 1987; Smith et al. 1998). Flexibility in orientation and width confer tolerance to variable light intensities (Bazazz 1996). Because its leaves are oriented at various angles and originate from vertical as well as horizontal shoots, *Linnaea* may thus tolerate a variety of moisture and light regimes. Because cordate-shaped leaves maintain a more inflexible perpendicular orientation (Givinish 1982, 1987), *Trillium*'s leaf architecture may confer the ability to capture low light but will subject this species to moisture stress and desiccation in direct light. *Tiarella*'s upper leaves range from cordate to palmate and thus may be able to orient themselves more flexibly to light. Consequently I hypothesized that *Trillium* is more sensitive to high light and moisture stress than *Tiarella*.

Allocations of limited photosynthates to thick cuticles may confer leaf longevity in sunny, arid, infertile areas by decreasing light absorption, transpiration rates and palatability (Givinish 1987, Perry 1995). Thus, reducing water loss and by by reflecting radiation during summer, *Linnaea*'s thick and shiny cuticles may prevent desiccation induced by surface temperatures in sites exposed to solar radiation. This waxy layer also may prevent desiccation induced by frozen soil during winter.

Slow-growing species with evergreen leaves tend to establish in nutrient poor sites (Givnish 1987) and thus cannot afford herbivory and annual construction of a complete leaf canopy. Deciduous leaves tend to be more palatable than long-lived leaves because of greater nitrogen and less lignin content, but annual construction of new leaves requires that the plant is established in resource-rich sites (Perry 1995). Deciduous species such as *Trillium*, may thus survive herbivory, although at smaller sizes in the year following this type of disturbance (Anderson 1992).

1.6.4.2 Stem architecture and physiology

Differences in stem morphology among the three species may affect fecundity and growth rates along gradients of light intensity, surface temperatures and soil moisture in gaps. Rates of increases in plant cover vary with the number and angle of branches on stolons or rhizomes (Bell 1979, 1980). All three species grow more slowly than early successional herbs (Bierzychudek 1982). However, *Linnaea*'s stolon growth and branching rate may allow rapid colonization of large areas that are repeatedly disturbed (Sobey and Barkhouse 1977). *Tiarella*'s short and rarely branching rhizomes have a slower (1 cm per yr) but denser growth pattern that may partially allow increases in cover in gaps. *Trillium*'s unbranching rhizomes have the lowest growth rates, similar species average about 0.6 cm per yr (Bierdychudek 1982).

Herbs with shallow rhizomes are more abundant where moisture is available, as in organic debris in forests (Antos 1988), and less abundant in soil horizons with high rates of drying and low rates of water recharge (Anderson and Loucks 1968). However, species with slow-growing, shallow rhizomes can be vulnerable to disturbances such as trampling at the soil surface and thus are less frequent where machinery has damaged growing meristems or compacted the soil (McIntyre et al. 1995; Rogers 1985). In contrast to herbs of eastern US which grow in spring to capture light under deciduous canopies, growth during spring may allow herbs to avoid summer drought that characterizes the Pacific Northwest region.

Morphological plasticity of stems in response to burial may allow *Linnaea* and *Tiarella* to occupy more habitats and disturbance regimes (thus wider resource gradients) than *Trillium*. After burial by 5 to 20 cm of volcanic tephra, *Tiarella*'s short rhizomes abruptly turned up and then elongated rapidly. Internodes that were usually 0.5 cm elongated to over 4 cm. *Linnaea* produces erect shoots that emerge above tephra and support extensive stolons that elongate rapidly and branch frequently unless they are buried. On the other hand, after burial by tephra most members of Liliaceae, including *Trillium*, die back to their rhizome at its original depth each year with no upward movement of perennating buds (Antos and Zobel 1984). Some individuals of these species may remain alive if rhizomes can sustain growth of leaves through the tephra.

The degree of connectivity, length of spacers and direction of growth determine where resource acquisition tissues (roots and shoots) are placed. Pooling of resources through connected spacers can increase growth rates, confer persistence of ramets in a variety of microsites and allow movement across unfavorable sites to new sites. Growth rates may increase under heterogeneous light if intact stolons transport water, photosynthates, and nutrients to and from other stolons rooted in in sun and shade, wet and dry soil. For example, studies of vegetatively spreading species, such as *Potentilla simplex,* showed that clones added more biomass when spacers (stolons) between rooted plants in pots with various amounts of nitrogen were kept intact than when they were clipped (Wijesinghe and Handel 1994). However, resource contrast increased total clone yield of *Glechoma heteracea* only for individuals that were rooted in large (25 x 25 cm) but not small (12.5 x 12.5 cm) patches of compost and sand (Wijesinghe and Hutchings 1999). Intact ramets of *Clintonia* spp. persist in low light by using light and soil resources acquired by other ramets in small canopy gaps (Pitelka and Ashmun 1985). Stolons of *Linnaea* can cross very hot and dry sites (Zobel and Antos 1984).

Species (e.g. *Linnaea*) with long rhizomes or stolons have more shoots, rooting nodes and thus sequester resources from larger areas and over longer lifespan with less dependance on sexual reproduction (Zobel and Antos 1984a). Species with variable length, growth rate and angle of spacers are considered “guerilla” species (Lovett-Doust 1994).

Some species with guerilla lifeforms, such as *Linnaea*, may forage by changing the length, growth rate and angle of spacers as levels of resources change. *Linnaea* thus can quickly exploit sites with recent and frequent canopy gap formation. Other guerilla species such as *Fragaria chileoensis* simply increase their chances of reaching favorable sites by "exploring" (continuously but randomly placing structures at any resource level) (Alpert 1996). "Phalanx" species such as *Clintonia borealis* (and possibly *Tiarella*) that maintain uniform lengths and growth rates of spacers are adapted to more stable habitats (Pitelka and Ashman 1985). Short and equal spacers keep stems close together and can increase in density in response to resources. A phalanx lifeform may thus prevent establishment of other species.

The direction of resource (e.g., carbon products, water, nutrients) flow can determine the direction of growth or movement to new sites. Flow to old portions of clones maintains the individual at original sites of establishment. For example, *Clintonia borealis* remains in the same locations within stable forests by directing resources to old shoots (Pitelka et al. 1985). Species with a consistent direction of resource flow to younger plant parts induce growth and or movement to new sites. For example, net transfer of N from old ramets rooted in nitrogen rich sites to young distal ramets allows growth and movement of *Fragraia chiloensis* to new, nitrogen poor sites on dunes (Alpert 1996). Rapid horizontal growth away from cool microsites may increase *Linnaea*'s chances of having new ramets reach warmer sites with moist rooting substrates. Heat in gaps can induce flowering and sustain seed production (Larcher 1995) for plants that have grown to reproductive size (Wesselingh et al. 1997); however, after nutrients are allocated to reproduction, growth rates may decrease for some species (Pitelka et al. 1985).

1.6.4.3 Root and symbiont architecture and physiology

Performance of herbaceous species may increase where soil moisture and litter from maple and cedar trees increase soil pH and thus nutrient availability (Perry 1995). Efficiency of water and nutrient uptake depend on (1) morphology and physiology of roots, (2) presence of mycorrhizal symbionts, and/or (3) diversity and root density of other herbs, shrubs, and trees that share resources and species of mycorrhizal fungi (van der Heijden 1998).

Roots of herbs remain shallower than roots of trees. Seedlings and young (but not old) ramets of *Tiarella* and *Linnaea* are rooted within a few cm from the soil surface (Antos and Zobel 1984a), where low soil moisture (Gray and Spies 1999) may subject the plants to moisture stress. Roots extend laterally and down to maximum depths of 0.25 m from scattered locations on older stolons of *Linnaea*(Antos and Zobel 1984a). Erikkson (1988) suggests that their low frequency (5 per m of stolon length), however, may subject this species to moisture stress. *Tiarella*'s roots occur all along the rhizome at a frequency of 176 per m. Large roots are especially concentrated on older parts of *Tiarella*'s rhizomes where the original seedling established where they reach maximum root depths of 0.21 m. Monocotyledons, especially members of the Liliaceae, such as *Trillium,* commonly have contractile roots that increase the depth of rhizomes and thus the depth of roots (Bierdzychudek 1982). Herbs such as *Oxalis cernua* move horizontally because of contractile roots (Bell and Tomlinson 1980).

Obligate symbiosis between fungi and roots of *Trillium* and *Linnaea* occurs, producing vesicular-arbuscular mycorrhizae (VAM). Although *Tiarella trifoliata* is apparently non-mycorrhizal (J. Trappe, personal communication, 1995), there is some evidence that *Tiarella cordifolia* may associate with mycorrhizal fungi (Rothwell and Vogel 1982). Hyphae of VAM fungi penetrate root cells of Liliaceae and exchange nutrients for vitamins and sugars (Linderman et al. 1975). The hyphae produce branches called arbuscules that increase nutrient and water exchange within cells but do not induce root branching or form rhizomorphs as do ectomycorrhizal fungi.

Presence of mycorrhizae may affect growth and fecundity of *Trillium* and *Linnaea* with "harvest" and "protective" mechanisms (Perry 1995). Harvest mutualisms occur when one species facilitates resource acquisition by another such as when mycorrhizae increase rates of water, nitrogen and phosphorous absorbtion and cycling. Some species can decompose organic matter and transfer usable nitrate directly to roots. Hyphae absorb water and nutrients more efficiently than roots because of their greater growth rates, surface area, length, and small diameters that allow water and nutrient extraction from pores that are too small for root penetration (Waring and Schlesinger 1985, Perry 1995). In addition to such functions, which protect roots from desiccation, other protective mutualisms extend vascular plant lifespans, during which additional resources can be acquired. Production of iron chelaters that act as an iimmune system, for example, could protect seedlings (Perry 1995).

Plants apparently tolerate stress and increase growth rates when plant roots are connected with a common hyphal network that allows sharing of resources and mycorrhizal symbionts. After additional herbaceous hosts with compatible mycorrhizae were experimentally introduced to plots of other species of herbs, the productivity of VAM herbs increased while the non-mycorrhizal species remained small or the plants died (van der Heijden 1998). Whether *Trillium* and *Linnaea* receive carbon compounds or mycorrhizal fungi from roots of other VAM species of herbs, shrubs, or trees (such as maples, yews, and cedars) in this gap experiment is not known.

Conditions that determine survival and functioning of mycorrhizae may determine fecundity and growth rate of herbs in forest gaps. Mycorrhizae depend on living hosts for food in the form of simple sugars (Perry 1995). Shade from living and fallen trees and retention of soil moisture in buried organic material can protect mycorrhizae from desiccation (Harvey et al. 1984). VAM hyphae may benefit from moisture in such debris more than ecotomycorhizal fungi that sequester water with long and fast-growing rhizomorphs. However, the low N availability in logs may inhibit uptake of P by VAM (Allen 1993). The presence of more mull soils in gaps could increase also mycorrhizal efficiency because VAM increase uptake of P where N is available (Allen 1993).

1.6.4.4 Dispersal rates, distances and modes

Partitioning of space in gaps may occur among some late-successional species (Bazazz 1996) that target seed dispersal to sites with favorable conditions for germination, survival, and growth. For example, direct dispersal of seeds by ants to specific microsites in shade (e.g., moist, decayed wood) may be advantageous for species such as *Trillium* with sensitivity to high light and moisture stress because of leaf architecture that confers tolerance to shade but not exposure, especially if fecundity is low (Hanzawa et al. 1988).

The number of safe germination sites, the distance between potential germination sites and the number of propagule sources relative to speed of species arrival determines species' colonization rate (Matlack 1994; Harper 1979). Thus, the location of previously established individuals may determine seedling density in and around gaps. Speed of arrival may also affect seedling density in gaps and is generally faster for seed than by vegetative propagules. For example, species of herbs with seeds that were dispersed after adhesion to moving objects or by the wind were found within second- growth forests at greater distances from the original forest edge than species with seeds dispersed by ants or passively (Matlack 1994).

The average distance between seedlings and the nearest reproductively mature *Trillium ovatum* was about equal to the height of the plant (*ca* 36 cm) for seeds that fell off the plant and less than a meter for seeds that were dispersed to ant nests (Mesler and Lu 1982). Dispersal distance of *Tiarella* is also low for individual seeds that simply fall off. Seedlings from individuals established on tephra within a stand can become a substantial part of the population within a decade (Antos and Zobel 1997). *Tiarella* can also move horizontally with growth of rhizomes at 0.5 to 4 cm per year (Antos and Zobel 1984a and 1984b). In contrast, *Linnaea* stolons may spread into gaps adjacent to growing meristems at an average of about 40 cm per year (Sobey and Barkhouse 1977; Antos and Zobel 1984a, b).

Long distance dispersal can occur for these species. For example, *Trillium* seeds are occasionally dispersed by hornets (Jules 1998), broken and dried *Tiarella* stalks are carried by mammals (pers. obs.) , and *Linnaea* seeds attach to birds (Pojar and MacKinnon 1994). Seed of these species, thus can establish at much greater distances from parent plants than when seeds simply fall off plants. Occasional dispersal by these modes may explain gene flow among metapopulations of populations of long-lived, shade-tolerant understory species over previously unfragmented landscapes (Cain 1998). Effects of currently fragmented landscapes on fitness of herb populations are not known.

1.6.4.5 Germination rates

Low germination and survival rates may contribute to the low seedling densities of all three species in spite of proximity to established individuals. Low densities of seedlings among microsites were documented for *Trillium* (Mesler and Lu 1983), who found that seedlings of this species germinated on ant mounds only in cool, moist forest interiors. Jules (1998) recorded an absence of germination in clearcuts even near parents.

Germination and survival rates for *Tiarella* are greater in old than in young stands. Survival rates were greater on logs than on the forest floor and increased with light (Tappeiner and Alaback 1989). Seedling density increased with time on tephra but was lowest where seed source was eliminated (Antos and Zobel 1986).

Germination rates for *Linnaea* are apparently low. All experimentally sown seeds (with no pretreatment) failed to germinate in the field, in spite of 18% viability after tests with light and alternating temperatures of 20/15 deg C (Clark 1990). None of six species with relatively rapid vegetative spread, including *Linnaea, Clintonia, Smilacina, Achlys, and Arnica* spp., could be traced to a seedling source in a study by Antos and Zobel (1984b), thus indicating the infrequentcy of seedling establishment.

1.7 Study design

This study was conducted in the H. J. Andrews Experimental Forest (H.J.A.) where a gap experiment was established by Spies (1990). The stand lies in the Willamette National Forest on the west slope of the central Western Cascades Mountain Range of Oregon in the *Tsuga heterophylla* Zone (Franklin and Dyrness 1988). Multiple layers of 500-year-old *Pseudotsuga menziesii* and a dense subcanopy of younger *Tsuga heterophylla* dominate the canopy.

Experimental gaps were created in the fall of 1990 by cutting all trees over 2 m tall (except for *Acer circinatum*) within the gap perimeter. The gaps were located in randomly selected sites with slopes less than 20%. All treatments were selected from stands with relatively dense canopies to minimize effects of recent natural gap-forming events. Trees were stage-felled into the northeast or northwest quadrants, and skidders winched fallen tree boles from the gaps with cables. Branches and foliage were trimmed and removed from the felled trees and from the gaps. Four gap sizes were created, with two replicates of each size. Gap diameter was measured between tree crown edges and scaled to the average height (50 m) of dominant trees. Ratios (of gap diameter to tree height) for the four sizes were 0.2, 0.4, 0.6, and 1.0. Thus 0.2 gaps were 10 m in diameter and 1.0 gaps were 50 m in diameter. Two control plots equal in area to the 1.0 gap size were also established in stands with dense canopy.

This experimental setting was used for observations of performance of all three species measured in this study. However, additional areas were sampled in sites bordering the gaps to compare response of all three herbs to direct light that penetrated areas north of crown edges in areas defined as the gap borders (Runkle 1992) and under canopy south of each gap treatment.

Fecundity and growth rates were measured along gradients of gap size and positions (within and bordering gap treatments) for all three species. Fecundity and growth of *Tiarella* and *Linnaea* were compared among five positions (north border, north, center, south and south border) for gap sizes 0.4, 0.6, and 1.0 and three positions (north border, center, and south border) for gap size 0.2. North, center, and south positions were established within control treatments. Because the density of *Trillium* was low, leaf area and fecundity were compared over larger areas (north border, north, south, south border) in and around all gap size and control treatments.

Performance of *Linnaea* and *Tiarella* were compared along gradients of light and soil moisture in gaps and controls with unpublished data collected by A. N. Gray and T. A. Spies. Because more *Trillium* occurred in natural canopy gaps and on gap borders, the study area for *Trillium* included the microsites in the stand surrounding the experimental gaps as well as locations within the gaps. Light and soil moisture were measured within 1 m of each

Trillium individual. Distinctness of individuals and presence of annual constrictions on rhizomes allowed measurements of age for *Trillium* only. Locations of seedlings were observed for all three species.

Table 1.1. Characteristics of *Linnaea borealis*, *Tiarella trifoliata*, and *Trillium ovatum*. Numbers in parentheses refer to the following references: (1) Antos and Zobel (1984a, 1984b), (2) Antos and Zobel (1986), (3) Hitchcock and Cronquist (1973), (4) Jules (1995, 1996), (5) Mesler and Lu (1986), (6) Sobey and Barkhouse (1977), (7) Clark (1990), (8) Givinish (1987), (9) Pojar and MacKinnon (1994), (10) Tappeiner and Alaback (1989), (11) Hanzawa and Kalisz (1993), and (12) Bierzychudek (1982).

Species and family	*Linnaea borealis* Caprifoliaceae	*Tiarella trifoliata* Saxifragaceae	*Trillium ovatum* Liliaceae
Potential longevity of genets (yr)	10 to 100 yr (1)	8 or more (10)	72 yr (4)
Age of first flowering (yr)	?	> 4 (10)	12 (11) (for *T. grandiflorum*)
Seed production	3 seeds per m^2; 2 seeds per flr (7) per year	profuse	1 to 150 seeds per capsule (5)
Seedling frequency	No seedlings found (1, 7)	6.6 per m^2 on tephra (2)	0 to 88 per 0.25 m^2 (5) in shaded, moist sites; absent in exposed sites (4)
Annual growth rates of stems 1. cm 2. no. branches	1. 48 (6); 38 (1) 2. 1 branch every 3 to 4 yrs (6)	1. 0.5 to 4 (2); 1 to 2 (10) 2. rare (1)	1. 0.6 (for *T. erectum and T. undulatum*) (12) 2. none (4)
Modes of dispersal: 1. major 2. minor	1. stolons (1, 6) 2. birds (9)	1. passive seed dispersal (9) 2. rhizomes (1)	1. ants, passively dehiscent (5) 2. hornets (4)
Leaf longevity (yr)	persistent (9)	basal leaves persistent upper leaves deciduous (9)	deciduous (9)
Maximum plant height (cm)	7 (9)	15 to 60 (3); 8 (1)	45 (9)
Leaf: 1. width (cm) 2. shape 3. orientation	1. 0.7 to 2.5 (3) 2. broadly elliptic to subrotund (3) 3. variable (3)	upper leaves: 1. 1.5 to 2.5 (3) 2. cordate to palmately lobed (3) 3. variable basal leaves: 1. 12 cm (3) 2. orbicular (10) 3. horizontal	1. 5 to 15 (3) 2. individual leaves are ovate (3); three leaves together are functionally cordate (8) 3. horizontal (3)
Root: 1. depth (m) 2. frequency (per length of rhizome)	1. oldest roots:0.25, young roots:near the soil surface (1) 2. 5 per m (1)	1. oldest roots: 0.21, young roots: near the soil surface (1) 2. 176 per m (1)	?

CHAPTER 2: FECUNDITY AND VEGETATIVE GROWTH RATES OF *LINNAEA BOREALIS* L. AND *TIARELLA TRIFOLIATA* L. IN DOUGLAS-FIR FOREST CANOPY GAPS

2.1 Introduction

Gaps in forest canopies add long-term structural diversity to landscapes that is essential for forest ecosystem function. For example, gaps can have an extensive influence on the productivity of the lower canopy in forests. Gaps in Douglas-fir forests of the Pacific Northwest cumulatively occur over acreage comparable to the area affected by historic wildfires (Spies et al. 1989). Gaps are especially prominent in old growth forests because they are relatively large and can persist many decades. Gaps in younger stands are usually more ephemeral because they are small and rapidly filled by expanding tree canopies (Spies et al. 1990).

According to the gap-phase regeneration paradigm (Watt 1947, Hubbell and Foster 1986), above- and belowground resource and microsite availability will be greater in canopy gaps until new trees replace the ones that died. Canopy gaps increase light intensity and the amount of precipitation that reaches the forest floor (Canham et al. 1990; Geiger 1965). Soil and air temperatures near the ground may consequently be higher and humidity may be lower in gaps than in surrounding forests (Chen et al. 1993; Runkle 1985; Hubbell and Foster 1986). Soil moisture can also be higher in gaps where root density and transpiration rates are low (Gray 1995; Toumey and Kienholz 1931).

Microclimatic and resource characteristics vary by a number of factors including gap size, shape, orientation; slope and height of surrounding vegetation; and by position within gaps (Pickett and White 1985). For example, temperatures and light intensity, are higher in large canopy gaps than in smaller gaps. Soil moisture is higher in small gaps than large gaps

(Gray and Spies 1996, 1997). In the northern hemisphere, northern positions within gaps receive more direct light and reach higher maximum temperatures than southern positions (Canham et al. 1990; Van Pelt et al. 1996). Soil moisture is greatest in gap centers (Gray and Spies 1996).

Shrubs, fallen trees, and pit and mound topography create additional microsites and resource variations within gaps (Lyford and MacClean 1968, Thompson 1985). Soil moisture and nutrients can be retained where fallen trees provide shade, store water, and trap organic debris. Root upheaval in gaps redistributes nutrients to the ground layer where newly exposed mineral soil provides substrates for root growth and germination of seeds (Harmon et al. 1986; Beaty 1984).

Gaps in the forest canopy may increase fitness of forest herbs by increasing resource availability necessary for growth and seed production (McConnaughay and Bazzaz 1990). Direct light in canopy gaps provides opportunities for production of photosynthates used for construction and maintenance of plants (Waring and Schleshinger 1985). Survival and growth rates can increase even at low light when sufficient soil moisture is available to roots (Atzet et al 1972; Fisher et al. 1991). Growth rates of forest herbs may be greater where direct light in sunflecks alternates with shade than in sites with continuous direct light because of the detrimental effects of long-wave radiation on moisture stress and evaporative loads (Chadzon and Pearcy 1991, Knapp et al. 1989, Pfistch and Pearcy 1992, Shultz and Adams 1995). Heat in gaps can induce flowering and sustain seed production (Larcher 1996) for plants that have grown to reproductive size (Wesselingh et al. 1997); however, after nutrients are allocated to reproduction growth rates may decrease for some species (Pitelka et al. 1985).

Gaps have been hypothesized as a mechanism for niche differentiation in forests (Bazazz and Pickett 1980; Denslow 1980) where differences in species performance (fecundity and growth) along light gradients lead to the coexistence of species. The hypothesis that species coexist because of vertical, horizontal, or temporal partitioning of gaps by size or position has been rejected for canopy trees in western coniferous forests because of the lack of short-lived, fast-growing "ruderal" trees in this region (Lertzman 1992). Differences in invasibility of gaps and partitioning of gaps by size, gap position, and time since gap creation may occur among shrubs and herbs that vary in (1) rates of response (e.g., growth and seed production) and (2) plasticity of types of response (e.g., seeds vs. vegetative growth) to habitats and disturbance regimes (Bazazz 1996; Antos and Zobel 1984b).

Several studies suggest that performance of species of herbs is differentiated by gap size and/or position. For example, the number of flowering *Erythronium* per area was significantly greater in single-tree gaps than under canopy but did not increase in multiple-tree gaps (Collins et al. 1988). Kotanen (1997) found that grassland species that reproduce largely by clonal growth were first to occupy gap edges but were subsequently crowded out by species with slow but dense growth. Recently disturbed sites are colonized by species with rapid vegetative spread such as *Linnaea*, but not by species with persistent buds buried to 2-3 cm (geophytes) (Sobey and Barkhouse 1977, McIntyre et al. 1995; Denslow 1985). Intense logging and burning in the central Western Cascade Mountain Range of Oregon in the *Tsuga heterophylla* Zone may have eliminated *Linnaea, Tiarella,* and other forest herbs for at least 20 yr (Clark 1990; Halpern and Spies 1994).

Different patterns of modular construction may explain why, in contrast to species of trees, rates of performance in gaps may differ among species of herbs by several orders of magnitude in gaps. Trunks of most tree species support branches that can project additional modules with sun leaves into direct light above the canopy, regardless of gap size or position.

In contrast, because the lack of trunks on herbs constrains their vertical growth, the intensity and duration of light affecting them is determined by the size and location of openings in taller vegetation. In addition, roots of trees can reach depths where soil moisture remains greater than near the surface, regardless of the size of current gaps in the canopy or roots.

A diversity of resource allocation patterns have evolved among species of herbs because of the wide range of light regimes in the herb layer. For example, herbs with flexible leaf and stem architecture (e.g., width, orientation, and size of leaves; number, angle and length of stems) can colonize young gaps with rapid rates of growth and reproduction. However, as sites with intense light become shaded by other plants, such species etiolate, retain photosynthate in shoots at the expense of roots, and produce thinner leaves and less dry matter (Grime 1979; Ryser 1996). On the other hand, herbs with lower rates and flexibility of performance (measured as fecundity, growth, dispersal, or germination) can persist under canopy where light, water, and other resources are less available but more stable, in spite of some temporal and spatial patchiness (Gadgil and Solbrig 1972; Grime 1979).

The overall goal of this study was to evaluate how small-scale disturbances affect forest herbs and to determine if herbaceous species differ in their response to resource gradients and gap size and position. I used *Linnaea borealis* and *Tiarella trifoliata* L. var. *unifoliata* to examine interactions of species, gap size and resources. The first objective was to determine whether fecundity and growth rates of these two forest herbs increase in gaps in these forests and, if so, to determine if the species differ in their response to gap size and position. The second objective was to compare fecundity and growth of the two species among the same gap sizes and positions.

I hypothesized that, based on their different morphologies and physiologies, performance of these two species would vary among gap size and position and that locations of peak performance would not be the same for *Linnaea* and *Tiarella.*

Linnaea and *Tiarella* are herbs that contrast in morphology and physiology but coexist in many of the same coniferous forest communities of the Pacific Northwest. *Linnaea* typically occupies warm sites at all moisture stress levels in Douglas-fir forests, while *Tiarella* typically occurs in cooler sites with lower moisture stress (Zobel et al. 1976). *Linnaea*'s cuticle-laden leaves which grow close to the ground may confer more tolerance to moisture stress in intense light than *Tiarella*'s palmate to cordate-shaped and thinner deciduous leaves (Givinish 1982, 1987). Although *Linnaea*'s fecundity increases with light (Eriksson 1988), seedlings are rare (Zobel and Antos 1986) because of low germination rates (Clark 1990). *Linnaea*'s stolons grow rapidly in disturbed forests (Sobey and Barkhouse 1977; Antos and Zobel 1984a) with relatively low light (Eriksson 1988). *Tiarella*'s rhizomes grow more slowly than *Linnaea*'s stolons (Antos and Zobel 1984a), and the foliage of *Tiarella* is taller and seedlings are more frequent (Antos and Zobel 1986). Root depth increases for both species with time and roots are more frequent on *Tiarella* than on *Linnaea* (Antos and Zobel 1984a). *Tiarella* produces more biomass in old forests with windthrow gaps where soil moisture (Hanley et al. 1997) and light (Alaback 1982; Tappeiner et al. 1989) are more available.

This study is the first to examine fecundity and growth of herbs relative to resources in forest gaps in an experimental setting. Most field studies of understory herbs compare their abundance among disturbance regimes or forest types or sites and do not evaluate the underlying biological causes (such as rates of seed production and growth) of those patterns. Although the averages and extremes of growth rates and fecundity have been measured for some species of herbs (e.g., Antos and Zobel 1984a), these measurements have rarely been taken in conjunction with measurements of resources (but see Eriksson 1988, Shultz and Adams 1995, Pitelka et al. 1980, Pfitch and Pearcy 1992) or gaps (Collins et al. 1985, 1988), let alone both resources and gaps (Hanley et al. 1997). Use of experimentally created gaps allows more control of gap size and shape than in naturally occurring gaps and provides a known history of plant abundance.

2.2 Methods

2.2.1 Site description

This study was conducted in the H.J. Andrews Experimental Forest (H.J.A.) where a gap experiment had been previously established by Spies (1990) at 900 m in elevation. H.J.A. lies in the Willamette National Forest on the west slope of the central Western Cascade Mountain Range of Oregon in the *Tsuga heterophylla* Zone (Franklin and Dyrness 1988). Multiple layers of 500-year-old *Pseudotsuga menziesii* and a dense subcanopy of younger *Tsuga heterophylla* dominate the forest. A moderately severe fire burned the stand in the 1840's (Teensma 1987) and understory was sparse before canopy gaps were created. Soil is a deep (depth to C horizon 1 m), well-drained, dark brown gravelly loam classified as a loamy skeletal, mixed, frigid Fluventic Dystrochrept (Gray and Spies 1996).

The climatic regime is characterized by summer drought and high temperatures from June to September, a pattern characteristic of the Pacific Northwest (Franklin and Waring 1980). Mean (15-year) annual precipitation is 224 cm, with only 8% of annual precipitation falling from June through September. Annual mean, minimum, and maximum air temperatures are 8.6, -3.1, and 27.0 deg C, respectively. Winter snowpacks accumulate to depths exceeding 1 m for only a few weeks.

2.2.2 Experimental design

Experimental gaps were created in the fall of 1990 by cutting all trees over 2 m tall (except for *Acer circinatum*) within the gap perimeter. The gaps were placed in locations with slopes less than 20% and with relatively dense canopies to minimize effects of recent gap events. Trees were stage-felled into the northeast or northwest quadrants, and skidders winched fallen tree boles from the gaps with cables. Branches and foliage were trimmed and removed from the felled trees. Four gap sizes were created, with two replicates of each size (Figure 2.1). Gap diameter was measured between tree crown edges and scaled to the average height (50 m) of dominant trees. Ratios for the four sizes were 0.2, 0.4, 0.6, and 1.0. Thus 0.2 gaps were 10 m in diameter and 1.0 gaps were 50 m in diameter. Two replicate control plots equal in area to the 1.0 gap size were also established under dense canopy in 1990 but included a few very small natural gaps in 1997.

The experimental gaps and their immediate surroundings were used for observations of performance of both species. Gaps were defined as the area between crowns of standing trees where the canopy had been experimentally removed (Gray 1995). Areas adjacent to these gaps were also sampled. In 1996, five positions (north and south borders, north, center, and south) were established for gap sizes 0.4, 0.6, and 1.0 and three positions (north and south borders and center) were established for gap size 0.2 (Figure 2.1). North, center, and south positions were established within control treatments. In each position, *Linnaea* and *Tiarella* were sampled within three 0.25-m^2 circular sample ring plots. The three sample units were randomly located within each position by establishing ring plots where cover of each species was highest within the center eastern, and western third of each experiement unit. The location of each sample plot for each species was mapped relative to coordinates used for other long-term studies.

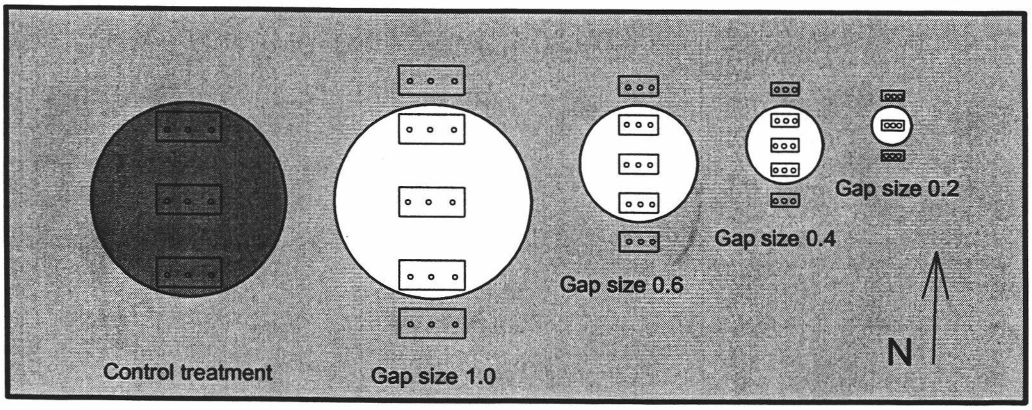


Figure 2.1. Experimental design for study of fecundity and growth of *Linnaea borealis* L. and *Tiarella trifoliata* L. in gap and control treatments. Gap size is the ratio of gap diameter and mean tree height (of 50 m). Positions are 192 m^2 in controls and gap size 1.0, 64 m^2 in gap size 0.6, 8 m^2 in gap size 0.4 and 4 m^2 in gap size 0.2.

2.2.3 Field measurements

2.2.3.1 Fecundity

The operational definition of fecundity for this study was the number of capsules per m^2 cover of each species. In each 0.25-m^2 sample plot of *Linnaea*, the number of stalks was counted in mid-July. All but a few stalks of *Linnaea* supported two capsules. For *Tiarella*, the total number of stalks per sample plot was recorded and the numbers of capsules per stalk of *Tiarella* was determined by counting all the capsules on five randomly selected stalks in each sample plot during the third week of July when capsules had formed, but before stalks broke off. The following equation was used to determine fecundity (F):

$$F = (\text{capsules} / \text{stalk}) * [(\text{stalks}/0.25\ m^2)*4] / (\%\ \text{cover}).$$

I estimated the percent cover of *Linnaea* and *Tiarella* for all 252 0.25-m^2 sample plots during the third week of July 1997. Cover guides were used to help estimate the area of leaves (Gray, pers comm. 1997). In addition, the number of seedlings were recorded within the ring plots for each species. Seedlings were identified by their palmately lobed leaves that developed after oblong cotyledon leaves had formed (Figure 2.2).

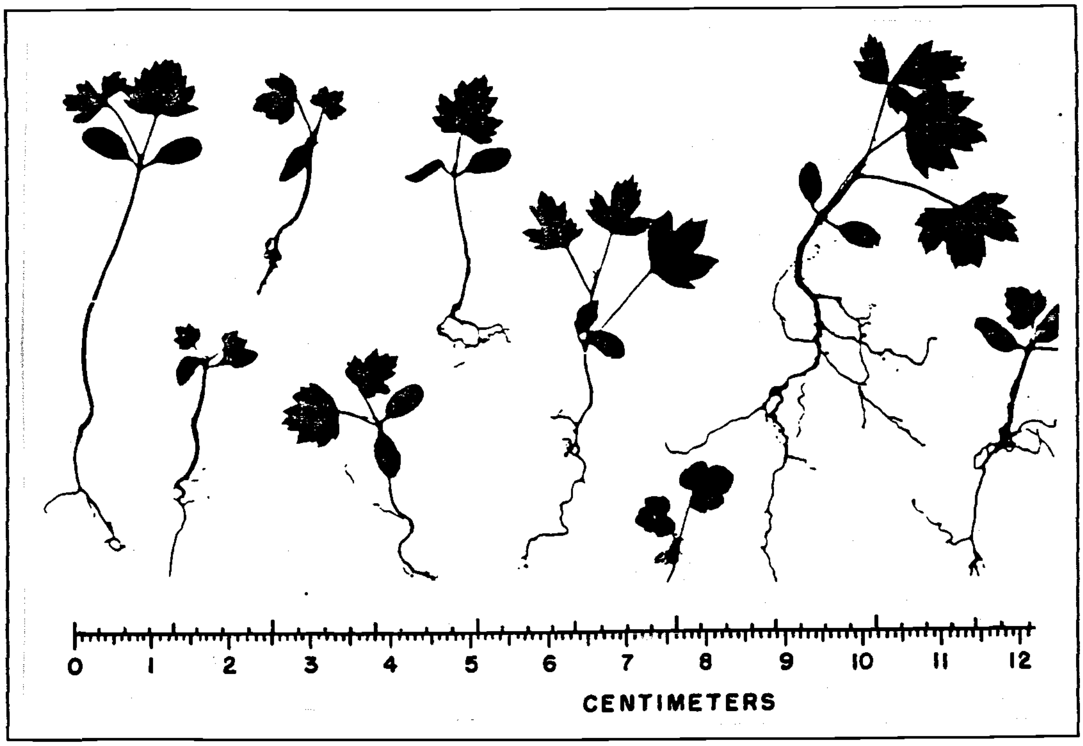


Figure 2.2. Outlines of *Tiarella* seedlings (actual size).

2.2.3.2 Growth rates

Two types of growth were measured for each species. First, to obtain a longer term estimate of growth rates within gap size 1.0 and controls, the relative change in frequency and cover of each species from 1990 and 1997 was calculated with data collected from permanent plots that were established by T. A. Spies in 1990. Percent cover of all herbs in each 0.25 m^2 plot was estimated annually or biannually from the area covered by one-sided each 0.25 m^2 plot was estimated annually or biannually from the area covered by one-sided vertical projections in plots that were established at 2 m intervals along main axes of each gap and control treatment and additionally along 4 m intervals on radial axes in primary replicates. Locations of all permanent plots, treatment boundaries, and cover (per 0.25 m^2 sample plot) of both species were graphed in Sigma Plot for each treatment. Percent frequency was calculated as the percent of sample plots in which either species was present relative to a total of 145 plots in each primary control and gap size 1.0 and relative to a total of 89 plots in the secondary treatments. Mean cover for each treatment was calculated as the average cover per plot. Mean and standard error of frequency and cover for the two replicate treatments were then calculated for each species in each treatment and year. Relative change in percent frequency (RCF) and percent cover (RCC) for each species was calculated as:

$\mathrm{RCF} = ((\%\ \mathrm{frequency}_{1997}) - (\%\ \mathrm{frequency}_{1990}))/((\%\ \mathrm{frequency}_{1997}) +$

$((\%\ \mathrm{frequency}_{1990})/2).$

$\mathrm{RCC} = ((\%\ \mathrm{cover}_{1997}) - (\%\ \mathrm{cover}_{1990}))/((\%\ \mathrm{cover}_{1997}) + (\%\ \mathrm{cover}_{1990})/2).$

The second estimate of growth was the current year's growth of individual plant parts. The distance between the end of each longest *Linnaea* stolon rooted in each sample plot and the point where growth had apparently resumed in spring of 1997 was measured in August 1997. Growth of stolons in 1997 was distinguished from that of 1996 by locating the point between the smallest leaf at the end of a series of progressively smaller leaves and a larger leaf. I assumed smaller leaves were produced during fall and winter (Sobey et al. 1977). Height growth of current year *Tiarella* was estimated from the mean height of five randomly selected stalks that were produced in June and remained intact in the third week of July.

2.2.3.3 Environmental data

Microsite conditions (fallen trees and shrubs, topography, and canopy cover) of each sample plot were described qualitatively and systematically photographed in 1997. Any subsequent major structural changes, such as windfall, were noted in 1998.

Measurements of photosynthetically active radiation (PAR) and soil moisture were made in 1992 at the treatment centers and under the dripline at the north, and south edges of gap sizes 0.2, 0.4, and 1.0 and equivalent positions in controls (Gray 1995). Gray (1995) measured PAR with calibrated quantum sensors and galium arsenide photodiodes placed 1.5 m above the forest floor during July and August of 1992. Data loggers sampled each light sensor at 10 s intervals and stored measurements as 2 hr means. Volumetric soil moisture content was estimated (Gray 1995) from Time Domain Reflectometry (TDR) using regressions that were developed for soils in one stand (Gray and Spies, 1995). One pair of 30 cm long TDR probes was placed in mineral soil seed plots at a 30° angle to sample the 0-15 cm depth at monthly intervals between May and September 1992.

2.2.4 Data analysis

2.2.4.1 Response to gaps

Species response to gaps was measured as the relative change of cover and frequency from 1990 to 1997 and as rates of fecundity and growth in 1997. Fecundity and growth of each species in the sample plots were averaged for 42 gap locations (gap size and position). Performance averaged among treatments with different positions would not be comparable because positions outside of gaps were analyzed for some but not all treatments. Analysis of growth and fecundity was therefore conducted in three ways. In the first approach (Analysis I) the effects of gaps were analyzed only within gaps (of all sizes but no border positions) and control treatments. In the second approach (Analysis II) the effects of position was analyzed within and outside of the large gap sizes 0.4, 0.6, and 1.0. In the third approach (Analysis III) positions were treated as separate treatment units and information from gaps of all sizes were analyzed.

In Analysis I, I averaged growth and fecundity during 1997 over north, center, and south positions within all sizes gaps and controls (Figure 2.3). For the smallest gap, the center position alone was used for estimating performance. ANOVA was conducted in SAS 6.10 (SAS Institute Inc. 1987) with the MIXED procedure to analyze how gap size affected each species. The LSMEANS statement in SAS computed means for each gap size (SAS Institute Inc. 1987). Dunnett's procedure (Steel and Torrie 1980) was conducted in order to observe differences between each treatment and the controls. Confidence intervals for treatment means and mean differences of performance relative to controls were constructed in SAS. Results were considered significant if the probability of a Type I error (α) was less than 0.05. Fecundity was log-transformed for both species and for growth for *Linnaea*.

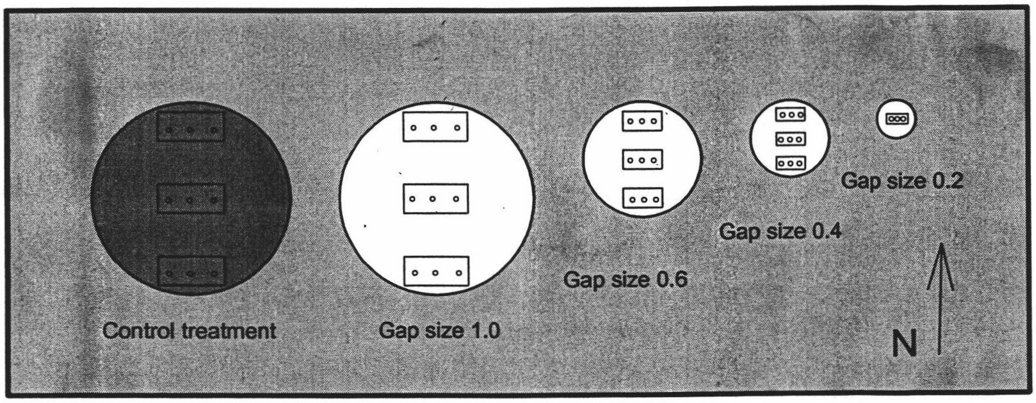


Figure 2.3. Experimental design for fecundity and growth of *Linnaea borealis* L. and *Tiarella trifoliata* L. within all gap and control treatments (Analysis I).

In Analysis II, I used gap sizes 0.4, 0.6, and 1.0, all of which had five positions. A split-plot ANOVA was conducted in SAS 6.10 (SAS Institute Inc. 1987) with the MIXED procedure to analyze how gap size, gap position, and interaction of gap size and position affected performance of each species. The LSMEANS statement in SAS computed means for each gap size, gap position, and interaction (SAS Institute Inc. 1987). Fisher's Protected Least Significant Differences (FPLSD; Fisher 1966) was conducted to determine which gap position, size, or interaction had significant effects on species performance. Results were considered significant if the probability of a Type I error (α) was less than 0.05. The numbers of capsules per m^2 cover were log-transformed for *Linnaea* and *Tiarella* because the range of response was large (the ratio of largest to smallest error values was greater than 10), producing a moderate funnel shape on residual plots. Before transformation, each value was increased by 1.0 to avoid log transformation of zero values. Transformation improved the residual plots. Growth rates were not transformed for either species because of the lower range of response and lack of zero values.

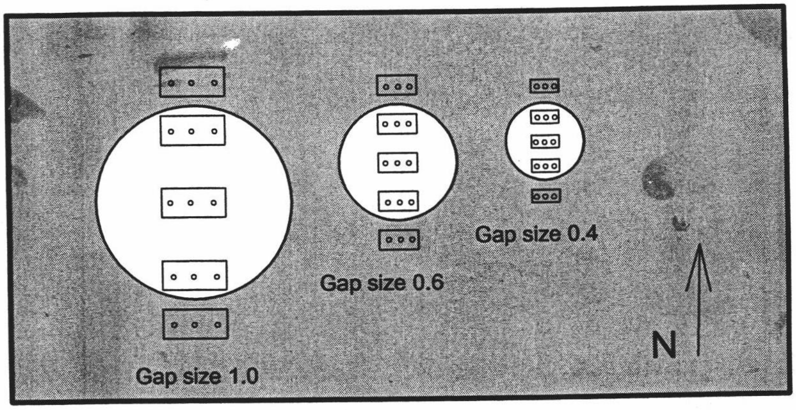


Figure 2.4. Experimental design for fecundity and growth of *Linnaea borealis* L. and *Tiarella trifoliata* L. within gap sizes 1.0, 0.4, and 0.2 (Analysis II).

In Analysis III, ANOVA was conducted in SAS 6.10 (SAS Institute Inc. 1987) with the MIXED procedure to analyze effects of all gap locations (gap position and size combination) on performance of each species (Figure 2.1). Thus border positions (absent from Analysis I) and controls and gap size 0.2 could be compared with locations within large gaps. The means for each location were used in FPLSD to determine which locations had significant effects on species performance ($\alpha < 0.005$). The numbers of capsules per m^2 cover were log-transformed, and each value was increased by 1.0 to avoid log transformation of zero values. Growth rates were not transformed for either species. Fecundity and growth rates of each species were plotted in decreasing order of magnitude to explore patterns of performance among locations.

2.2.4.2 Response to resource gradients

The effects of resources on species performance were conducted by regressing both soil moisture content and light with data collected in 1992 by Gray (1995; see section 2.2.3.3) on mean fecundity and growth of both species in the north, center and south positions of controls and gap sizes 0.2, 0.4, and 1.0. Most plots of *Linnaea* and *Tiarella* were in equivalent locations. Plots of *Linnaea* in south positions of gap size 0.4 were elevated on rootwads. Stepwise regression analysis was conducted in SAS 6.10 (SAS Institute Inc. 1987) to select variables to include in the model. Criteria for model selection was $\alpha \leq 0.15$.

2.3 Results

2.3.1 Response to gaps

2.3.1.1 Growth from 1990 to 1997 in large gaps and controls

The percent frequency of both species increased in both control and gap size 1.0 treatments from 1990 to 1997. The increase in frequency of *Linnaea* in 1997 relative to 1990 was about four times greater in gap size 1.0 than in controls and almost twice that of *Tiarella* in gaps. The relative increase in frequency of *Tiarella* in gaps was slightly greater in gaps than in controls (Table 2.1).

Table 2.1. Mean and standard error (in parentheses) in percent frequency of *Linnaea* and *Tiarella* in gap size 1.0 and control treatments from 1990 to 1997 (n=2) and changes during this period relative to the mean frequency in both yr (rel. ch.).

Treatment	*Linnaea*			*Tiarella*		
	1990	1997	rel. ch.	1990	1997	rel. ch.
Control	0.13 (0.12)	0.16 (0.13)	19%	0.11 (0.11)	0.15(0.12)	31%
1.0	0.11 (0.09)	0.25 (0.13)	75%	0.13 (0.13)	0.20(0.15)	43%

The percent cover of *Linnaea* increased in controls but increased more in gap size 1.0 from 1990 to 1997. Cover of *Tiarella* increased at about twice the rate in gap size 1.0 as in controls and at slightly greater rates in gap size 1.0 than did *Linnaea* (Table 2.2).

Table 2.2. Mean and standard error (in parentheses) in percent cover of *Linnaea* and *Tiarella* in gap size 1.0 and control treatments from 1990 to 1997 (n = 2) and changes during this period relative to the mean cover in both yr (rel. ch.).

Treatment	*Linnaea*			*Tiarella*		
	1990	1997	rel. ch.	1990	1997	rel. ch.
Control	57 (68)	76 (141)	29%	15 (17)	30 (40)	68%
1.0	21 (16)	212 (285)	164%	12 (14)	128 (155)	167%

2.3.1.2 Analysis I: Growth and fecundity within gaps

Mean fecundity of *Linnaea* varied among treatments at a significance level of P = 0.09. The difference in fecundity in controls and in gaps was marginally significant (P = 0.09) in gap size 0.4. Fecundity was low and not significantly different from controls in smaller gaps. Differences were not significant in larger gaps (Table 2.3a).

Mean fecundity of *Tiarella* varied among treatments at a significance level of P = 1.0 (Table 2.3b). The difference in fecundity in controls and in gaps was marginally significant for gap size 0.6 (P = 0.06), gap size 1.0 (P = 0.09), and gap size 0.4 (P = 0.08). Fecundity among the two replicates of gap size 1.0 differed the most.

Table 2.3a. Mean fecundity (capsules per m^2 cover) of *Linnaea* within all treatments and mean differences of fecundity in gaps compared to controls (n = 2). Values were averaged for north, center, and south positions in all treatments except gap size 0.2, for which values for the center position were used. Data are back-transformed values of logged least square means. Confidence intervals are in parentheses.

	Linnaea	
Trt.	back-transformed means	ratio to control
Ctl.	6.16 (0.76, 49.93)	1
0.2	8.06 (1.0, 65.37)	1.31 (0.024, 71.62)
0.4	182.0 (22.51, 1475.57)	29.55 (0.54, 1616.63)
0.6	61.8 (7.62, 501.00)	10.03 (0.183, 548.89)
1.0	134.3 (16.56, 1088.44)	21.8 (0.40, 1192.49)

Table 2.3b. Mean fecundity (capsules per m^2 cover) of *Tiarella* within all treatments and mean differences of fecundity in gaps compared to controls (n = 2). Values were averaged for north, center, and south positions in all treatments except gap size 0.2, for which values for the center position were used. Data are back-transformed values of logged least square means. Confidence intervals are in parentheses.

	Tiarella	
Trt.	back-transformed means	ratio to control
Ctl.	0.85 (0.04, 18.13)	1
0.2	45.34 (2.13, 964.30)	53.2 (0.15, 18403.6)
0.4	112.6 (5.3, 2395.15)	132.1 (0.38, 45715.8)
0.6	197.2 (9.27, 4194.8)	231.4 (0.67, 80065.5)
1.0	137.2 (6.45, 2917.84)	161.0 (0.47, 55692.5)

Mean growth of *Linnaea* stolons varied among treatments at a significance level of P = 0.17. Differences in growth rates in controls and gap size 0.2 were marginally significant at P = 0.08. Differences in controls and other gap sizes were significant at P = > 0.2 (Table 2.4a). Mean stolon growth in gaps was about twice (15 cm longer) the means in controls.

Table 2.4a. Mean growth (cm) of *Linnaea* stolons within all treatments and mean differences of growth in gaps compared to controls (n=2). Values were averaged for north, center, and south positions in all treatments except gap size 0.2, for which values for the center position were used. Data are least square means that were back-transformed from logged values. Confidence intervals are in parentheses.

	Linnaea	
Trt.	back-transformed means	ratio to control
Ctl.	17.86 (11.93, 26.74)	1
0.2	34.92 (23.33, 52.27)	1.96 (0.90, 4.23)
0.4	24.70 (16.5, 36.97)	1.38 (0.64, 2.99)
0.6	28.52 (19.05, 42.7)	1.60 (0.74, 3.45)
1.0	28.60 (19.11, 42.82)	1.60 (0.74, 3.46)

Differences in growth rates among treatments and controls differed at significance levels of (P = 0.1) for *Tiarella*. Differences were marginally significant in gap size 1.0, 0.2, and 0.6 at P = 0.07, 0.07, and 0.1 respectively. Height of *Tiarella* stalks generally were about twice as tall (5 cm taller) in gaps than in controls.

Table 2.4b. Mean growth (cm) of *Tiarella*'s shoots within all treatments and mean differences of growth in gaps compared to controls (n=2). Values were averaged for north, center, and south positions in all treatments except gap size 0.2, for which values for the center position were used. Data are least square means that were back-transformed from logged values. Confidence intervals are in parentheses.

	Tiarella	
Trt.	back-transformed means	ratio to control
Ctl.	5.30 (3.57, 7.85)	1
0.2	10.48 (7.07, 15.54)	1.98 (0.93, 4.20)
0.4	7.07 (4.77, 10.48)	1.33 (0.63, 2.83)
0.6	9.85 (6.65, 14.60)	1.86 (0.88, 3.95)
1.0	10.42 (7.03, 15.44)	1.97 (0.93, 4.17)

2.3.1.3 Analysis II: Response to gap position within and bordering large gaps

Fecundity of *Linnaea* varied significantly among positions (P < 0.05) but not among gap sizes nor in interactions among gap sizes and position. Fecundity of *Tiarella* also varied significantly among positions (P < 0.0001) but not among gap sizes nor in interactions among gap sizes and position (Table 2.5).

Table 2.5. Results of split-plot ANOVAs on capsules per m^2 cover for separate tests of *Linnaea* and *Tiarella*.

Source	df	*F*	*P*
Linnaea			
Gap size	2	2.45	0.234
Error: gap size	5		
Position	4	3.28	0.049
Error: Position	4		
Gap size x position	8	1.53	0.243
Error: Gap size x position	6		
Total	29		
Tiarella			
Gap size	2	0.13	0.885
Error: gap size	5		
Position	4	16.55	0.0001
Error: Position	4		
Gap size x position	8	1.94	0.145
Error: Gap size x position	6		
Total	29		

Among the five gap positions, fecundity was significantly greater for both *Linnaea* and *Tiarella* in at least one position within gaps than it was in border positions (Figure 2.5, Table 2.6). Fecundity of *Linnaea* was greatest in the north and south positions and lowest in south borders. Fecundity of *Tiarella* was greatest in south positions within the gaps and decreased northward.

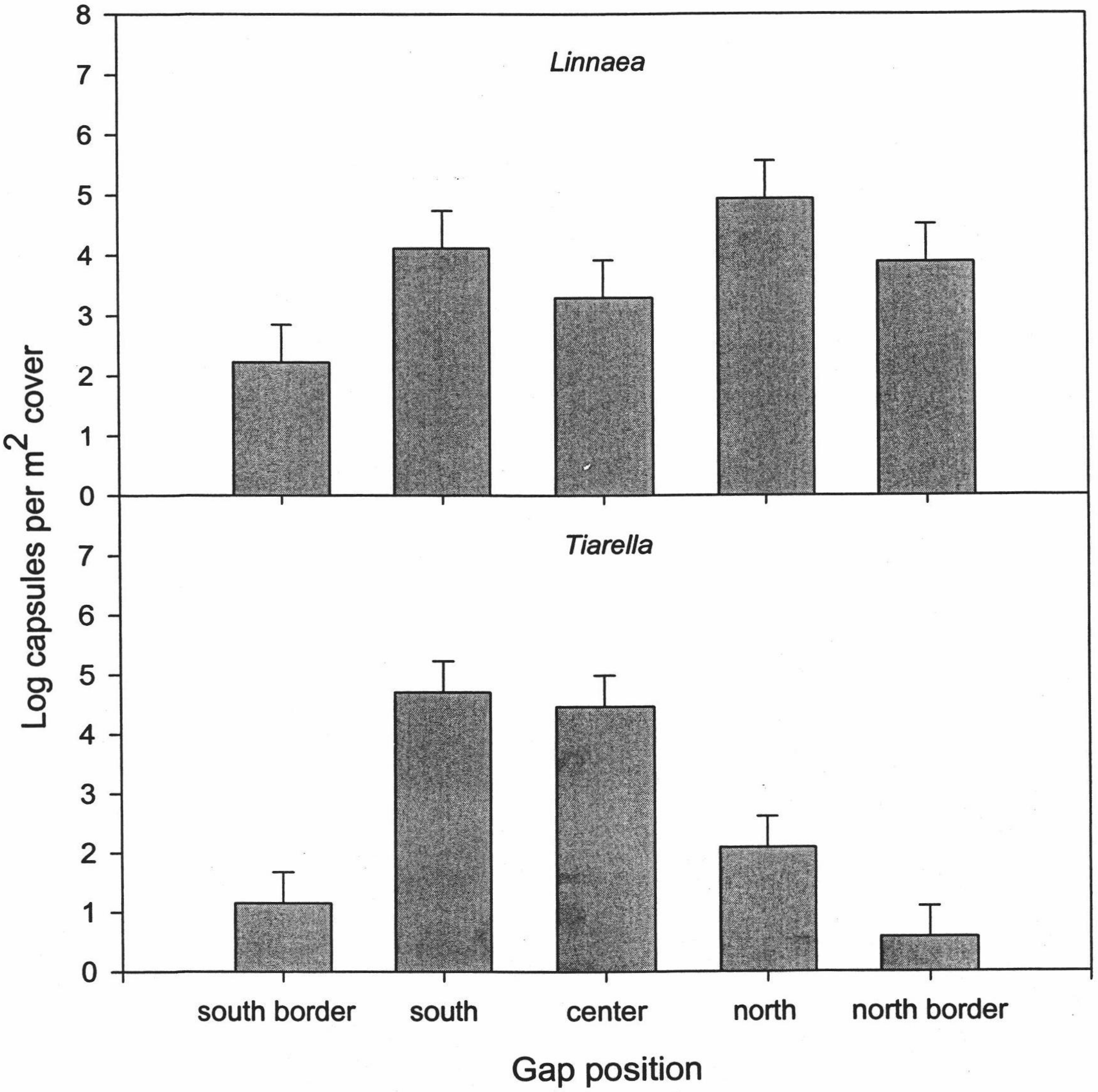


Figure 2.5. Capsules per m^2 cover in five positions in and around gap sizes 0.4, 0.6 and 1.0 in separate tests of *Linnaea* and *Tiarella*. Values are least-square means with standard errors of log-transformed fecundity data (n=6).

Growth rates also varied significantly for both species among positions but not among gap sizes nor in interactions among gap sizes and position (Table 2.7). Mean growth of *Linnaea* was significantly ($P < 0.02$) different in at least one position. Differences in mean growth of *Tiarella* was more sensitive to gap position and differed at significance of $P < 0.002$.

Table 2.6. Significance levels for differences in pairwise comparisons of fecundity of *Linnaea* and *Tiarella* in five positions of large gaps.

Gap positions	*Linnaea*	*Tiarella*
south border/south	0.0339	0.0002
south border/center	0.1995	0.0003
south border/north	0.0049	0.1780
south border/north border	0.0566	0.3987
south/center	0.3204	0.7234
south/north	0.3153	0.0019
south/north border	0.7806	0.0001
center/north	0.0592	0.0036
center/north border	0.4667	0.0001
north/north border	0.2074	0.0398

Table 2.7. Results of split-plot ANOVAs on growth rates (cm per growing season) for separate tests of *Linnaea* and *Tiarella*.

Source	df	*F*	*P*
Linnaea			
Gap size	2`	0.23	0.8081
Error: gap size	5		
Position	4	4.92	0.0139
Error: Position	4		
Gap size x position	8	1.23	0.3615
Error: Gap size x position	6		
Total	29		
Tiarella			
Gap size	2	0.37	0.72
Error: gap size	5		
Position	4	8.84	0.0015
Error: Position	4		
Gap size x position	8	0.57	0.782
Error: Gap size x position	6		
Total	29		

Among positions within and around gaps, mean growth rates for both species were significantly greater within gaps than in border plots (Figure 2.6, Table 2.8). *Linnaea* stolons grew longer in in all positions within gaps than on south borders. Growth in south (but not center and north) positions were significantly greater than on the north border. *Tiarella* stalks grew taller in center positions of gaps than in border positions. Growth rates in north than positions differed from rates on north borders but not from south borders.

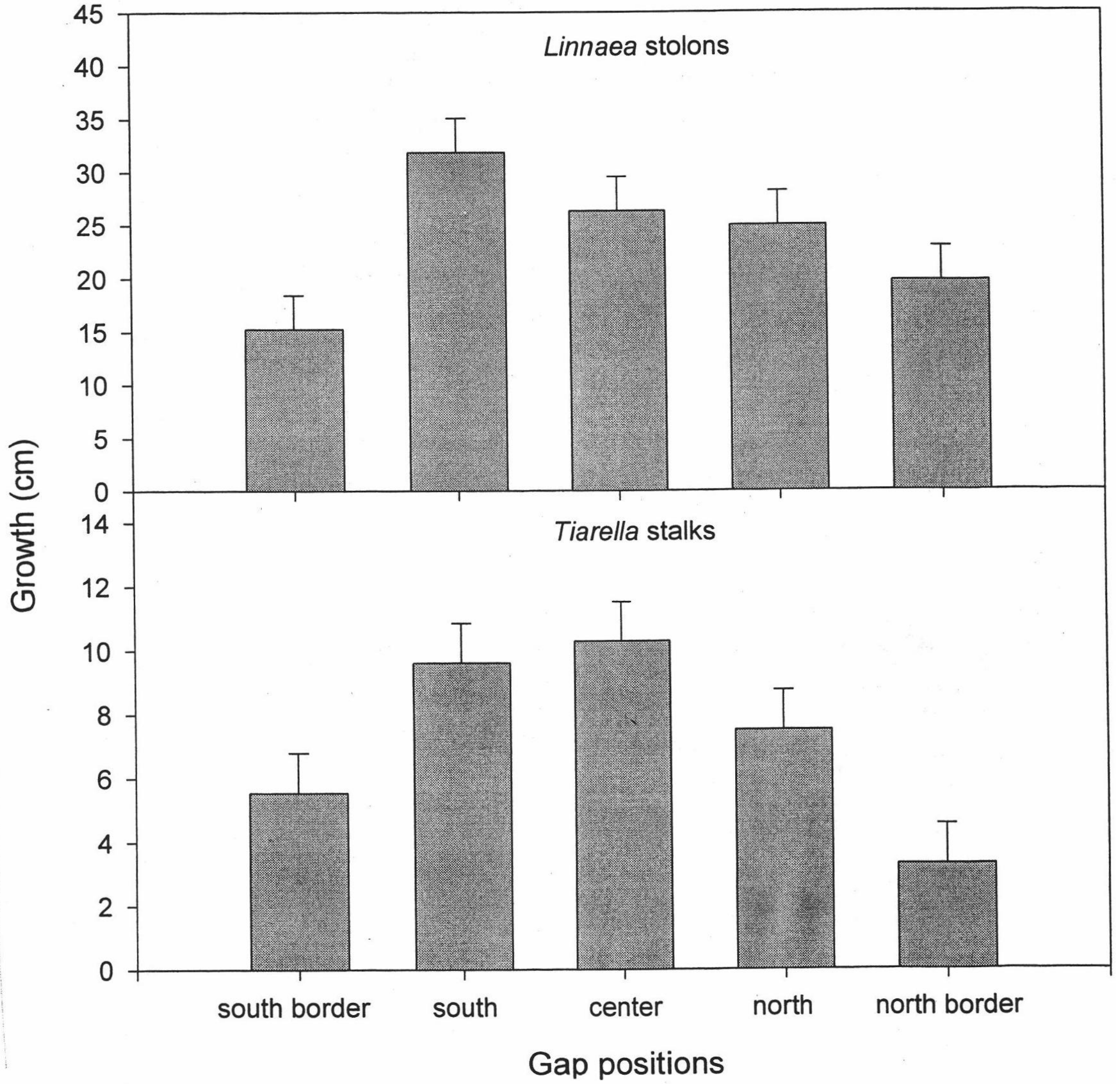


Figure 2.6. Mean growth (cm) in five positions in and around gap sizes 0.4, 0.6, and 1.0 for separate tests of *Linnaea* stolons and *Tiarella* stalks. Values are least-square means and standard errors (n = 6) of growth data.

Table 2.8. Significance levels for differences in pairwise comparisons of growth rates of *Linnaea* and *Tiarella* in five positions of large gaps.

Gap positions	*Linnaea*	*Tiarella*
south border/south	0.0015	0.0119
south border/center	0.0182	0.0049
south border/north	0.0341	0.1799
south border/north border	0.2899	0.1271
south/center	0.1985	0.6381
south/north	0.1144	0.1505
south/north border	0.0113	0.0006
center/north	0.7386	0.665
center/north border	0.1301	0.0003
north/north border	0.2234	0.0098

2.3.1.4 Analysis III: Response to all treatment locations

Mean fecundity varied significantly among locations for both *Linnaea* and *Tiarella* (Table 2.9). In general, fecundity of *Linnaea* was greater in northern positions within gaps than on gap borders or in controls (Figure 2.7, Table 2.10). Fecundity of *Tiarella* was generally greater in south and center gap positions than on gap borders or in controls (Figure 2.6, Table 2.11).

Mean growth rates varied significantly among locations for both *Linnaea* and *Tiarella* (Table 2.12). In general, growth rates of *Linnaea* stolons were greater in south and center gap positions than in north positions (except where stolons were under fallen trees in the north). Lowest growth rates occurred on gap borders or in controls except where natural gaps had formed (Figure 2.5, Table 2.13). Mean growth rates of *Tiarella* were generally greatest in south and center gap positions, except where one of the replicates of gap size 0.4 had been enlarged by inadvertant knockdown on the east during logging. Rates were lowest on gap borders and in controls but were somewhat higher in controls where natural gaps occurred (Figure 2.8, Table 2.14).

Table 2.9. Results of ANOVAs on fecundity among 21 locations (gap size and position combinations) for separate tests of *Linnaea* and *Tiarella* (n=2).

Source	df	*F*	*P*
Linnaea			
Location	20	3.25	0.005
Error	21		
Total	41		
Tiarella			
Location	20	3.52	0.003
Error	21		
Total	41		

Table 2.10. Pairs of locations where differences in mean fecundity (log of capsules per m^2 cover) of *Linnaea* are significant ($P < 0.005$). Numbers refer to gap size (0 = control) and letters refer to position (n = north, nb = north border, c = center, s = south, sb = south border).

	0.4s	1.0n	0.4c	0.4nb	0.4n	6.0n	1.0nb
0.2nb	0.0013	0.0014	0.0015	0.0018	0.0026	0.0034	0.0037
0.2sb	0.0016	0.0017	0.0019	0.0023	0.0033	0.0043	0.0046
0.6c	0.0040	0.0044	0.0048				
0s	0.0040	0.0044	0.0048				

Table 2.11. Pairs of locations where differences in mean fecundity of *Tiarella*(log of capsules per m^2 cover) are significant ($P < 0.005$). Numbers refer to gap size (0 = control) and letters refer to position (n = north, nb = north border, c = center, s = south, sb = south border).

.	0c	1.0sb	6.0nb	1.0nb	0.4nb	0s	0n	0.4sb	0.2sb	0.4n	0.6sb
0.6c	0.0002	0.0002	0.0004	0.0004	0.0006	0.0009	0.0021	0.0022	0.0023	0.0037	0.0042
1.0s	0.0004	0.0006	0.0009	0.0011	0.0014	0.0015	0.0021	0.0047	0.0049		
0.4s	0.0021	0.0027	0.0042								

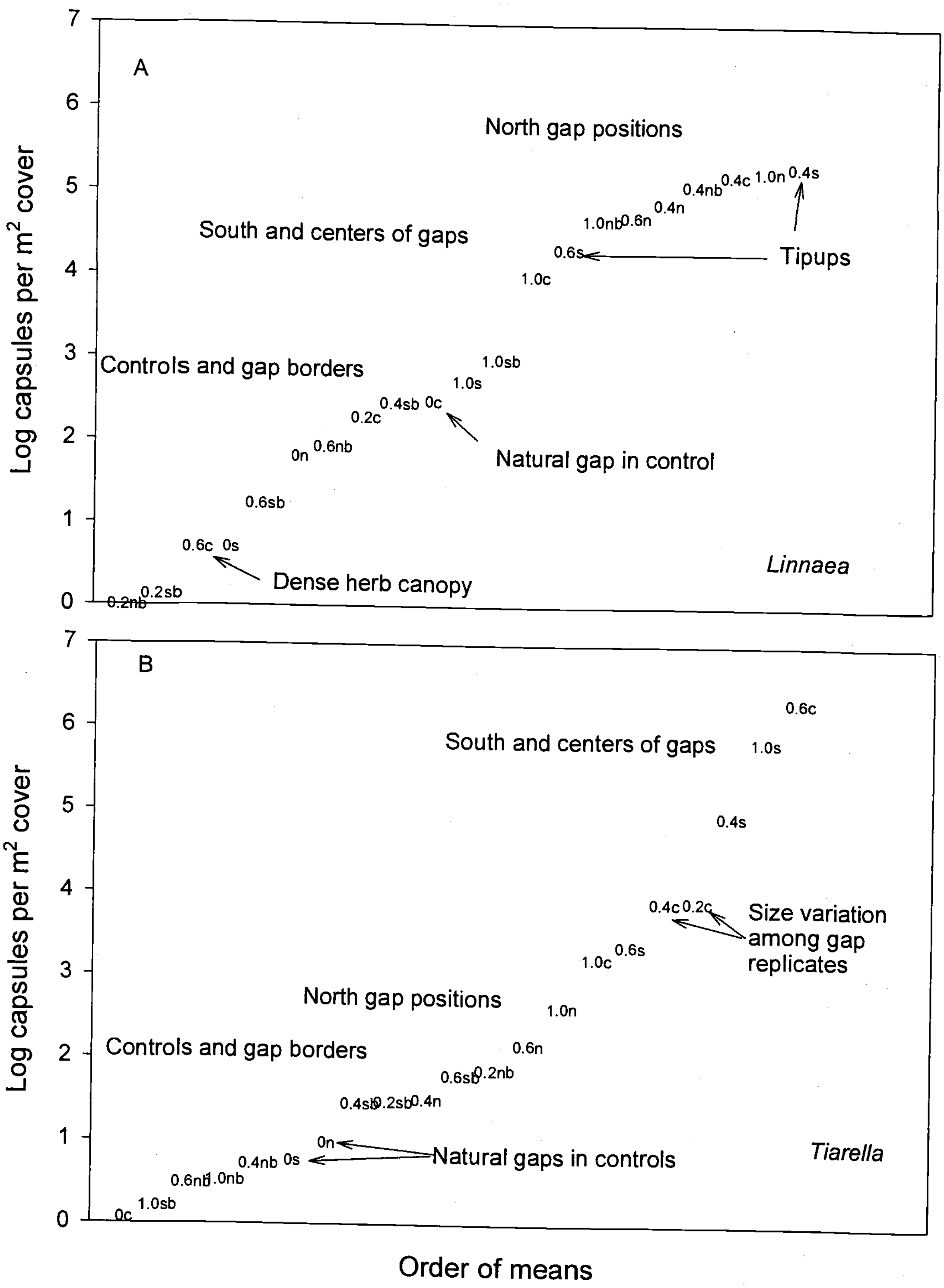


Figure 2.7. Fecundity of *Linnaea* (A) and *Tiarella* (B) at individual positons arranged in order of means from lowest to highest. Notes in figure refer to general patterns and possible causes of why a position did not fit the general pattern. Numbers refer to gap size (0 = control) and letters refer to position (n = north, nb = north border, c = center, s = south, = south border).

Table 2.12. Results of ANOVAs on growth rates among 21 locations (gap size and position combinations) for separate tests of *Linnaea* and *Tiarella* (n=2).

Source	df	*F*	*P*
Linnaea			
Location	20	2.46	0.0232
Error	21		
Total	41		
Tiarella			
Location	20	2.03	0.0582
Error	21		
Total	41		

Table 2.13. Pairs of locations where differences in mean growth (cm) of *Linnaea* stolons are significant (P < 0.005). Numbers refer to treatments and letters refer to position.

	0.2c	1.0s	0.6n	0.6s	1.0c
0.2nb	0.0008	0.0008	0.0012	0.0014	0.0017
6.0sb	0.0057	0.0058			

Table 2.14. Pairs of locations where differences in mean growth (cm) of *Tiarella* stalks are significant (P < 0.005). Numbers refer to gap size and letters refer to position.

	0c	1.0sb	0.6nb	1.0nb	0.4nb	0s	0n	0.4sb	0.2sb	0.4n	0.6sb
0.6c	0.0002	0.0002	0.0004	0.0004	0.0006	0.0009	0.0021	0.0022	0.0023	0.0037	0.0042
1.0s	0.0004	0.0006	0.0009	0.0011	0.0014	0.0015	0.0021	0.0047	0.0049		
0.4s	0.0021	0.0027	0.0042								

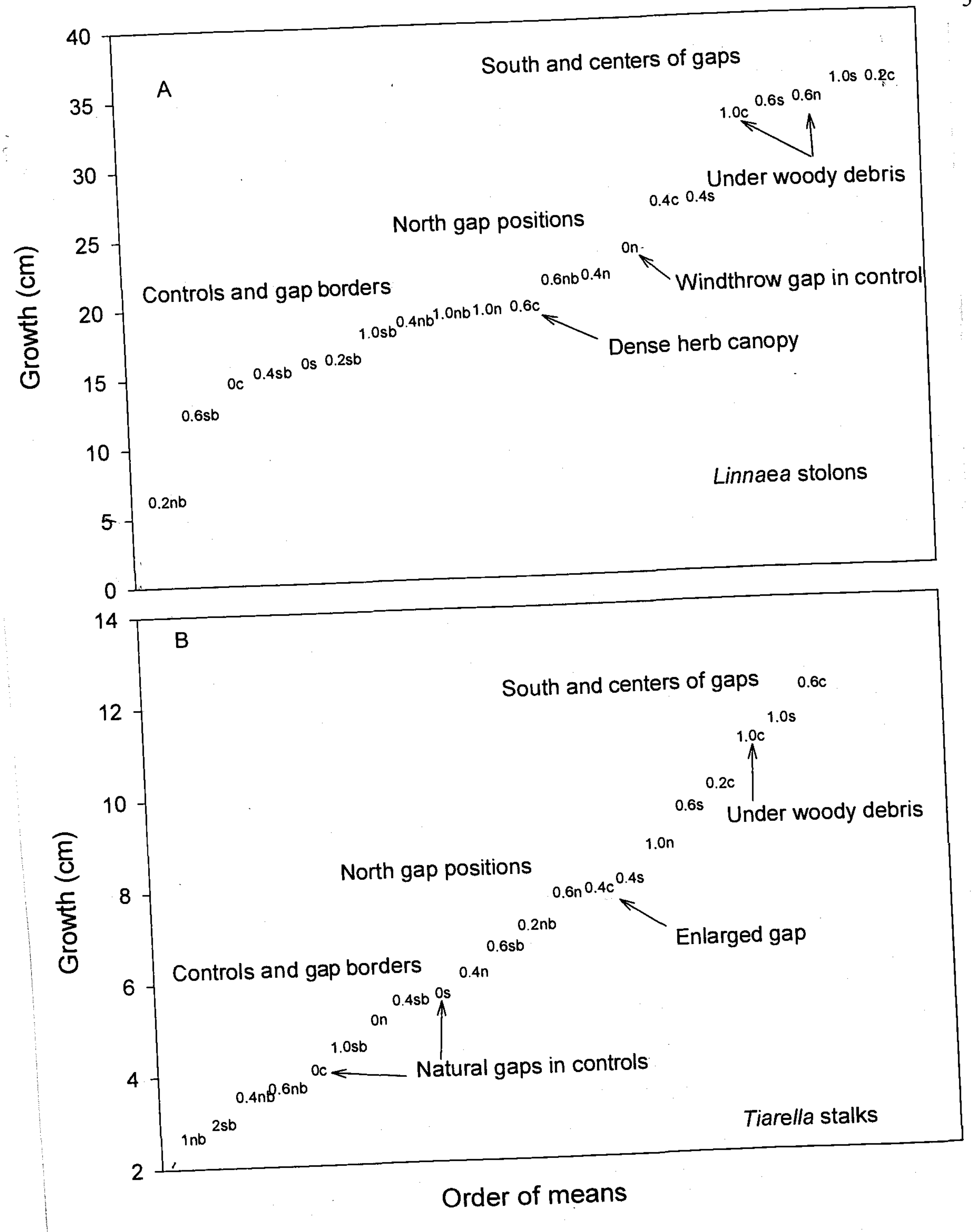


Figure 2.8. Growth rates (cm) of *Linnaea* stolons (A) and *Tiarella* stalks (B) of *Linnaea* (A) and *Tiarella* (B) at individual positons arranged in order of means from lowest to highest. Labels along the horizontal refer to general patterns. Notes refer to possible causes of why a position did not fit the general pattern. Numbers refer to gap size (0 = control) and letters refer to position (n = north, nb = north border, c = center, s = south, sb = south border).

2.3.2 Response to resource gradients

Performance of both species was explained by 1992 light and soil moisture resources. Stepwise regressions that entered soil moisture, light intensity and an interaction term for soil moisture and light intensity) indicated that fecundity increased with an interaction between light and soil moisture for *Linnaea* (F = 3.96, $P < 0.0818$) and with soil moisture (F = 8.52; $P < 0.0193$) for *Tiarella* (Figure 2.9, Table 2.15). Growth increased with soil moisture at significance levels of ($P < 0.0904$) for *Tiarella* and at ($P < 0.1011$) for *Linnaea* (Figure 2.10, Table 2.16).

Table 2.15. Best variables and coeffiecients of determination from stepwise multiple regression of resource variables on fecundity of *Linnaea* and *Tiarella*. Values in parentheses are signs of the regression coefficients and partial R^2s. The regression with * is significant at $P < 0.05$.

Species	Total R^2 (adjusted)	Independent variables
Linnaea	0.33	Interaction: light and soil moisture (+) (0.33)
Tiarella	0.52	Soil moisture (+) (0.52)*

Table 2.16. Best variables and coeffiecients of determination from stepwise multiple regression of resource variables on growth rates of *Linnaea* and *Tiarella*. Values in parentheses are signs of the regression coefficients and partial R^2s. Regressions are not significant at $P < 0.05$.

Species	Total R^2 (adjusted)	Independent variables
Linnaea	0.30	Soil moisture (+) (0.30)
Tiarella	0.32	Soil moisture (+) (0.32)

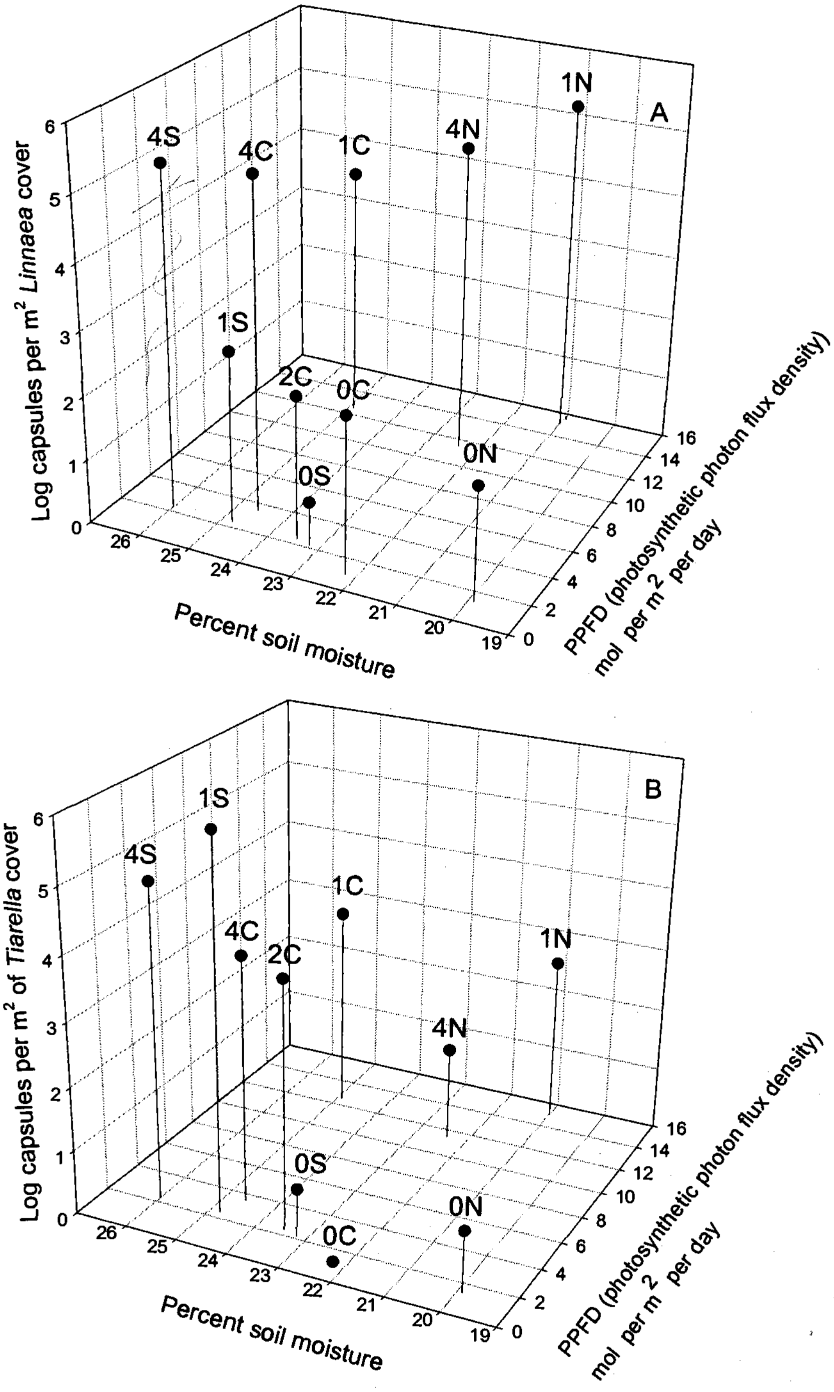


Figure 2.9. Fecundity of *Linnaea* (A) and *Tiarella* (B) along light and soil moisture gradients measured in 1992 by Gray (1995) within gap and control treatments.

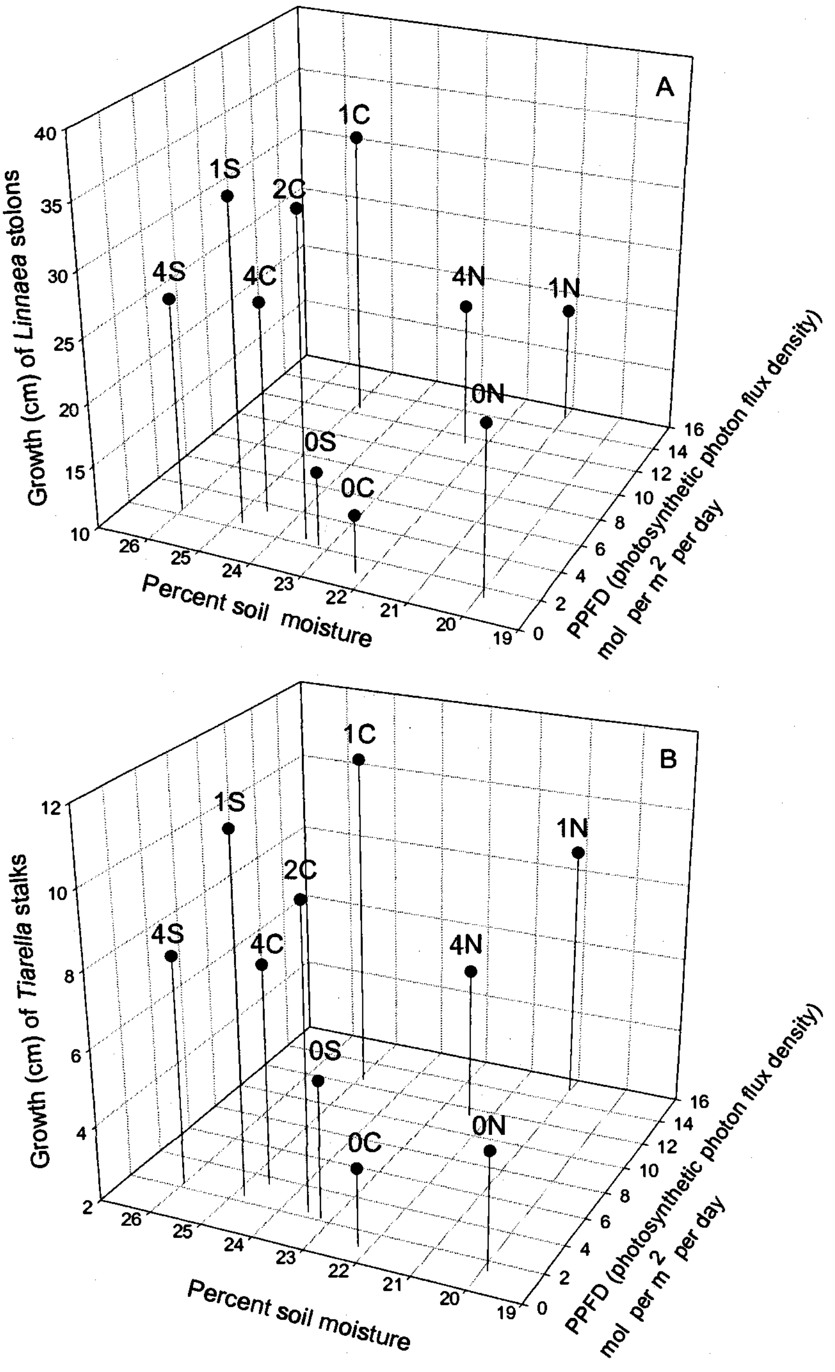


Figure 2.10. Growth of *Linnaea* (A) and *Tiarella* (B) along light and soil moisture gradients measured by Gray (1995) within gap and control treatments.

2.3.3 Seedling presence

Tiarella seedlings were rare. Those present occurred sporadically within most gap treatments but were not in control areas (Table 2.17). Seedlings were present on gap borders and in south and center but not north positions of gap sizes 0.4, 0.6, or 1.0. No *Linnaea* seedlings were observed.

Table 2.17. Presence of *Tiarella* seedlings in all gap and control treatments. Numbers are totals of seedlings in all three subplots per position in both treatment replicates.

	south border		south		center		north		north border	
Treatment	rep 1	rep 2	rep 1	rep 2	rep 1	rep 2	rep 1	rep 2	rep 1	rep 2
Controls	--	--	0	0	0	0	0	0	--	--
0.2	7	0	--	--	0	17	--	--	2	3
0.4	0	0	0	0	3	0	0	0	3	0
0.6	0	18	0	7	0	0	0	0	5	0
1.0	0	0	5	0	0	0	0	0	1	0

2.4 Discussion

This study demonstrates that gaps can increase fecundity and growth of *Linnaea* and *Tiarella*. It also shows that response of *Linnaea* is different from *Tiarella*. *Linnaea*'s fecundity and growth among gap sizes were generally small and not sequential. *Tiarella* increased fecundity somewhat consistently with gap size until gap size 0.6. Minimum gap size threshold for increases in fecundity appeared to be larger for *Linnaea* than for *Tiarella*. On the other hand, growth rates of both species increased substantially, even in small gaps. Rates of fecundity and growth of each species within control treatments where natural gaps had formed were occasionally equivalent to rates in gaps. Thus, while relative changes of frequency and cover (over 7 yr) were also greater in gap size 1.0 than in control treatments, cover of both species and frequency of *Tiarella* also increased slightly in controls. Rates of fecundity within gaps were greater for *Tiarella* than for *Linnaea*. Within all treatments, especially in gaps, the total, absolute amount of growth (cm) in 1997 was greater for *Linnaea* stolons than for height *Tiarella* stalks. Relative growth rates cannot be compared because thes structures did not exist before the 1997 growing season.

Despite the effect of gaps, performance varied more with gap position and resources than with gap size. Fecundity and growth rates of both species were especially greater within gaps than in positions that bordered the gaps. Within large gaps, fecundity of *Linnaea* was greatest in northern positions. Fecundity of *Tiarella* was greatest in southern positions. Growth rates of *Linnaea* and *Tiarella* were greater in southern than in northern positions. Exceptions to these trends occurred in large gaps where canopy and substrate cover varied among equivalent positions among replicate treatments. Resources may explain the horizontal axes of the plots with all gap locations and performance. For example, fecundity increased with light for *Linnaea* and with soil moisture for *Tiarella.* Growth rates increased with soil moisture for both species.

2.4.1 Response to gaps and resources in gaps

These results demonstrate *Linnaea's* ability for rapid horizontal spread and *Tiarella's* ability to exploit vertical space after light and soil moisture become available in gaps (Figure 2.11) to dense canopy areas. Fecundity of *Linnaea* also increased with light in a study by Eriksson (1988). Similarly, Hanley et al. (1997) found that biomass production by *Tiarella* increased where soil moisture was available in windthrow gaps in Alaska. Anderson (1968) found that moisture in the form of throughfall was more important than light to leaf area of herbs in gap openings in deciduous forests of the Midwest.

Gaps may increase abundance of these herbs as long as individuals are located in microsites or positions where rates of their major mode of reproduction increase. For example, despite the large number of capsules produced, *Linnaea*'s germination rates are low (Clark 1990). No seedlings were observed for *Linnaea* in any treatment during 1997 or 1998. On the other hand, growth rates of 60 cm in length of stolons per year were recorded for individuals in unoccupied space of gap fringes. Therefore, horizontal growth of *Linnaea*'s stems, not sexual reproduction, may explain increases in frequency for *Linnaea* from 1990 to 1997. However, growth rates of stolons in 1997 were lower under dense herb canopy. Therefore, differences in *Linnaea*'s growth rates in gaps compared to controls or gap borders may currently be lower than such differences for *Tiarella*. *Linnaea* may also quickly reach new sites by changing the length, growth rate and angle of spacers as levels of resources change if it has "guerilla" growth patterns (Lovett-Doust 1981). Mean and variation of the number of *Linnaea* branches (per segment stolon produced during a growing season) and length (cm) were 2.2 (+/-0.5) and 5.84 (1.46) respectively (Antos and Zobel 1984a). Whether rates of branching and total length varied in gaps vs. controls was not measured in this study.

Rhizome growth patterns and low distance of seed dispersal may partially explain why relative increases of frequency in gap size 1.0 between 1990 and 1997 were much lower for *Tiarella* than for *Linnaea*. Unlike *Linnaea*'s stolons, *Tiarella* rhizomes rarely exceed lengths of *ca* 2 cm and they rarely branch (Antos and Zobel 1984a,b). *Tiarella* may persist within or near areas of original establishment because of short and equal spacers that increase in density rather than length in response to resource availability. Such a "phalanx" lifeform (Lovett-Doust 1981) may allow *Tiarella* to compete with other herbs as resources become available in gaps. *Clintonia borealis*, for example, prevents establishment of other herbs by keeping stems close together (Pitelka and Ashman 1985). *Tiarella*'s passively-dispersed seeds (van der Pjil 1969) also would not be likely to travel far.

On the other hand, vertical growth of *Tiarella* stalks (not growth from horizontal growth of rhizomes from individuals established at further distances) may explain why relative increases in cover (from 1990 to 1997) of *Tiarella* increased in gaps as well as why fecundity of *Tiarella* was greater than for *Linnaea*. Rapid growth of *Tiarella* in gaps resulted in tall stalks that produced more and longer branches (and branchlets) that covered more area and supported more capsules (per m^2 cover) than did the shorter shoots of *Linnaea*. Such growth patterns of new individuals may result in increased cover in just a few years. For example, at the end of a decade, Antos and Zobel (1997) found that *Tiarella* populations near Mount St. Helens included a substantial proportion of seed-origin plants probably dispersed from adjacent individuals, not by vegetative spread (Antos and Zobel 1997).

Conditions in the seedling environment may explain current variations in abundance as well as the presence of *Tiarella* seedlings in south positions of gap size 1.0 and centers of gap sizes 0.2, 0.4, and 0.6 and absence in controls and north positions of gaps. Soil moisture in north positions of gaps and controls and light intensities of controls (Figure 2.11) and under dense herb and shrub canopy may have been too low for germination and survival. Tappeiner et al. (1989) found that rates of seed germination and survival of *Tiarella* seedlings increase with light intensity. Hanley et al. (1997) found that soil moisture is associated with increases of biomass of *Tiarella.*

Rates of response of *Linnaea* and *Tiarella* to gaps measured in this study generally corresponded to rates of response to other types of disturbance. After burial by 5 to 20 cm of volcanic tephra, for example, *Linnaea* produced extensive stolons that elongated rapidly and branched frequently unless they were buried (Antos and Zobel 1984b). *Tiarella*'s short rhizomes abruptly turned up and then elongated rapidly. Internodes that were usually 0.5 cm elongated to over 4 cm.

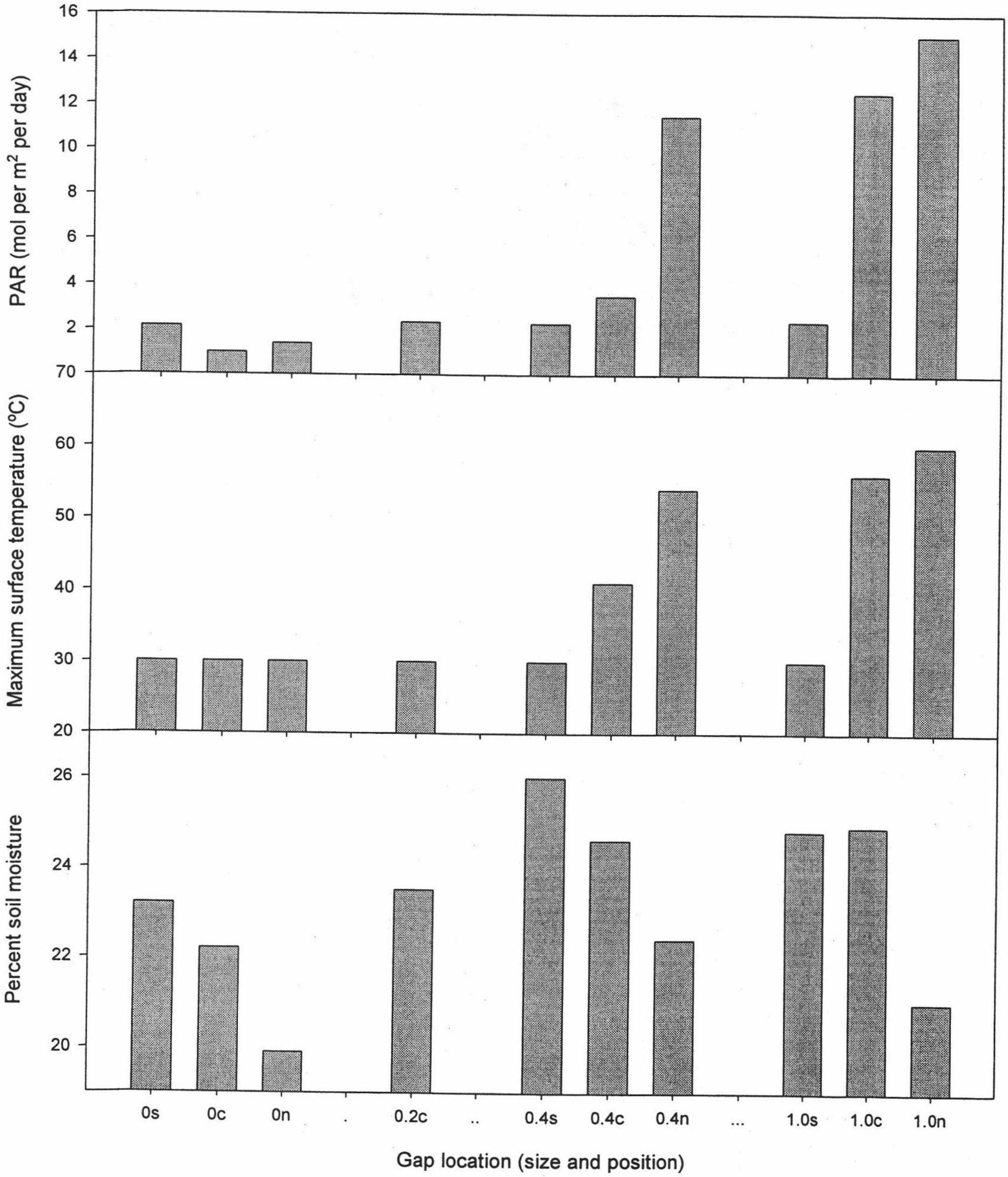


Figure 2.11. Averaged conditions (percent soil moisture, maximum soil surface temperature and photosynthetic active radiation (PAR)* in standardized mineral soil plots in August (Gray 1995). PAR, measured with photo fluence rates between 400nm and 700nm, is expressed in mol photons per m^2 per day.

Both species responded somewhat to gap size. Fecundity was greatest in gap size 0.4 but flowers were nearly absent in gap size 0.2 for *Linnaea* probably because light and thus temperatures of the larger gap size may be required for flower and seed production by *Linnaea*. In larger gaps, some of this heat may be dissipated by wind (Smith 1986). Smaller gaps may not produce contrasting conditions that induce plant response. For example, Wijesinghe and Hutchings (1999) found that root density increased with gap sizes because larger areas with contrasting conditions allowed the plant to "sense" increased nutrient availability.

Fecundity of *Tiarella* increased in gap size 0.2, then increased sequentially with gap size but declined somewhat in gap size 1.0. This trend may have occurred because soil moisture, not light, was significantly associated with fecundity of *Tiarella* and because soil moisture is low in the north portions of gap size 1.0 (Figure 2.11). Soil moisture may be low, even under coarse woody debris in exposed portions of large gaps (Gray 1995).

Variation in *Tiarella*'s fecundity among replicates of the largest gap sizes may also be explained by variations in temperatures among replicates that induce moisture stress in leaves. Maximum temperatures of gaps increase with size (Gray 1995) because more of the forest floor is exposed to direct light than in smaller gaps. Variations in topography and microsites affect temperature more than they affect soil moisture. Thus temperatures that are higher on south-facing and convex topography (Larcher 1996) may explain why fecundity for *Tiarella* was much lower in the replicate of gap size 1.0 with convex topography.

Growth for both species increased in gap size 0.2 (compared to controls) but did not vary among gap sizes. Soil moisture increased in small gaps (Figure 2.11) and was associated with growth of *Tiarella* and somewhat associated with growth of *Linnaea*. On the other hand, increases in light (compared to controls) occurred in larger gaps and only increased slightly in small gaps. Thus fecundity of *Linnaea* (which was associated with light) increased in gap size 0.4.

Differential performance of the two species among similar gap size and positions suggests that the two species are adapted differently to available light and soil moisture. My study suggests that fecundity and growth of both species increases with light intensity until high surface temperatures, low soil moisture, or both induce moisture stress. Differences in performance among similar locations for the two species may be explained by different tolerances for moisture stress conferred by morphology and physiology of their leaves, stems, and roots (Chapter 1).

Growth and fecundity may have been more responsive to gap position than to gap size because light, soil moisture, and temperature are more heterogeneous within whole gaps than within portions of gaps (Figure 2.11). Fecundity of *Linnaea* may have been greatest in north positions that experience the longest daily durations of direct light and thus highest maximum temperatures (Gray and Spies 1997) if temperature thresholds are necessary for flower formation and high heat sums are necessary for fruit and seed ripening (Larcher 1996). *Linnaea* may tolerate moisture stress in such sites because of the thick, shiny layers of cuticle on its leaves (Givinish 1987) and because it roots in buried, decayed debris. The low mean fecundity in gap centers might be explained by lower light intensity and temperatures created by dense layers of herbs that colonize moist gap centers but not drier positions at the extreme edges of gaps. Lower maximum temperatures in controls suggest that fecundity found under closed tree canopies in positions bordering the south side of gaps and in controls may also be limited by lower heat sums.

Microsite variation within gaps may contribute to variation in response. Exceptions to these general trends for fecundity of *Linnaea* in central and southern positions occurred where large "rootwads" projected patches of this species at least 2 m above the ground. At such heights direct sunlight would probably persist longer than on the forest floor. Fecundity was also greater in positions north of some gaps that had been enlarged by windfall that exposed the herbs and in natural gaps occurring in some control treatments than in equivalent treatments with denser canopy.

Growth rates for *Linnaea* may have been greatest in south positions of large gaps because maximum temperatures, and thus moisture stress, are lower in the diffuse light characteristic of south positions. Growth rates may have been slightly lower in gap centers (where slimy and rotting stolons were observed) than in south positions because taller herbs (e.g., *Tiarella*) may deplete moisture if they have efficient root systems and light if they cast dense shade in the centers. The lowest growth rates which occurred in northern positions with longer durations of direct light, were probably caused by both moisture stress and translocation of nutrients to flowers and fruit construction (Pitelka and Ashmun 1985). Similar declines in growth rates have been found for *Linnaea* in Sweden above light intensities of *ca* 9 mol per m^2 per day (Eriksson 1988) which are somewhat comparable to the north and center of large gaps and north of gap sizes 0.4 and 0.6 (Figure 2.11). Exceptions to these spatial trends in *Linnaea* growth occurred where stolons were shaded by logs in north positions or rooted in windfall in control treatments. These structures may have reduced moisture stress of leaves and roots, respectively.

Fecundity and growth of *Tiarella* may have been greatest in gap centers, lower in north positions, and lowest on gap borders and in controls because *Tiarella*'s thin, elevated, and somewhat horizontal cordate- to palmate shaped leaves subject the plant to moisture stress in direct light, especially where soil moisture is unavailable (Givinish 1982, 1987). Such architecture also may explain why *Tiarella's* fecundity and growth rates were higher in centers of gap size 0.6 than in any other gap location. Above- and belowground conditions in centers of gap size 0.6 may result in low moisture stress for leaves and roots, which would explain why *Tiarella*'s performance was greatest in this location. Because center positions of gap size 0.6 are shaded by trees on the south border, durations of direct light and thus maximum temperatures are lower in gap size 0.6 than in larger gaps. Soil moisture content may be greater in centers of large gaps than either in north positions of large gaps or where tree roots have recolonized in centers of smaller gaps or on gap edges (Figure 2.11).

Low soil moisture and high maximum temperatures (Figure 2.11) probably explain *Tiarella*'s lower mean performance rates in north positions of large gaps. Moisture stress resulting from depletion of soil moisture by live tree roots may explain *Tiarella*'s low fecundity and growth on gap borders and in controls. Direct light that increases temperatures of *Tiarella*'s thin, deciduous leaves explain fecundity and growth rates being lower in border positions north of gaps than in more shaded south border plots.

Greater rates of fecundity and growth occurred where *Tiarella* was established under logs in north positions and in small natural gaps in controls. Lower rates of fecundity and growth may have occurred in the center of one replicate of gap size 0.4 because it was really a 0.5 from logging and it thus exposed the leaves of individuals in gap centers to direct sunlight. Evapotranspiration induced by the heat associated with direct light may not have been offset by soil moisture if tree roots recolonized the center position and depleted moisture. On the other hand, soil moisture available in root gaps of larger canopy gaps may compensate for moisture stress on leaves.

2.4.2 Effects of structural heterogeneity on performance among gap size and position

Amounts of light (and temperatures) are predictable in gaps of different sizes with equivalent geometry and suntracks (Canham et al. 1990). The length of exposure (total daily PPFD) also varies predictably among positions. Changes in temperature and light along gradients of slope and aspect are also predictable (Larcher 1996). However, these predicted patterns are altered by variations in gap size, internal structure (e.g. shrubs and debris) and topography among replicates, and these variations explain why plant response to gap size varied among replicate treatments.

The heterogeneous, patchy distribution of both of herbs and fallen trees within gaps may also explain variations of response to both gap size and gap position. The naturally skewed (mean > median) size and age distributions of *Linnaea* and *Tiarella* (Antos and Zobel 1984a) and trees (Harmon et al. 1986) result in only a few large or old individuals of each lifeform being present. Seedlings and young (but not old) ramets of *Linnaea* and *Tiarella* are rooted near the soil surface (Antos and Zobel 1984a), where low soil moisture (A.N. Gray, pers. comm., 1999) may subject the plants to moisture stress. Older ramets rooted at depths with more soil moisture may become patchy because they persist only (1) where roots penetrate logs that have been buried long enough to decay to stages that retain soil moisture and (2) where leaves will be shaded by large fallen trees before desiccation. Effects of gap size on growth rate of seedlings may have been more predictable for Gray and Spies (1997) because both seedbeds and coarse woody debris were located in equivalent areas among replicate treatments.

2.4.3 Gap dynamics

Growth and fecundity measured during the time of this study will change because canopy and root gaps are dynamic structures. Year-to-year and site-to-site variability in seed production and demography of understory occur as canopy gaps open, enlarge, and close (Valverde et al. 1998; Bierzychudek 1982). *Tiarella* and, to a lesser degree, *Linnaea* apparently can persist for years under closed canopy at low light and soil moisture. Disturbances that remove taller herbs, shrubs and tree canopy may favor vegetative reproduction of *Linnaea* (Sobey et al. 1977) as they do other species with rapid vegetative growth rates (Denslow 1985). Formation of gaps that increase soil moisture and light may result in rapid increases in fecundity of established *Tiarella*. Delays before such changes in growth and fecundity occur and durations of each response will depend on the flexibility of species response (Bazazz 1996). Growth and branching rates of *Linnaea*'s stolons may have immediately increased in frequency and extent of growth in unoccupied space of new gaps compared to the low growth and branching rates of *Tiarella's* rhizomes. Rates of *Tiarella*'s fecundity and vertical growth in gaps may eventually produce dense cover that reduce growth rates of *Linnaea*'s stolons.

Although both species are found in old growth forests, each may respond to gaps more rapidly than *Trillium* (Chapter 3). Resource levels within gaps may continue to result in greater abundance of both *Linnaea* and *Tiarella* than *Trillium* within gaps. For example, rapid growth of numerous, branching shoot structures of *Tiarella* conferred immediate support of hundreds of seeds per m^2 plant cover within gaps. On the other hand, from maximum to minimum, *Trillium*'s seed production varied by about one hundred seeds per plant (2 per m^2 plant cover) because each rhizome generally produced one unbranching stem that only supported one capsules and maximums for *Trillium* generally on borders of gaps.

Maximum horizontal growth (cm per growing season) were clearly greater for *Linnaea* than maximum additional length of rhizomes documented for *Tiarella* and *Trillium*. Average maximum growth of *Linnaea* stolons of 35 cm reached more than 60 cm in length per season for some individuals, far exceeding the increases of less than 1 cm per year per *Trillium* rhizome or even the maximum rates of 4 cm per yr for *Tiarella* rhizomes. In addition, *Linnaea* stolons (unlike *Tiarella*'s rhizomes) branch frequently (Antos and Zobel 1984a) but there was no evidence of branches on any *Trillium* rhizome in this study.

Observations of *Linnaea* and *Tiarella* in 1998 suggest that in future years, both species may persist in gap sizes 0.2 and 0.4 (which are more common in old growth forests than larger gaps) because of the absence of taller herb and shrubs such as *Senecio, Circium*, and other wind-dispersed species that were found in larger gaps, according to data collected by A.N. Gray and T. A. Spies. At the time of this study, *Tiarella* was almost completely covered by shrubs such as *Berberis* spp. and a variety of early successional herbs in some areas of center portions of gap size 1.0 and no seedlings were observed under the dense foliage. In 1997 *Linnaea* did not flower or fruit, and growth rates were lower under taller herbs in gap sizes 0.6 and 1.0 as observed in other studies (Antos and Zobel 1984a).

2.4.4 Limitations of study

This study only measured growth and fecundity over 2 yrs and changes in frequency and cover before and 8 yrs after treatment. Long-term calculations of fecundity per area would integrate effects of growth and fecundity among gap sizes and positions. Long-term effects of competition from other species of understory herbs and creation of new microsites may produce different patterns of performance.

Comparisons of species performance within and bordering large gaps demonstrated gap effect and gap size more clearly than comparisons of control and gap treatments because of additional degrees of freedom in statistical calculations. Additional replication would have increased statistical power of tests of gap size, but to create more than two replicates for each gap size would have required logging additional acres of old forests. To rigorously test the effects of gap size alone on herbs, field experiments would need to control locations of plants, coarse woody debris, root gaps and seepages, height and density of adjacent canopy, and topography.

2.5 Conclusions

This study supports the hypotheses that fecundity and growth of *Linnaea* and *Tiarella* will increase within forest canopy gaps and that their performance will vary somewhat with gap size but especially along gradients of gap position and resources. Small gaps are important for fecundity of *Tiarella* but not *Linnaea*. Growth of both species increases in small gaps. On the other hand, differences in the effects among larger gap sizes (within the range measured in this study) on species performance can be overridden when plants happen to be located where light, temperature or soil moisture levels are altered by variations in the topography, canopy and internal structure (shrubs and woody debris).

Linnaea and *Tiarella* respond to the positions within forest canopy gaps in spite of microsite variability. Both species increase rates of their major mode of reproduction within gaps but not on gap borders. Fecundity of *Tiarella* is greatest in southern locations while fecundity of *Linnaea* is greatest in northern positions in gaps. Within gaps, growth rates for *Tiarella* are lowest in and seedlings are absent from northern positions.

Although effects are light and soil moisture on species performance are difficult to separate out because of their similar patterns among treatments, some patterns did emerge. Fecundity and growth of *Tiarella* are most affected by soil moisture. Fecundity of *Linnaea* is affected by light. Effects of soil moisture and light in center positions will vary with gap size unless overridden by structural heterogeneity.

Patterns of fecundity and growth (which include changes of frequency and cover) suggest that *Linnaea* can spread quickly into unoccupied space in gaps and that *Tiarella* rapidly increases cover in gaps. Maximum increases in stolon length (per season) observed in unoccupied locations of gaps for *Linnaea* may partially explain why relative increases in frequency 7 yr after gap creation are greater for *Linnaea* than for *Tiarella*. Rapid increases in stalk height result in greater fecundity in gaps for *Tiarella* than for *Linnaea*. The rates and locations of performance of these two species do not represent behavior of forest herbs (e.g., *Trillium*) with lower potential rates of growth and seed production that increase on gap borders and in root gaps under dense canopy but not within gaps.

In conclusion, gaps are important for growth and fecundity of both *Linnaea* and *Tiarella*.

CHAPTER 3: FECUNDITY, SIZE, AND GROWTH OF *TRILLIUM OVATUM* PURSH. ALONG GRADIENTS OF LIGHT, SOIL MOISTURE, AND TIME IN DOUGLAS-FIR FOREST CANOPY GAPS

3.1 Introduction

Forest succession and disturbance in the mid-elevation zone on the west slope of the central Cascade Mountain Range of Oregon often leads to a mix of dense, shade-tolerant western hemlock and -intolerant Douglas-fir (Franklin and Dyrness 1988; Stewart 1986). Wind and wildfire, insect and fungal attacks have historically produced openings in these forests ranging from 0.01 ha to over 100,000 ha. Smaller gaps (0.1 to1 ha) are a distinctive feature of mid- to late-successional forests. Canopy gaps created by the deaths of two or more large trees in old stands can persist for many decades. By contrast, because of rapidly expanding tree canopies, gaps of one or two trees in young stands are much more ephemeral (Spies et al. 1990).

Gaps can control the environment and resource patterns that understory plants experience. According to the gap-phase regeneration paradigm (Hubbell and Foster 1986), above- and belowground resource and microsite availability will be greater in canopy gaps until new trees replace the fallen ones. Canopy gaps increase light intensity and the amount of precipitation that reaches the forest floor (Canham et al. 1990; Gray and Spies 1996, 1997). Soil and air temperatures near the ground may consequently be higher and humidity may be lower in gaps than in surrounding forests (Chen et al. 1993; Runkle 1985; Hubbell and Foster 1986). Soil moisture can also be higher in canopy gaps where root density and transpiration rates are low (Gray 1995; Toumey and Kienholz 1931).

Microclimatic and resource characteristics vary by gap size, shape, and orientation; by slope and height of surrounding vegetation; and by position within gaps (Pickett and by slope and height of surrounding vegetation; and by position within gaps (Pickett and White 1985). For example, temperatures, light intensity, and soil moisture are higher in large canopy gaps than in smaller gaps (Gray and Spies 1996, 1997). In the northern hemisphere, northern positions within gaps receive more direct light and reach higher maximum temperatures than southern positions (Canham et al. 1990; Van Pelt et al. 1996). Soil moisture is generally greatest in gap centers (Gray and Spies 1996).

Shrubs, fallen trees, and pit and mound topography create additional microsites and resource variations within gaps (Lyford and MacClean 1968, Thompson 1985). Soil moisture and nutrients can be retained where fallen trees provide shade, store water, and trap organic debris. Root upheaval in gaps redistributes nutrients to the ground layer where newly exposed mineral soil provides substrates for root growth and germination of seeds (Harmon et al. 1986; Beaty 1984).

The timing and spatial distribution of canopy tree death (e.g. the frequency and size of canopy gaps) may explain variations in the distribution and performance of understory species (Pickett et al. 1985). Year-to-year and site-to-site variability in seed production of understory herbs, for example, may depend on location of gaps (Bierzychudek 1982). Frequently or recently disturbed sites are dominated by species with rapid vegetative spread but lack geophytes (species with persistent buds buried to 2-3 cm) (McIntyre et al. 1995; Denslow 1985). Slowly dispersed species are last to colonize gap centers (Kotanan 1997).

The relatively high amounts of direct light in forest canopy gaps (Canham et al. 1990; Gray and Spies 1996), especially sunflecks (Chadzon and Pearcy 1991), can increase rates of photosynthesis, growth, and flower and seed production for even the most shade-tolerant understory herbs. Light in canopy gaps created by the loss of even a single tree may increase flowering rates of *Erythronium* in eastern deciduous forests (Collins and Pickett 1988). Elevated temperatures near the ground and lower humidity in gaps during the day (Chen et al. 1993; Runkle 1985; Hubbell and Foster 1986) contribute to increased transpiration rates for herbs in gaps. Intense heat in gaps elevates evaporative loads (Shultz and Adams 1995) and induces moisture stress, especially for species with wide leaves (Waring and Schlesinger 1985).

Increased availability of soil moisture in gaps due to lower tree root density may also increase growth rates, fecundity, and abundance of understory species. Low soil moisture near the soil surface (Gray and Spies 1999) may otherwise expose young and shallow-rooted plants to moisture stress. The abundance of several species of forest herbs increased in plots where tree roots were experimentally severed (Toumey and Kienholz 1931). Growth rates of tree seedlings increase with soil moisture (Gray and Spies 1996), and moisture will also increase survival of seedlings that would otherwise die in low light (Aztet et al. 1972; Fisher et al. 1991). For instance, *Streptopus roseus* is most abundant in accumulations of moist organic debris (Antos 1988), probably because the roots of this species never reach depths where soil moisture is greater and less variable. As long as decayed logs, litter, and humus remain in contact with moist soil, they may keep roots moist (Harmon et al. 1986).

Some late-successional forest herbs may be less common than early successional species because they have low rates of fecundity, growth, dispersal, germination, and architectural or physiological flexibility (Primack and Miao 1992; Bierzychudek 1982). However, low allocation of resources to reproductive and growth functions enable shade-tolerant species to conserve resources and thus persist even where light, water, and other resources remain relatively unavailable (Gadgil and Solbrig 1972; Grime 1979). For example, allocation of limited photosynthates to a few but large and heavy seeds provides resources for germination and growth in nutrient-depleted, shady sites and for penetrating leaf litter that tends to accumulate under the forest canopy (Tilman 1988; Sydes and Grime 1982). Resource allocations to non-photosynthetic mechanical tissues that support large, wide blades confer persistence in shade (Givinish 1982). Allocations to tissue density of stems may confer longevity (Ryser 1996). Continuation of low growth rates in spite of sudden resource increases prevents development of large structures that cannot be sustained when conditions deteriorate (Bazzaz 1996).

The goal of this study was to explore how forest gaps and variation in resource levels in old-growth forests affect performance and abundance of *Trillium ovatum* Pursh., a shade-tolerant forest herb. Resources made available by gaps in the forest canopy and root gaps may aid growth of shade-tolerant herbs such as *Trillium* to sizes that increase performance (rates of seed production and seedling survival) of cohorts. On the other hand, growth and fecundity may decrease in extreme levels of environmental factors in large gaps. The objectives of this study were to compare rates of seed production and growth of *Trillium* 1) in locations within and bordering canopy gaps of different sizes and under forest canopy, 2) along resource gradients and 3) in relation to plant age and size of *Trillium*.

Trillium ovatum Pursh. is a shade-tolerant herb that occurs at low to middle elevations in the West, ranging north to British Columbia, south to California, and east to Colorado (Hitchcock and Cronquist 1973). It occurs frequently but at much lower relative cover than compared with other forest herbs in all age classes of the *Tsuga heterophylla* Zone of the western Cascades (Franklin and Dyrness 1988; Spies 1991). In old redwood forests, *Trillium* and other ant-dispersed herbs account for 50% of the sparse herb layer (Mesler and Lu 1983). Habitats range from shaded to open areas on stream banks and in moist to wet woods that become "boggy" in spring (Hitchcock and Cronquist 1973). *Trillium* and other species with similar leaf architecture are associated with partial shade (Givinish 1987) and are more frequent in stands that were never clearcut (Bailey et al. 1998).

I hypothesized that seed production, growth, and recruitment of *Trillium* would increase in response to gaps in the forest canopy. I also hypothesized that such increases would be greater in intermediate light and soil moisture than in intense or low light where soil moisture is low. Finally, I hypothesized that plant characteristics such as size of rhizomes and leaves and age would affect rates of flower and seed production.

Most field studies of understory herbs have compared abundances of herbs among disturbance regimes, but have not studied their performance in terms of growth and fecundity. Although average and extreme growth rates and fecundity have been measured for some species of herbs (e.g., Antos and Zobel 1984), these measurements have rarely been taken in conjunction with measurements of resources (but see Eriksson 1988; Shultz and Adams 1995; Pitelka et al. 1980; Pfitsch and Pearcy 1992) or gaps (Collins et al. 1985, 1988). Consequently, this study is the first to relate fecundity and growth of herbs to plant characteristics (e.g., age and size) and the heterogeneity of resources and structure that is characteristic of late-successional forests. Use of experimentally created gaps allows more control of gap size and shape than in naturally occurring gaps and provides a known history of plant abundance, light and soil moisture, disturbance and other factors in forests that may affect species performance.

3.2 Methods

3.2.1 Site description

This study was conducted in the H.J. Andrews Experimental Forest in the Willamette National Forest. The site lies at 900 m in the *Tsuga heterophylla* zone (Franklin and Dyrness 1988) on the west slo7pe of the central Cascade Mountain Range of Oregon. The canopy is dominated by multiple layers of 500-year-old *Pseudotsuga menziesii* and a dense subcanopy of *Tsuga heterophylla.* A moderate-severity fire burned this stand in 1886 (Teensma 1987). Understory was sparse before canopy gaps were created in 1990. Soil is a deep (depth to C horizon 1 m), well-drained, dark brown gravelly loam classified as a loamy skeletal, mixed, frigid Fluventic Dystrochrept (Gray 1995).

The climatic regime, recorded by a nearby meteorological station at a similar elevation, includes summer drought and moderately high temperatures from June to September, a pattern characteristic of the Pacific Northwest (Franklin and Waring 1980). Mean (15-year) annual precipitation is 224 cm, with only 8% of annual precipitation falling between June and September. Winter snowpacks at 500-1000 m in the Cascades only temporarily accumulate to depths exceeding 1 m. Annual mean, minimum, and maximum air temperatures were 8.6, -3.1, and 27.0 deg C during the 2 yr of my study.

I conducted this study in a previously established gap experiment to examine the response of *Trillium* to resource heterogeneity. Experimental gaps were created in the fall of 1990 (Gray and Spies 1996) in areas with relatively dense canopies and slopes less than 20%. Four sizes of circular gaps were created, with two replicates of each size. Gap diameter measured between tree crown edges was scaled to the average height (50 m) of dominant trees.

The ratios of gap diameter to tree height for the four gap sizes were 0.2, 0.4, 0.6, and 1.0. Two control plots equal in area to the 1.0 gap size were also established under dense canopy and included few or no natural gaps in 1990. Gaps were created by cutting all trees over 2 m tall (except for *Acer circinatum*) within the gap perimeter. Trees were stage-felled into the northeast or northwest quadrants. Skidders that were parked outside the gaps winched fallen tree boles out from the gaps with cables. Branches and foliage were trimmed and removed from the felled trees.

I also made observations in a trench plot experiment that was established by A. N. Gray and T. A. Spies in 1990. In this experiment, all roots were severed and soil was cut down to 1 m in two replicate 3 x 3 m plots. To prevent reinvasion of roots, black Mylar plastic and stainless steel mesh screen liners were installed on sideslope sides of the plots before excavated soil was returned to the trench plots. One control of equal size was established for each replicate. Four treatments each were randomly located in a 1 ha stand under dense canopy and in gap equivalent to gap size *ca* 0.4.

After an initial survey of the entire experimental study area, I concluded that the density and sizes of *Trillium* within experimental canopy gaps were too low for study. I therefore expanded the study area to include areas outside of the gap and control treatments so that I could study a greater number and size range of individuals at wider gradients of light and soil moisture than occurred in the gaps. Two studies of *Trillium* were conducted. In the first study, I compared mean and maximum rates of fecundity and leaf area and seedling density in 1997 among equally-sized positions within and adjacent to each gap size and control treatment. In the second study, I compared seed production, growth and size of vegetative plant parts, and age along resource gradients within the canopy and trench plot experiments and in various microsites at greater distances from the treatments in the surrounding stand during 1998.

3.2.2 Study #1. Spatial patterns of performance in relation to gap size and position

3.2.2.1 Mean and maximum seed production and leaf area

Mean rates of seed production and leaf area were calculated for areas within and immediately bordering control treatments and gap sizes 0.2, 0.6, and 1.0 to determine whether and where canopy and gaps in the forest canopy might affect *Trillium*. The maximum rate of seed production and leaf area per individual were also compared among these locations to determine whether any treatment location consistently limited rates of seed production or leaf size as well as to determine whether maximum performance occurs in similar locations. To maintain an equivalent probability of finding large, productive individuals among experimental units, it was necessary to establish positions of equal size within and surrounding each gap size and control and then to analyze each gap size separately.

For each treatment and control, four positions were designated as experimental units (Figure 3.1). Because of *Trillium*'s patchy distribution, the sizes of these sampling areas were larger than (but included) the areas where growth and fecundity were measured for *Linnaea* and *Tiarella* (Chapter 2). Two positions (north and south) were established within the gaps (defined as the area between crowns of standing trees where the canopy had been experimentally removed (Runkle 1992)) and control treatments. Border positions of equivalent area were established 0.5 radius north and south of each gap and control treatment. The position north of each gap replicate was established in order to evaluate performance in the direct light that penetrated areas north of crown edges. The south border position was established under forest canopy south of each gap treatment. Equivalent areas were also sampled in each control treatment.

All *Trillium* that were present within each location (treatment and position), a total of 185, were flagged and numbered in May 1997. Individuals and position were then mapped using surveyed grid points (posted at 2-m and 4-m intervals along central and secondary axes within and a few meters north and south of each treatment). The number of seeds and leaf area of all intact individuals (except seedlings) were measured in June 1997 with methods described in section 3.2.3.3. When *Trillium* occurred in patches of 10 or more similar-sized individuals, leaf area was estimated from measurements of one individual selected with a random numbers table. Mean and maximum values of seed production and leaf area per individual were calculated for each gap location.

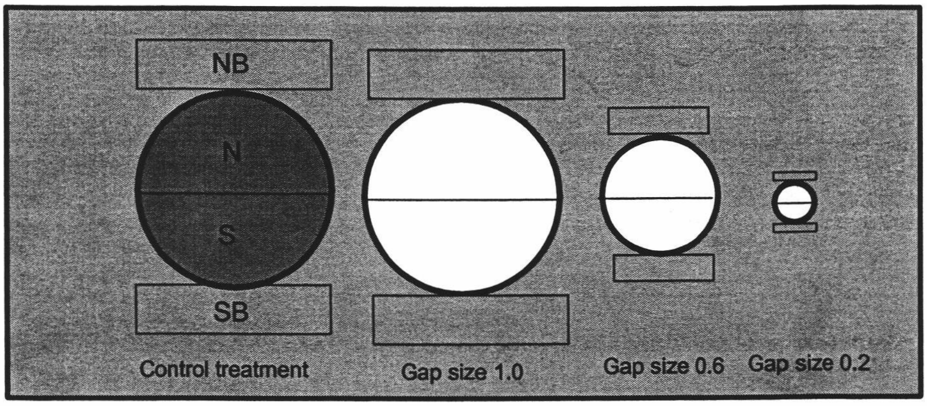


Figure 3.1 Experimental design for measurements of mean and maximum seed production and leaf area among controls and gap sizes 0.2, 0.6, and 1.0 for *Trillium*. Each position is equal to half of the treatment area (981.25 m^2 for gap size 1.0 and controls, 353.25 m^2 for gap size 0.6, and 39.25 m^2 for gap size 0.2). Border positions extend 1/2 of treatment radius north and south of each treatment.

3.2.2.2 Seedling density

All positions for each gap size and control treatments were systematically surveyed for seedlings during a period from May to July 1997. The oblong leaf shape was used to identify seedlings (Figure 3.2). Seedling density was calculated as the number of individuals per m^2 for each position in each gap and control treatment. The area of each position in this analysis varied by gap size (Figure 3.3).

Figure 3.2. Photograph of *Trillium* seedlings. Length of cotyledons in this photograph range from *ca* 2 to 3 cm.

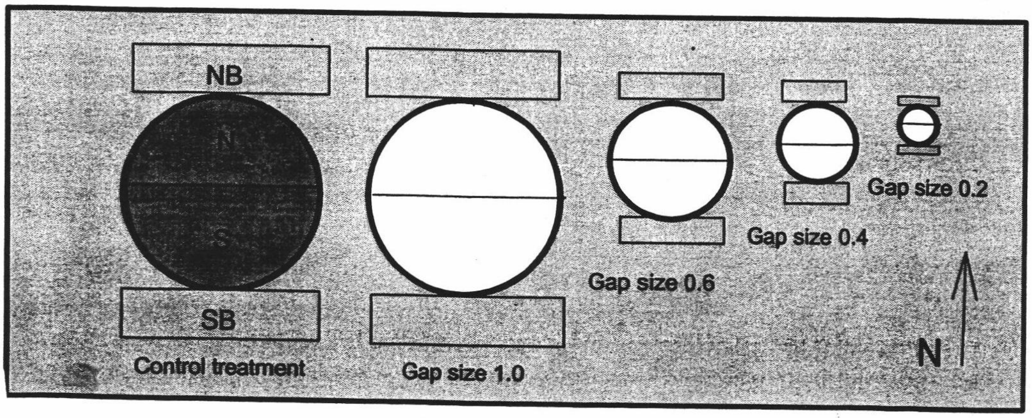


Figure 3.3 Experimental design for comparisons of seedling density among all gap sizes and positions for *Trillium*. Each position is equal to half of the treatment area (981.25 m^2 for gap size 1.0 and controls, 353.25 m^2 for gap size 0.6, 157.0 m^2 for gap size 0.4 and 39.25 m^2 for gap size 0.2. Border positions extend 1/2 of treatment radius north and south of each treatment.

3.2.3 Study #2: Performance in relation to resources, plant age and plant size

3.2.3.1 Experimental design

Because the ranges of light intensity, soil moisture, and size and density of *Trillium* were low within gaps and controls, this study also included additional types of microsites in the area immediately surrounding the experiments. In 1998 I selected 101 individuals from 75 sites from a range of canopy density for the full range of light and soil moisture conditions in this stand. These sites include all (1) canopy gap treatments, (2) experimental trench plots and (3) control treatments for both canopy and root gap experiments. Sites within experimental gaps were either exposed to direct light or shaded by topography, shrubs, or fallen trees. I also located *Trillium* that were established in drier soil and that were partially shaded by forest canopy and woody debris in sites north of each experimental gap. I next surveyed the area immediately surrounding each control treatment and located all *Trillium* in the nearest (1) seepages and windthrow pits under dense canopy and (2) canopy gaps that remain open because of topography.

In 1997 and 1998 all *Trillium* within 0.5 m of environmental measurements (described in section 3.2.3.2) taken at these 75 sites were flagged, numbered, mapped, and measured for leaf area and seed production. All 101 individuals present in 1998 were excavated for measurements of various plant parts as described in section 3.2.3.3. Individuals present and intact in both 1997 and 1998 (59) were used to analyze relative growth rates and to compare leaf area and seed production for the two years.

3.2.3.2 Environmental measurements

At each of the 75 sites, mean photon flux density during the growing season was estimated from hemispherical photographs taken directly above each plant but below the heights of sub-shrubs, brush piles, and fallen trees (Easter and Spies 1994). These photographs were taken on cloudy days or early in the morning during June 1998, to ensure greatest contrast between foliage and sky. To take the photographs a 35-mm camera was aligned on a tripod so that the image would have true north at the top (Pfitsch and Pearcy 1992). Black-and-white film and a red filter were used to maximize contrast between canopy and sky. The resulting images were digitized from negatives to estimate diffuse and direct components of daily photosynthetic photon flux density (PPFD) in mol per m^2 per day. Total PPFD (Qt) was calculated with dry-season equations using Excel as

$$Qt = [(6.42 \times 10^6) \text{ ISF}] + [(1.97 \times 10^7) \text{ DSFm}]$$

where ISF represents the indirect site factor and DSF is the direct site factor (Rich 1989).

In August 1998 volumetric soil water content was estimated with time domain reflectometry (TDR) (Gray and Spies 1995). At 61 sites, one 29-cm probe was inserted at a 45 degree angle to a depth of 15 cm using preformed blocks as a guide. Mean percent soil moisture at 0 to 15 cm was computed with regressions that were developed for soils in the H.J. Andrews stands:

$$\text{Soil moisture} = \{-3.1952 + 10.0463 * [\text{TDRDIST}/(0.99 * 0.29 \text{ cm})]\}$$

where TDRDIST is the time required for an electromagnetic wave to pass between a pair of metal probes in the soil (Gray and Spies 1995).

As the rhizomes were excavated, the substrate immediately surrounding each was coded as (1) mineral soil, (2) coarse woody debris, (3) rock, or (4) humus. Depth of overlying litter was measured with calipers from the ground surface to the mineral soil in the hole.

3.2.3.3 Plant measurements

Aboveground measurements of 101 individuals in 1998 included flower presence, seeds per capsule, and leaf width, length, and height. Plants missing flowers or capsules were distinguished from individuals that had not produced flowers by the presence of severed peduncles where flowers had been. The maximum width and length of the middle leaf and leaf height were measured with calipers after capsules formed and growth stopped in early June. Capsules were collected in paper bags in late June before dehiscence, which was observed when air temperatures exceeded *ca* 25 deg-C in exposed areas. The number of seeds per capsule was counted within 24 hours.

I developed equations to predict leaf area from measures of leaf width and length. For the 101 individuals excavated, leaves were grouped into 15 size classes. For one individual randomly selected from each size class, leaf area was measured with an Area Measurement System (Delta-T devices LTD; Cambridge, England) connected to a video camera (Ikegamic, Model no. ITC510). The empirical equation

$$\text{Leaf area (cm}^2) = \text{leaf width} + \text{leaf length}^2 + \text{leaf length}$$

was used to predict total leaf area of individuals with three leaves ($F = 475.437$; $P < 0.0001$, $r^2 = 0.99$, $MSE = 78.99$, $n = 15$) The shape of leaves of seedlings and of single- and two-leafed individuals differed from shapes of leaves of large, three leaved individuals. Therefore their leaf areas were calculated using graph paper for single and two-leafed individuals. Leaf area and seed production were compared for the 59 individuals that were intact in both 1997 and 1998. The relative growth rate of leaves (RGR) was calculated as rings (detected with a dissecting microscope) from the oval initial growth structure (Figures 3.4 and 3.5) out to the base of the petiole (Christian 1961; Jules 1995). Rhizome volume was measured by water displacement in 25-ml flasks after severing all roots. Volumes were recorded within ±0.5 cm^3. To record growth patterns and shapes, plants were subjectively assigned to one of three classes of rhizome growth patterns. Changes in rhizome diameter after gap treatment in 1990 were coded as changes noted at 8 annual rings from the base of each petiole. Changes were evaluated by ocular estimation. Increases were coded as 1 and decreases as -1; 0 was the code for no change (Figure 3.4). Individuals younger than 8 yr were coded as 1. Rhizome depth was measured from the point on each stalk at the mineral soil surface to the lowest point on the bottom of each rhizome.

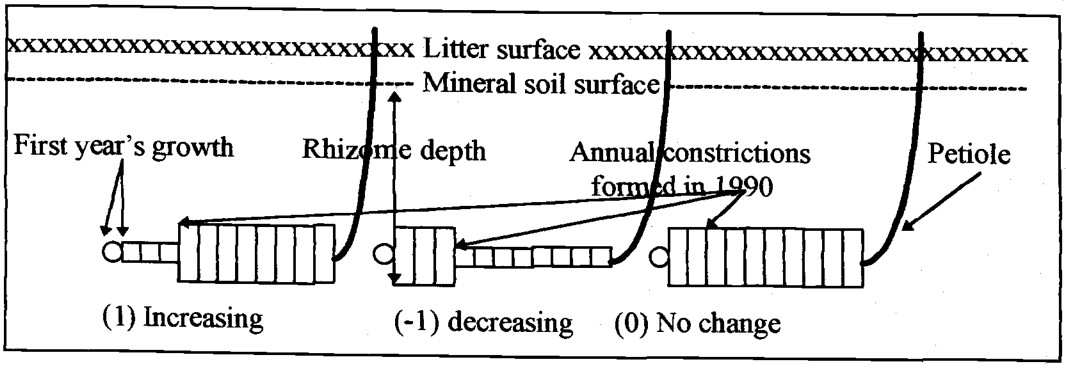
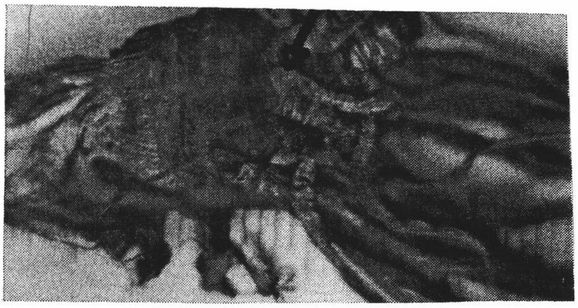
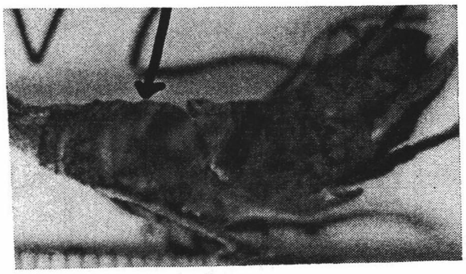


Figure 3.4a. Three categories of rhizome growth.

Increasing diameter (1):



Decreasing diameter (-1):



No change in diameter (0):

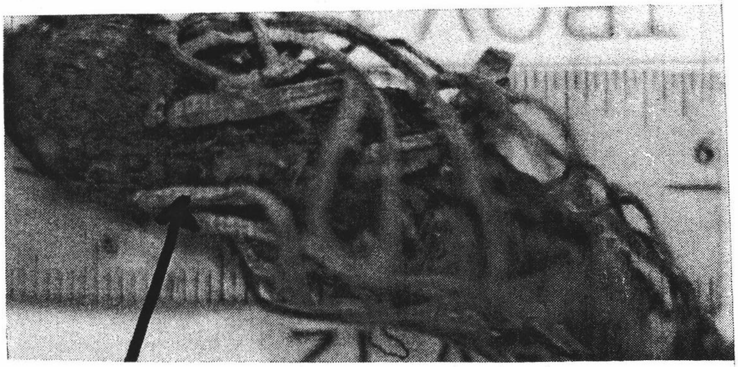


Figure 3.4b. Actual rhizomes excavated with increasing, decreasing and no change in diameter after 1990. Arrows indicate growth in 1990 and lines illustrate where petioles emerged from rhizome. Calipers under rhizome show scale in mm.

3.2.4 Statistical analyses

3.2.4.1 Spatial patterns

Mean and maximum rates of seed production and leaf area for each of the four positions for controls and gap sizes 1.0, 0.6, and 0.2 were calculated using Excel. Split-plot ANOVAs were conducted with SAS 6.10 (SAS Institute Inc. 1987) using the MIXED procedure to analyze effects of these four positions on the maximum leaf size and seed production per plant. Leaf area and seeds per individual were square-root-transformed. The LSMEANS statement in SAS computed means for each gap treatment, position, and interaction. Fisher's Protected Least Significant Differences (FPLSD; Fisher 1966) was conducted to determine whether treatment, position, or interaction of treatment and position had significant effects on performance. Results were considered significant if the probability of a Type I error (α) was less than 0.005.

3.2.4.2 Performance, resources, and age

The effects of resources, age, and size of various plant parts on rates of seed and flower production were analyzed for the dependent variables listed below. Seed production, size and growth rates of leaves and rhizomes were also regressed on the following independent variables (except for themselves):

- leaf area
- relative growth rate of leaves
- rhizome volume
- rhizome depth
- rhizome growth pattern (0, -1, or 1)
- age
- soil moisture
- light intensity
- substrate type
- litter depth.

Stepwise regression analysis with a forward and backward procedure was conducted in SAS 6.10 (SAS Institute Inc. 1987) to select variables to include in each model ($\alpha \leq 0.15$). Flower presence and rhizome growth patterns were analyzed with logistic regression. Linear regressions were conducted for seed production, relative growth rate, leaf area, rhizome volume, and rhizome depth.

The numbers of seeds per individual that flowered in 1998 were square-root-transformed and all values were increased by one to avoid transformation of zero values (flowers without seeds). Leaf area, rhizome volume, and rhizome depth were log-transformed.

3.3 Results

3.3.1 Fecundity, leaf area, and recruitment in relation to gap locations

3.3.1.1 Seed production and leaf area

Mean seed production was lowest in controls and lowere within gaps than on northern borders of gap sizes 0.2 and 0.6. Mean seed production was greater in southern positions than in positions north of gaps gap size 1.0 because of a single productive individual which was under dense hemlock canopy within the gap and because of the presence of of young (thus non-flowering) individuals on gap borders.

Maximum seed production was greater on north borders of all gap sizes than in north or south positions within gaps (Table 3.1). Maximum seed production varied significantly ($F = 6.72$, $P = 0.024$, $df = 6$) with interactions of gap treatment (gap size 1.0 and control) and position, but not with treatment or position.. Among the four positions within and bordering controls and gap size 1.0, maximum seed production differed significantly ($\alpha < 0.005$) from zero in positions north of gap size 1.0 only (Table 3.2) Maximum seed producton was greater and less variable north of gap size 1.0 than in south positions within gap which also had high maximum values (Table 3.1).

Mean leaf area was less variable among treatment locations than fecundity and within gaps, generally decreased with gap size (Table 3.1). Maximum leaf area was greatest north of gaps of all size than in north or south positions within gaps (Table 3.3). Within gaps, mean and maximum leaf area was greater in southern positions than in northern positions of gaps. Among the controls and gap size 1.0, maximum leaf area varied with interactions of gap treatment and position ($F = 4.38$, $P = 0.059$, $df = 6$) but not with treatment or position alone. Maximum leaf area differed significantly significantly ($\alpha < 0.005$) from zero in all locations except north positions of gap size 1.0 and in south positions of control treatments (Table 3.4). Among all eight locations, maximum leaf area was greatest and least variable north of gap size 1.0 (Table 3.3).

3.3.1.2 Seedling density

Only 39 seedlings were found. Most of these seedlings were present on borders of gaps. Two were found within controls near natural gaps (Table 3.5). None were present within the gaps.

3.3.2 Performance in relation to resource gradients, plant size and age

3.3.2.1 Multivariate analysis of resource, plant size and age variables

This section describes a possible sequence of development of *Trillium*'s plant parts based on the results of stepwise logistic (Table 3.6) and linear (Table 3.7) regressions involving seed production, leaf area, rhizome volume and depth, age, and resource variables.

The presence of flowers varied significantly with leaf area ($\chi^2 = 19.98$, $P = 0.0001$, $n = 84$; Table 3.6). Individuals with small leaves did not flower. Rhizome growth (coded as increasing, decreasing, or no change in diameter) varied with light and litter depth ($\chi^2 = 19.42$, $P = 0.0035$, $n = 66$). Thus seedlings and individuals with abrupt increases in rhizome diameter occurred in intermediate light with some litter. Individuals with decreasing rhizome diameters were in found in intense light and in low light. Seedlings were present in low light where litter was at least 4 cm deep, but not in intense light.

A chain of relationships emerged from the stepwise regressions. Seed production per individual increased with leaf area, light, rhizome depth, and rhizome volume ($F_{4,21} = 58.28$, $P = 0.0001$, $MSE = 0.9$, Table 3.7). Leaf area was by far the most important variable in the model. Variation in leaf area in turn was explained by a combination of rhizome volume, rhizome depth, soil moisture, and light ($F_{4,33} = 42.7$, $P = 0.0001$, $MSE = 0.23$). Rhizome volume explained most of the variation in leaf area. Relative growth rates of leaves were partially explained by rhizome volume, light, and soil moisture ($F_{5,34} = 11.68$, $P = 0.0001$, $MSE = 0.07$). Rhizome volume increased with age ($F_{1,67} = 215.70$; $P = 0.0001$, $MSE = 0.95$). Rhizome depth increased with both age and light ($F_{3,74} = 44.79$, $P = 0.0001$, $MSE = 0.21$).

Table 3.1. Mean and maximum number of seeds per individual in four positions of gap and control treatments in 1997 (n=2). Standard errors are in parentheses. Number (no.) of *Trillium* in replicate treatments (rep 1 and 2) are listed for each location.

Gap size	Position	no. *Trillium*		mean	maximum
Control	Within treatments:	rep 1	rep 2		
	north	10	8	0.6 (1.1)	2.5 (0.7)
	south	6	3	0 (0)	0.0 (0.0)
	total	*16*	*11*	*0.4 (0.9)*	*1.5 (2.1)*
	Bordering treatments:				
	north	2	6	0.3 (1.0)	1.5 (2.1)
	south	6	10	6.3 (10.6)	19.0 (21.2)
	total	*8*	*16*	*4.2 (8.9)*	*19.0 (21.2)*
0.2:	Within treatments:				
	north	1	6	4.3 (7.3)	8 (11.3)
	south	1	2	9.7 (12.7)	12 (17.0)
	total	*2*	*8*	*5.9 (8.9)*	*12 (17.0)*
	Bordering treatments:				
	north	1	3	11.3 (22.5)	22.5 (31.82)
	south	2	6	23.8 (34.7)	47.5 (67.2)
	total	*3*	*9*	*19.6 (30.7)*	*47.5 (67.2)*
0.6:	Within treatments:				
	north	1	6	2.3 (4.9)	6.5 (9.2)
	south	1	17	3.6 (7.4)	16 (9.9)
	total	*2*	*23*	*3.2 (6.6)*	*16 (9.9)*
	Bordering treatments:				
	north	1	5	19.7 (19.7)	32 (39.6)
	south	2	11	2.7 (5.7)	42.5 (37.5)
	total	*3*	*16*	*8.1 (14.1)*	*64.5 (6.4)*
1.0:	Within treatments:				
	north	13	7	0.8 (2.4)	7 (4.2)
	south	2	3	15.0 (30.3)	37.5 (44.6)
	total	*15*	*10*	*3.8 (14.1)*	*39.5 (41.7)*
	Bordering treatments:				
	north	9	10	9.1 (21.3)	68 (8.5)
	south	1	17	0.1 (0.32)	0.5 (0.7)
	total	*10*	*27*	*4.7 (15.7)*	*68 (8.5)*

Table 3.2. Least square means of the square root of the maximum fecundity (per individual) in gap and control treatments (n = 2) in 1997. Means marked with an asterisk (*) are significantly greater than zero at the 0.005 level.

Gap size	south border	south	north	north border
Control	3.91 (1.31)	0.00(1.31)	1.57 (1.31)	0.87 (1.31)
1.0	0.50 (1.31)	5.38 (1.31)	2.58 (1.31)	*8.24 (1.31)

Table 3.3. Mean and maximum leaf area per individual in four positions for gap and control treatments in 1997 (n=2). Standard errors are in parentheses. Number (no.) of *Trillium* in replicate treatments (rep 1 and 2) are listed for each location.

Gap size	Position	no. *Trillium*		mean	maximum
Control:	Within treatments:	rep 1	rep 2		
	north	10	8	71.8 (48.2)	154.9 (9.0)
	south	6	1	36.7 (32.4)	45.1 (47.6)
	total	*16*	*9*	*62.0 (46.6)*	*154.9 (9.0)*
	Bordering treatments:				
	north	2	6	54.4 (66.1)	141.4 (89.4)
	south	6	1	143.1 (37.6)	176.0 (54.4)
	total	*8*	*7*	*95.8 (69.9)*	*176.0 (54.4)*
0.2:	Within treatments:				
	north	1	6	54.8 (87.1)	86.1 (63.3)
	south	1	2	87.1 (68.4)	91.2 (96.2)
	total	*2*	*8*	*64.5 (52.1)*	*100.2 (83.3)*
	Bordering treatments:				
	north	1	4	105.6 (122.4)	232.8 (75.2)
	south	2	7	136.9 (109.6)	213.3 (186.3)
	total	*3*	*11*	*125.7(110.6)*	*262.3(117.0)*
0.6:	Within treatments:				
	north	1	6	53.7 (18.4)	62.7 (24.9)
	south	1	16	59.0 (31.9)	113.4 (40.2)
	total	*2*	*22*	*57.4 (28.1)*	*82.6 (3.3)*
	Bordering treatments:				
	north	1	5	124.6 (53.8)	186.5 (9.4)
	south	2	12	75.4 (38.3)	101.6 (31.9)
	total	*3*	*17*	*90.2(48.0)*	*186.5 (9.4)*
1.0:	Within treatments:				
	north	12	7	32.2(21.5)	64.2 (7.3)
	south	2	3	94.6(103.1)	175.5 (143.6)
	total	*14*	*10*	*45.2(53.7)*	*175.5 (143.6)*
	Bordering treatments:				
	north	10	12	95.75 (65.2)	233.31 (64.6)
	south	1	17	40.24 (13.0)	56.8 (35.7)
	total	*11*	*29*	*70.77(56.1)*	*233.31 (64.6)*

Table 3.4. Least square means of the square-root of maximum leaf area per individual (cm^2) in gap and control treatments (n=2) in 1997. Means marked with an asterisk (*) are significantly greater than zero at the 0.005 level.

Gap size	south border	south	north	north border
Control	*13.19 (2.3)	6.13(2.3)	*12.44 (2.3)	*11.01 (2.3)
1.0	7.34 (2.3)	*12.62 (2.3)	8.01 (2.3)	*15.20 (2.3)

Table 3.5. Density (mean and standard error per m^2) and total number of seedlings (no.) in treatment replicates (a and b) in four positions of controls (ctls.) and all gap sizes.

	south border			south			north			north border		
Gap sz.	mean	no.		mean	no.		mean	no.		mean	no.	
		a	b		a	b		a	b		a	b
Ctls	0.002 (0)	2	2	0.0005 (0.0007)	1	0	0 (0)	0	0	0 (0)	0	0
0.2	0.13 (0.14)	1	9	0 (0)	0	0	0 (0)	0	0	0.05 (0.09)	0	5
0.4	0.03 (0.031)	1	8	0 (0)	0	0	0 (0)	0	0	0.01 (0.02)	0	1
0.6	0.017(0.004)	4	1	0 (0)	0	0	0 (0)	0	0	0.002 (0.004)	0	1
1.0	0.0 (0)	0	0	0 (0)	0	0	0 (0)	0	0	0.0004 (0.001)	2	1

Table 3.6. Best variables from stepwise multiple logistic regressions of flower presence and rhizome growth pattern on resources, age and size. Values in parentheses are signs of the regression coefficients.

Dependent variables	Independent variables
Flower presence	leaf area (+)
Rhizome growth pattern	light*light (+), litter depth (+)

Table 3.7 Best variables and coefficients of determination from stepwise multiple regression of fecundity, growth, leaf area and rhizome volume on resources, age and size of other plant parts. Values in parentheses are signs of the regression coefficients and partial R^2s. All regressions are significant at $P < .05$.

Dependent variable	R^2 (adjusted)	Independent variables
Seed production	0.92	leaf area in 1998 (+) (0.83), light (+) (0.04), rhizome depth (+) (0.03), and rhizome volume (+) (0.03)
Leaf area	0.84	rhizome volume (+) (0.69), rhizome depth (+) (0.05), soil moisture (+) (0.03), and light (+) (0.06)
Relative growth rate of leaves	0.69	rhizome volume (+) (0.29), light (+) (0.17), light and soil moisture (+) (0.23), and 1997 leaf area (-) (0.08)
Rhizome volume	0.76	age (+) (0.76)
Rhizome depth	0.65	age (+) (0.63) and light (+) (0.02)

3.3.2.2 Relationships of individual variables and age

This section will illustrate and discuss patterns of plant development over time in relation to individual variables. Measurements were taken from a population of 96 *Trillium* that exhibited a wide range of ages (Figure 3.5). The age distribution of these excavated individuals showed a negative slope after age 25. Most individuals were less than 24 years old. Although at least 45 growth rings were observed for the oldest indiviudals, breakage suggested that some of these *Trillium* could have been older.

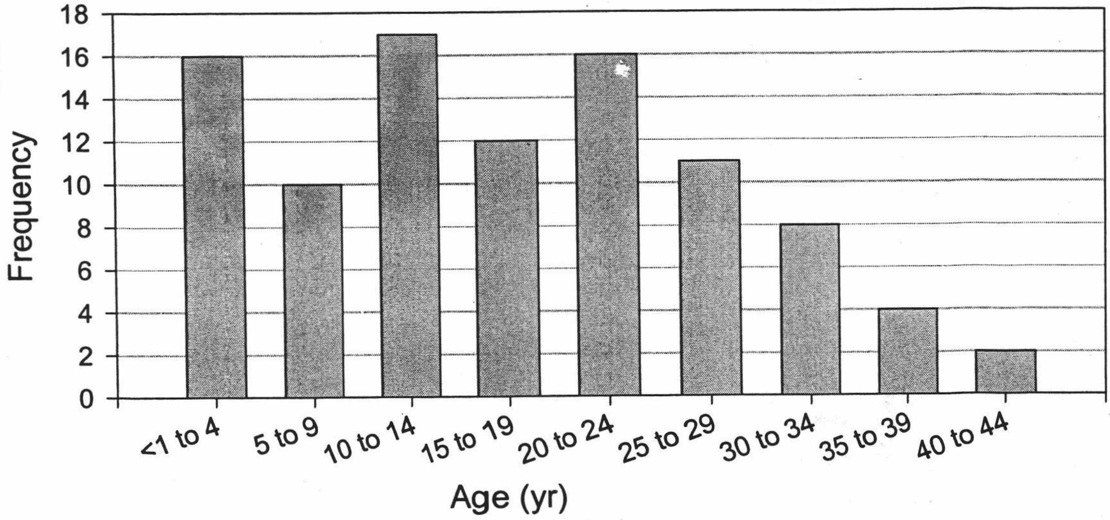


Figure 3.5 Age distribution of 96 *Trillium* individuals excavated from 75 sites in 1998.

Although flower production is most dependent on leaf area (Table 3.7), flower presence increased with age when the variables were individually regressed ($\chi^2 = 22.51$, P = 0.0001). No flowering individuals were less than 12 years old (Figure 3.6). However, among flowering individuals only, seed production was not related to age (F = 2.42, P = 0.1299), in spite of a slight trend of increase with age (Figure 3.7). About ten individuals over 15 yr produced most of the seeds. All individuals over 30 years produced seeds.

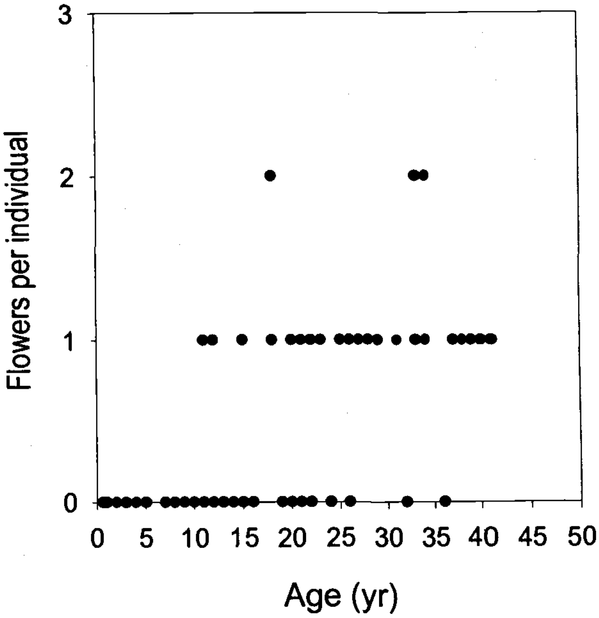


Figure 3.6. Relationship between age and number of flowers per individual (in 1998).

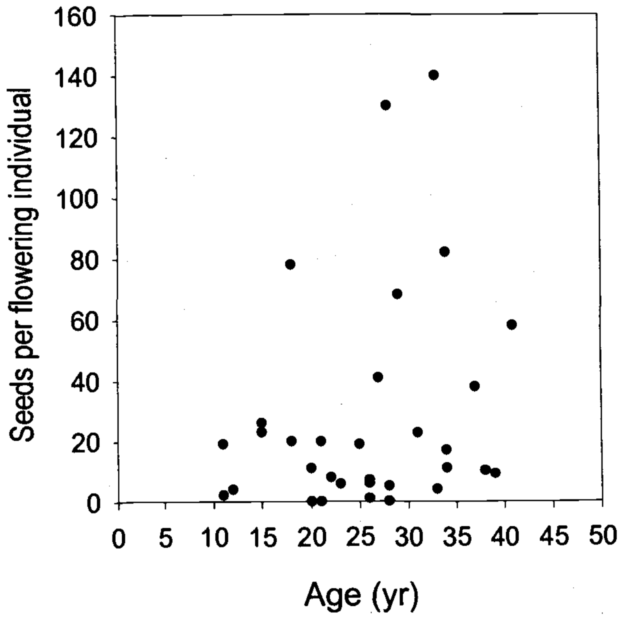


Figure 3.7. Number of seeds per flowering individual of *Trillium* and age.

Leaf area was under 10 cm^2 for individuals younger than 8 years old (Figure 3.8). Leaf area varied widely among older individuals. Most individuals between 30 and 40 years had leaf areas of at least 100 cm^2.

Rhizome volume increased with age (Figure 3.9) after a lag time of about 8 yr. Rhizome depth also increased with age but there was no lag (Figure 3.10).

3.3.2.3 Patterns of fecundity and growth in relation to plant size

Flowering individuals had larger mean leaf areas than did non-flowering individuals (Tables 3.6 and 3.8). No individual with leaf area less than 55 cm^2 flowered, but all individuals larger than 130 cm^2 flowered.

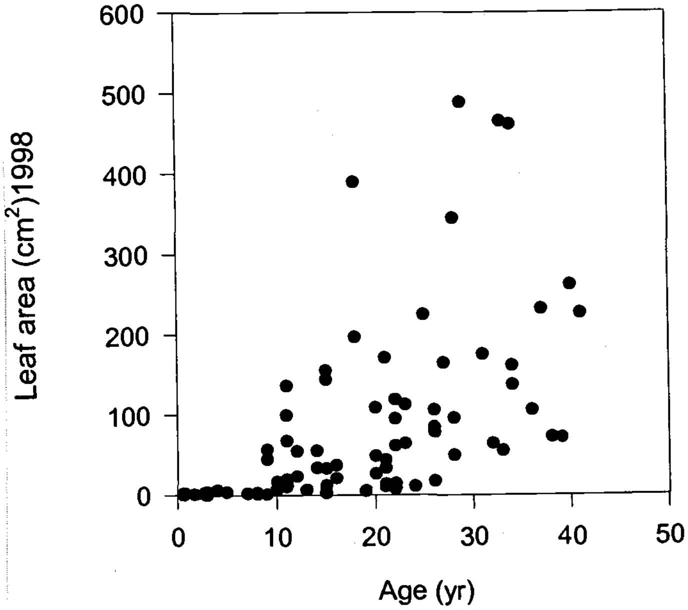


Figure 3.8. Relation between leaf area and age of *Trillium*

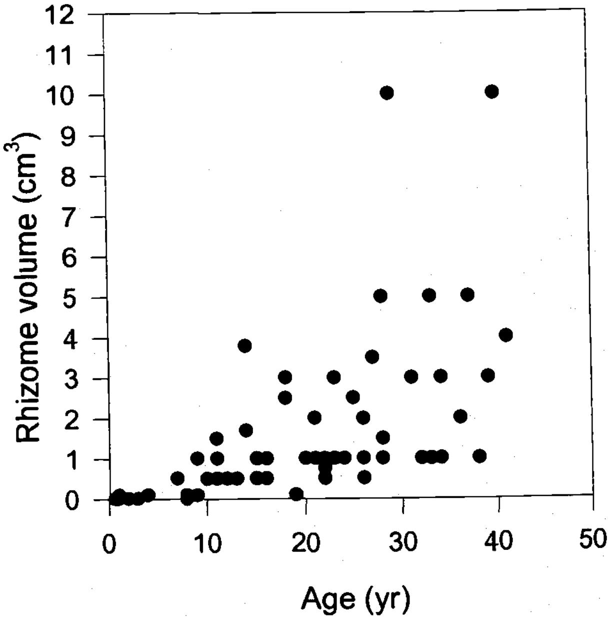


Figure 3.9. Rhizome volume in relation to age.

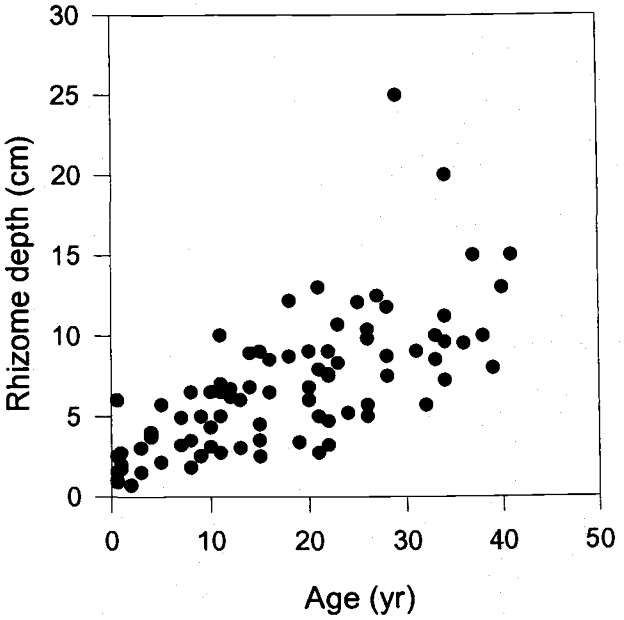


Figure 3.10. Rhizome depth (in mineral soil below the litter layer) in relation to age.

Table 3.8. Mean leaf area (cm^2) of flowering and non-flowering *Trillium*. Standard errors are in parentheses.

Presence of flowers	Leaf area (cm^2)
Non-flowering	18.52 (25.57)
Flowering	157.85 (115.97)

The number of seeds per flowering individual in 1998 was predicted somewhat better by leaf area in 1998 ($F_{1,31} = 98.496$, P = 0.0001, MSE = 0.41, $r^2 = 0.075$) than by leaf area in 1997 ($F_{1,29} = 69.804$, P = 0.0001, MSE = 0.38, $r^2 = 0.70$). Small (10 to 150 cm^2 in leaf area) individuals produced 1 to 20 seeds. Individuals with leaf area larger than 250 cm^2 produced 60 to 120 seeds (Figure 3.11).

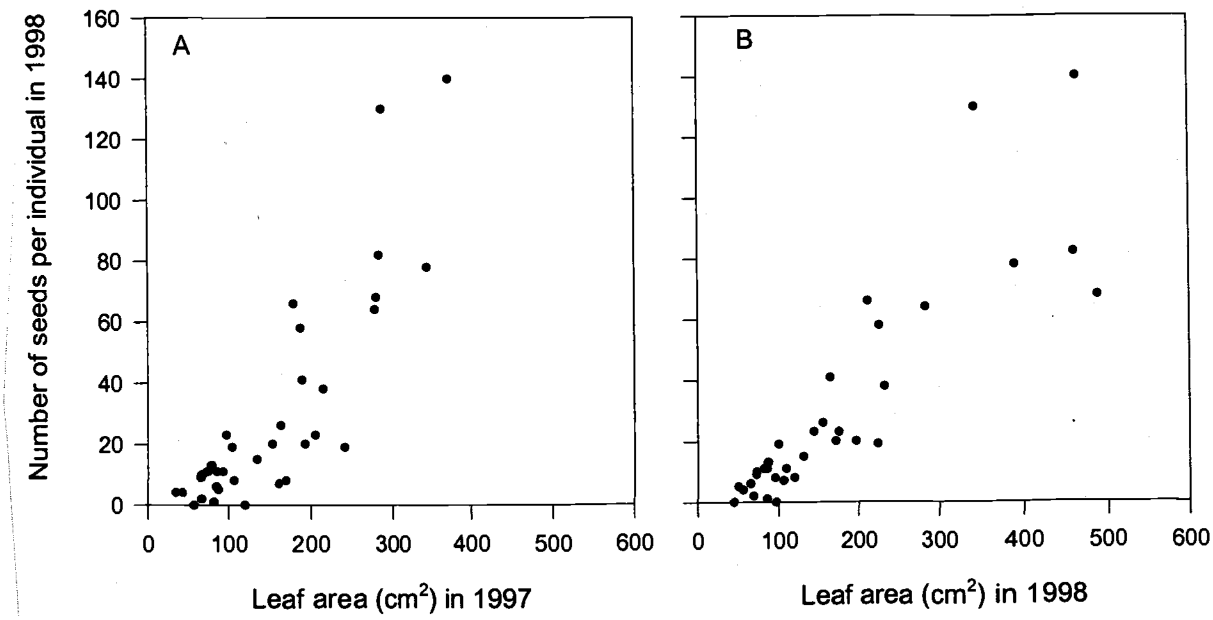


Figure 3.11. Number of seeds per individual in 1998 relative to leaf area in (A) 1997 and (B) 1998.

Leaf area increased with both rhizome volume and with rhizome depth (Figure 3.12). Leaf area increased linearly with rhizome volume with more variability at larger sizes. Leaf area increased curvi-linearly with rhizome depth.

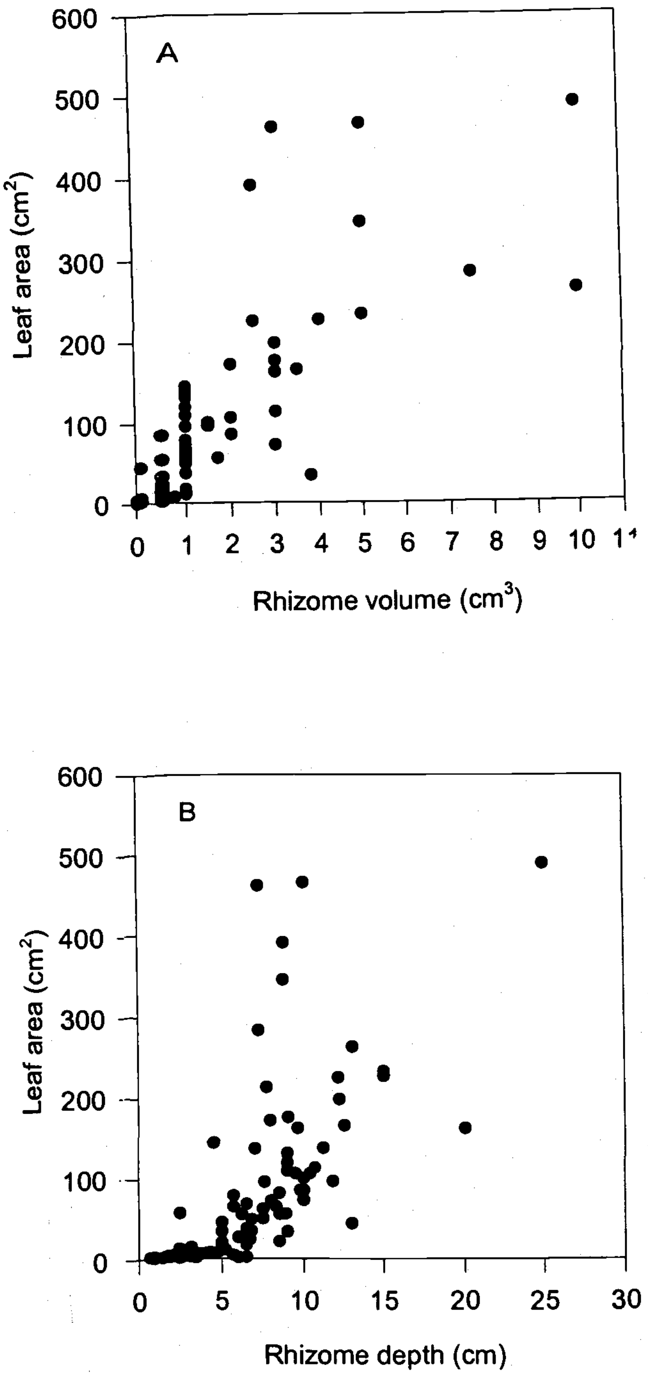


Figure 3.12. *Trillium* leaf area relative to (A) rhizome volume and (B) depth.

For individuals measured in both years, seed production and leaf area in 1998 was similar to that in 1997 (Figure 3.13). All individuals over 250 cm^2 in 1997 were even larger in 1998.

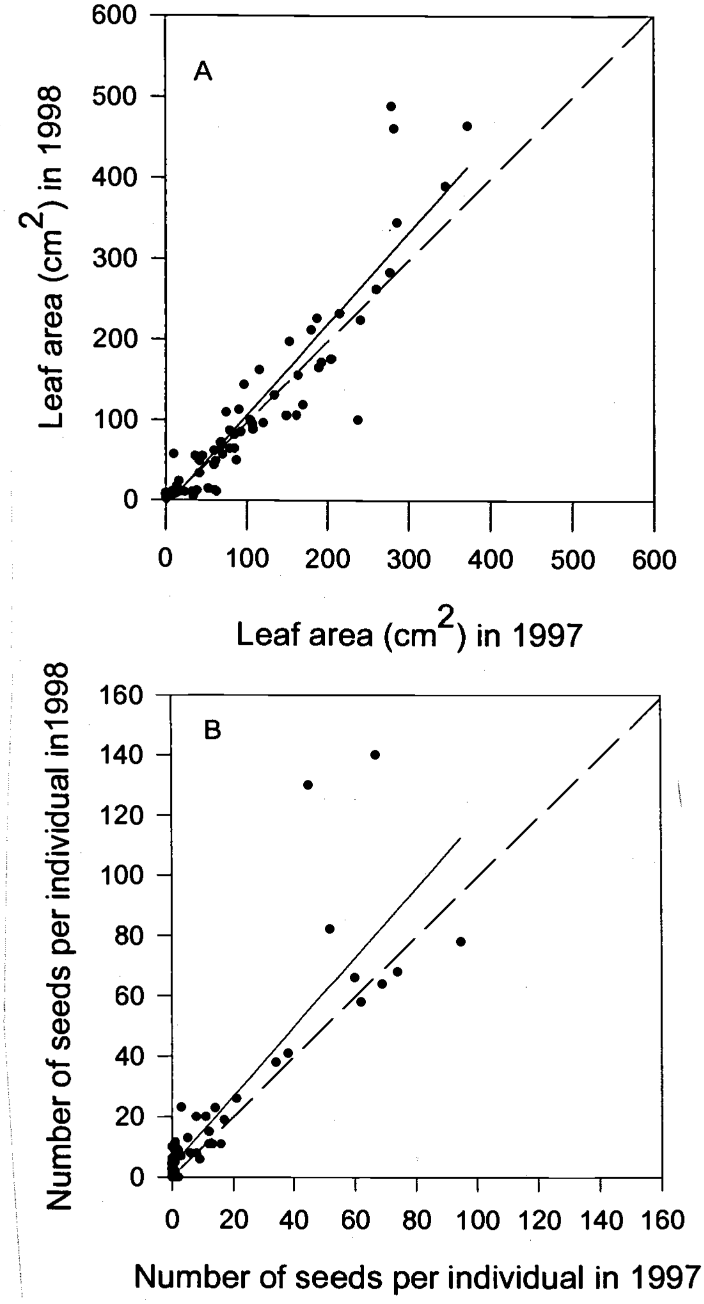


Figure 3.13. Number of seeds per individual (A) and leaf area (B) in 1997 and 1998. Dashed line indicates the line for equal rates of seed production or leaf area in 1997 and 1998. Solid line represents the actual regression for 1997 vs. 1998.

3.3.2.4 Patterns of fecundity and growth along resource gradients

This section discusses patterns of *Trillium*'s response to resource gradients. Both seed production and leaf area per individual (when values for flowering and non-flowering individuals were averaged for each interval of 0.8 mol of photon flux density per m^2) were greatest at light intensities of about 6 mol per m^2 per day (Figure 3.14). Seeds were absent at light intensities greater than 12 mol per m^2 per day and few seeds were produced at light intensities greater than 8 mol per m^2 or less than 2 mol per m^2. All individuals at light intensities greater than 10 mol per m^2 per day had leaf areas smaller than 50 cm^2. Seed production and leaf area were highest and most variable at intermediate light levels of 3 to 8 mol per m^2 per day.

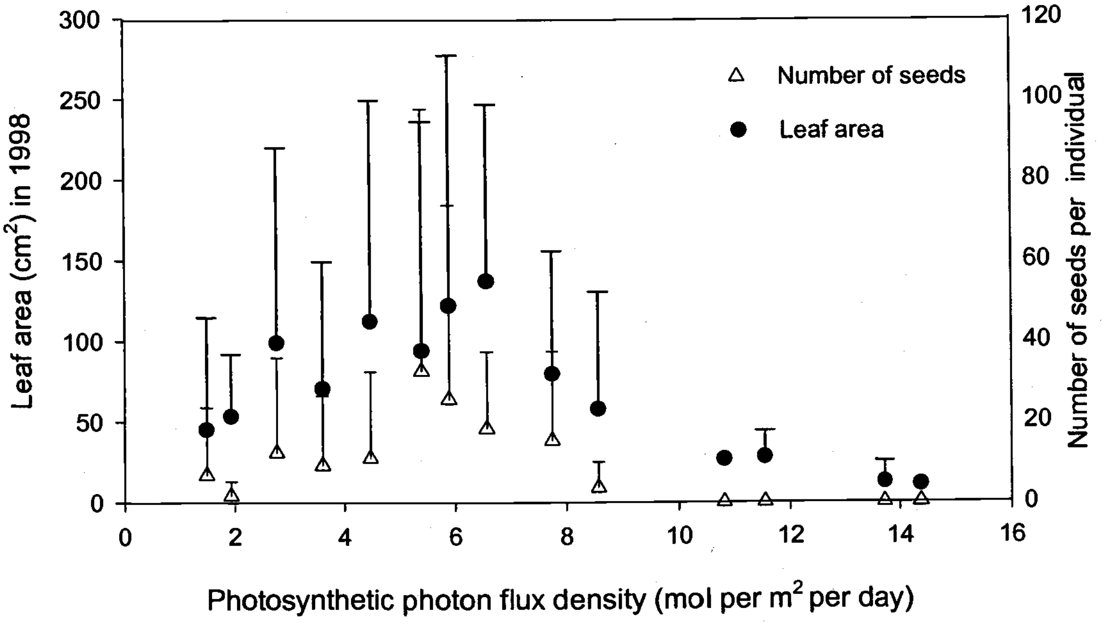


Figure 3.14. Mean seed production and leaf area per individual *Trillium* for each interval of 0.8 mol of photon flux density per m^2 (measured only at locations of *Trillium* in this study; maximum light intensity in Oregon can reach 20 mol per m^2 per day). Standard deviations of seed production and leaf area for each light class are represented by bars. Sample sizes in each interval ranged from 1 to 12.

Increases in rhizome diameter occur in intermediate light (e.g., north of gap borders, south portions of gaps) and decreases occur at high and low extremes of light where soil moisture is low (e.g., in north positions in gaps) (Figure 3.15). Seedlings occur in low light.

Individuals younger than 10 yr were absent from sites where light intensity exceeded 9 mol per m^2 per day (Figure 3.16). Soil moisture (Figure 3.15) and litter depth (Figure 3.17) were never high at high light intensities and were frequently low in low light.

3.4 Discussion

3.4.1 Performance and plant development

Responses of *Trillium* to gaps and other microsites were a function of both plant development and resources (Figure 3.18). This section describes how plant development may operate. Regressions of all variables and the scatterplots of plant parts and age suggest that after seedlings germinate, a sequence of growth begins with increases in rhizome depth, then increases in rhizome volume, and finally increases in leaf area. These delays in leaf and rhizome growth appear to delay the energy-expensive process of flower production for about 10 yr. Low growth rates also may prevent formation of vegetative structures that would be too large to be sustained in the low soil moisture and low light characteristic of forest understory. During periods of declining resources, rates of seed production, flower presence, leaf area, then rhizome volume appear to decrease (in that order). Dynamics of each of these plant parts will first be discussed separately. This discussion will be followed by a summary of how size of plant parts may affect modular growth of the whole plant.

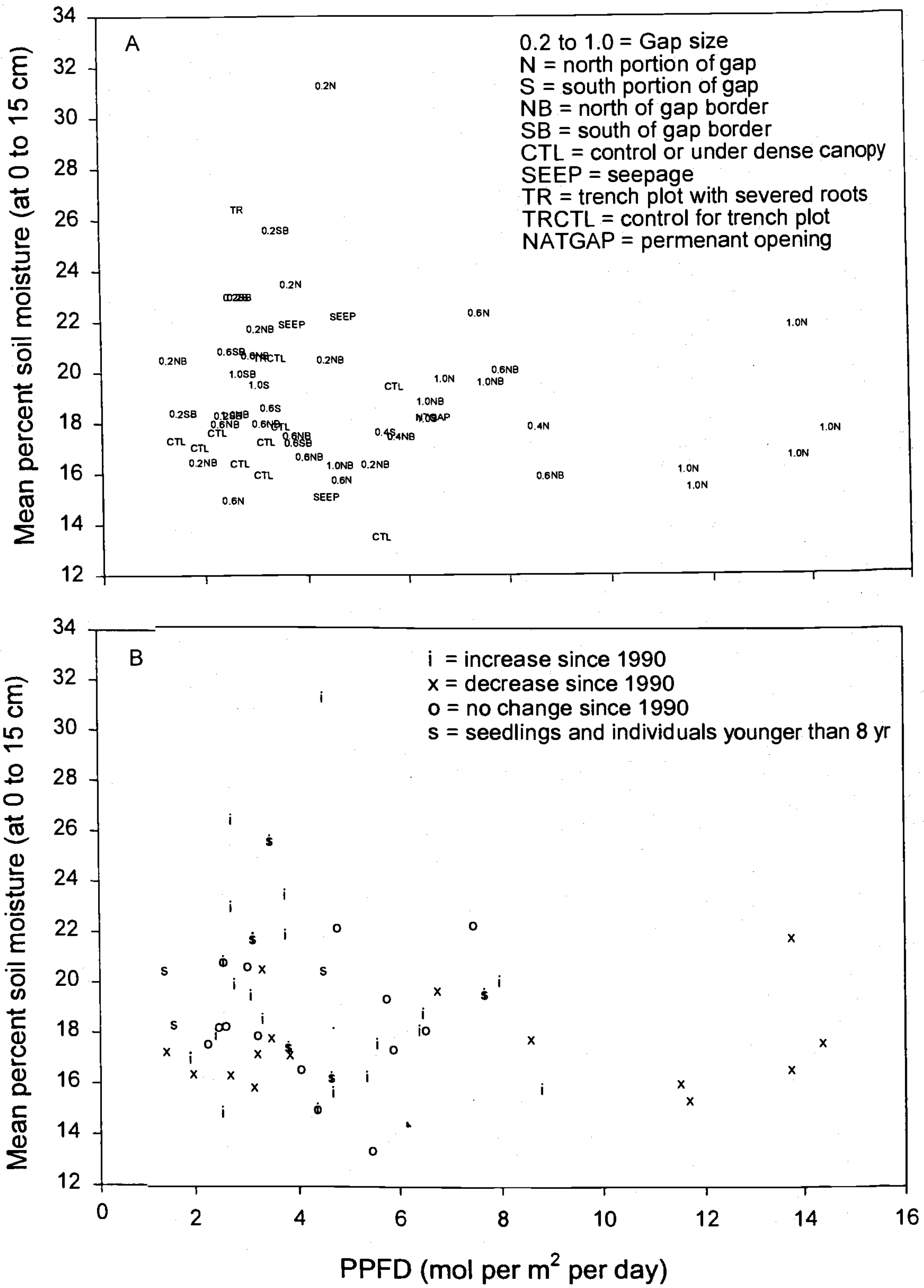


Figure 3.15. Change in rhizome diameter 8 yr after gap treatments along gradients of light and mean soil moisture (at 0 to 15 cm). Gap size and position or other locations are indicated on the upper figure.

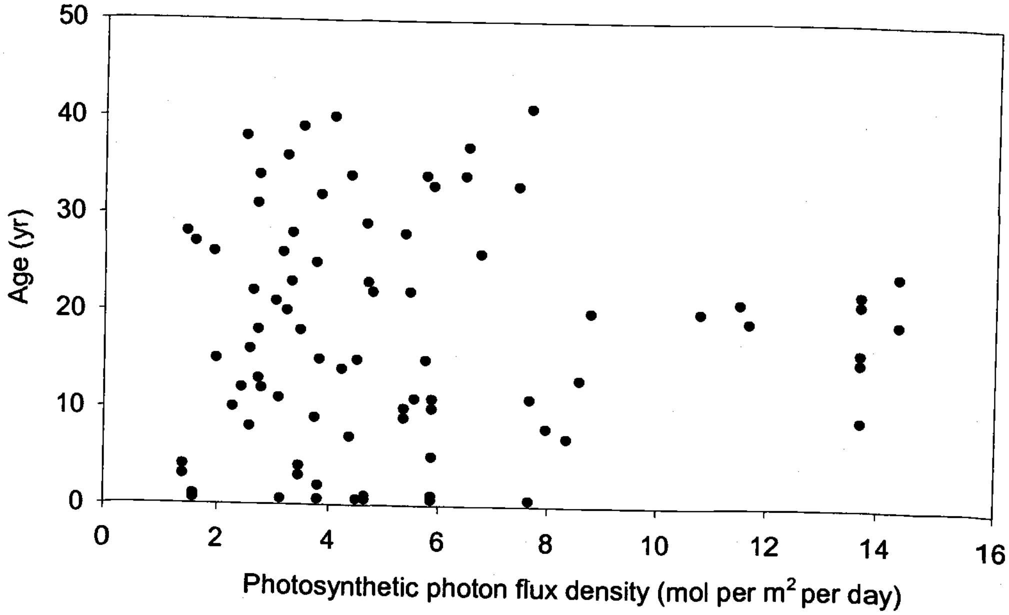


Figure 3.16. Age of *Trillium* and light intensity.

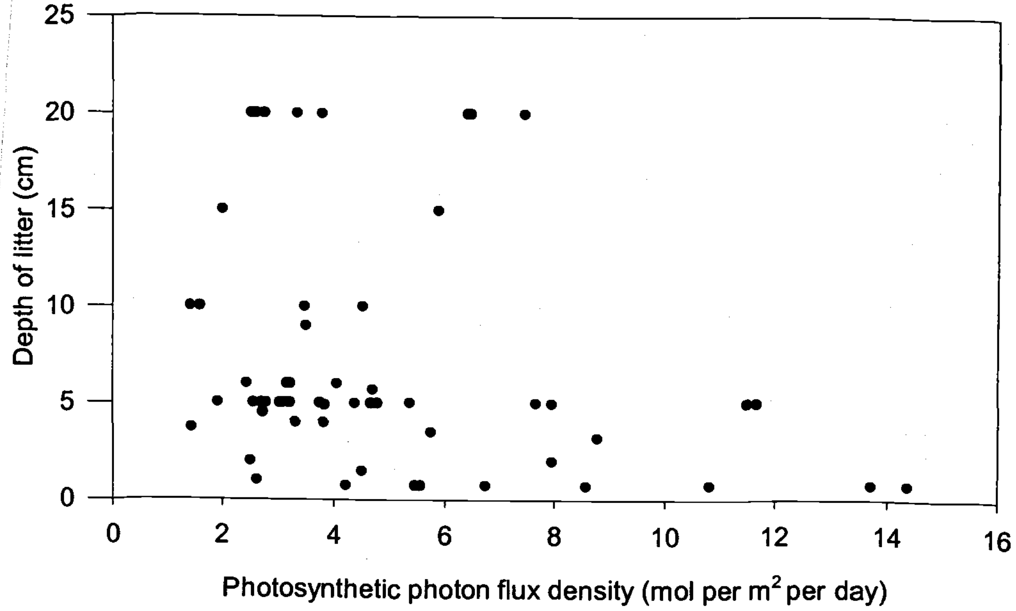


Figure 3.17. Depth of litter (cm) and light intensity (where *Trillium* were established).

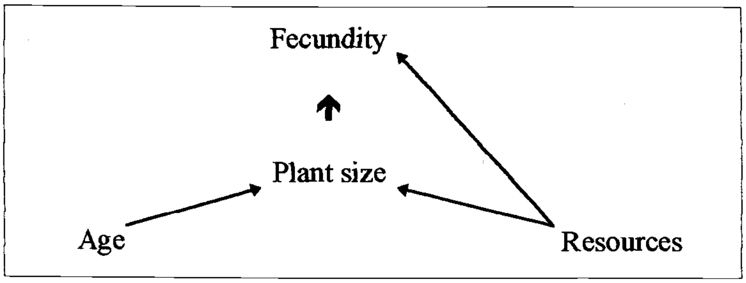


Figure 3.18. Model of general relationships among factors affecting *Trillium* fecundity.

Flowers were absent from all individuals younger than 10 years old probably because their leaf area (of less than 10 cm^2) were too small for the amount of energy capture that would sustain flower production and their rhizomes were too small (e.g., < 0.1 cm^3) and shallow (e.g. less than 5 cm deep) to capture consistently available belowground resources. Individuals older than 10 years with leaf area less than 55 cm^2 similarly did not flower. These data generally correspond with the age of first flowering (of about 10 years) of other species of forest herbs in the eastern US (Bierzychudek 1982) and the minimum plant size threshold of 36 cm^2 reported for flowering *Trillium grandiflorum* (Hanzawa et al. 1993).

Seed production also increased with leaf area, as reported for *Trillium grandiflorum* (Hanzawa et al. 1993) and *Aster acuminatus* (Pitelka et al. 1980). A few large individuals produced most seeds, as is typical for most plant species (Hutchings 1986). Although flowers are formed during the growing season before the one in which they appear (Hanzawa et al. 1993), the correlation between seed production and current year leaf area may be explained by relatively high energy costs of seed-meristems that must be immediately supplied by photosynthates from growing leaves. Seed production may also be limited by physiological traits that determine ovule production, availability of pollinators, and amount of resource flow to developing ovules (Hanzawa et al. 1993).

Leaf area (in contrast to seed production) was mostly explained by rhizome volume and increased one or two years earlier (e.g., 9 yrs) than flower production. Leaf area was also associated with rhizome volume of *Trillium grandifolium* (Hanzawa et al. 1993). Carbon products stored for future leaf construction may increase with rhizome size until the older end of the rhizome start to die (Jules 1996). Water stored in large rhizomes may provide a buffer (capacitance) to water loss during periods of rapid transpiration but probably do not contain enough water to supply leaves for longer periods (D. Zobel, pers. comm.). Leaf area also increased somewhat with rhizome depth probably because rhizomes were at depths with higher and less variable soil moisture (pers. comm., Gray 1999).

Relative growth rates of leaves also increased with rhizome volume but showed stronger relationships to resources (e.g. light and an interaction of light and soil moisture) than leaf area did. This suggests that leaf area can increase after a threshold rhizome volume is reached, but only where resources are available. The greatest growth rates were recorded for a 9-yr-old established in the intermediate light and moist soil of a small gap. Relative growth rates of leaves were negative, on the other hand, for individuals in controls and portions of large gaps that are least shaded by the forest canopy.

Rhizome volume increases with time as more tissue is added to this structure after age 8. Wide variation in rhizome volume of older individuals is probably caused by variations in resource availability. Abrupt increases in rhizome diameter at the time of gap creation (as well as the presence of rhizomes younger than gaps) were associated with intermediate light and litter depth characteristic of, for example, gap borders. Radical increases in rhizome diameter that appeared in trenched plots suggest that growth rates can also increase abruptly with additional soil moisture. The lack of statistical significance between rhizome growth pattern and soil moisture may have been caused by the rarity of moist sites and by the inability of the TDR probes to measure moisture at depths of older rhizomes. The small, gradually decreasing diameters of rhizomes of 20-yr-old individuals suggest that *Trillium* can persist at low growth rates in low light for many years. Consistent diameters in persistent gaps (e.g., borders of streams) suggest that individual *Trillium* in such sites may be very long-lived if ends of rhizomes do not die. Silvertown and Lovett-Doust (1993) state that some clonal herbs can even be "immortal".

Rhizome depth (measured in mineral soil, not under twigs and leaves on soil surface) is the only plant characteristic to increase immediately and consistently after germination. Increasing rhizome depth could be explained by three phenomena: differential survival, contractile roots, and burial. First, seeds located at shallow depths may have lower survival rates than more deeply buried seeds. However, since no seedling in this study was traced deeper than 0.5 cm and because tiny rhizomes may not sustain growth from such depths, it does not seem likely that any *Trillium* could germinate from seeds at such depths.

Secondly, rhizome depth in mineral soil could have increased with age if contractile roots displace the rhizome (Esau 1960). Monocotyledons, especially members of the Liliaceae, commonly have contractile roots that increase the depth of rhizomes (Bierdzychudek 1982). Members of other plant families such as *Oxalis cernua* move horizontally because of contractile roots (Bell and Tomlinson 1980).

Third, accumulations of fallen trees could also contribute to rhizome depth of older *Trillium* in some cases. For example, several individuals were excavated from depths of over 20 cm where they were rooted in moist, rotted logs. Seeds from which these individuals germinated may have been directly dispersed by carpenter ants to logs that were close enough to the ground surface for the first leaves to emerge. After additional debris accumulated in subsequent years, *Trillium* with sufficient rhizome volume may have emerged only if their rhizomes had enough volume to support growth of petioles from the increased depths. The number and width between growth rings and the consistently large diameters on rhizomes indicated that these *Trillium* have been growing at extremely rapid rates in such sites for at least 35 yr.

The largest *Trillium* added the greatest amount of leaf area and number of seeds per individual. While leaf area and seed production were generally quite similar for most individuals in 1997 and 1998, as predicted for plants with low plasticity (Bazzaz 1996), those individuals with leaf area greater than 300 cm^2 added at least 100 cm in leaf area and produced 30 to 50 more seeds per plant from 1997 to 1998. Such opportunistic growth occurred in partial shade where (1) greater surface area and height of leaves let plants acquire more light, (2) larger rhizomes stored more nutrients, and (3) deeper rhizomes accessed more water. Because plant growth is modular, growth rates generally increase where parts are in the right place at the right time, especially after the plants become large (Crawley 1986).

Other characteristics of large plants such as tissue toughness of the stems appeared to provide protection against herbivory by slugs (not deer) and trampling. *Trillium* that had showed evidence of herbivory in 1997 were smaller, did not flower, or produced fewer seeds in 1998. Raw data also indicated that individuals consumed by slugs in 1997 were smaller and shorter in 1998, as predicted by Anderson (1994) and Hanzawa et al. (1993).

3.4.2 Performance in relation to resources

Fecundity was a function of resources as well as size of plant parts. Large and productive *Trillium* have large rhizomes and occur in sites with intermediate light and soil moisture or low light and high soil moisture. However, as previously discussed, growth of leaves and flower construction are delayed for about 10 yr, even in sites where light and soil moisture are associated with extremely high rates of seed production and growth of older *Trillium* possibly because *Trillium* first allocates resources to belowground parts before flower and leaf construction. Because both time and resources both affect rhizome volume, seed production and growth may continue in less optimal conditions at the soil surface for individuals with large, deep rhizomes (Figure 3.19) that are located at depths with higher percent moisture. Leaf area and relative growth rates of leaves may have been correlated with soil moisture because individuals established in sites that remain moist after leaf expansion in June continued to allocate and store carbohydrates in rhizomes through September. *Trillium grandifolium* continues activity in fall (Hanzawa et al. 1993), in spite of completing leaf expansion in spring after light intensity decreases under deciduous canopies.

Seed production and leaf area show a non-linear, skewed response to gradients of light. This may be because *Trillium*'s leaf architecture allows capture of some light even under dense forest canopies. *Trillium* may be able to grow and survive in shade because its cordate-shaped leaves (in conjunction with erect stems) maintain large horizontal areas of photosynthetic tissue (Givinish 1987, 1982). However, in exposed sites, maintaining such horizontal positions may subject the plant to desiccation, because the wide leaves dissipate less heat and provide more area for transpiration than narrow leaves. In full sun with no wind, leaves over 100 mm wide were warmer than narrower leaves, even when stomates are open (Waring and Schlesinger 1985). The light intensities in Figure 3.19 and in the following discussion could also be categorized as "very low", "low", and "intermediate" because light intensities in Oregon can reach 20 mol per m^2 per day (S. Chan, pers. comm., 2000).

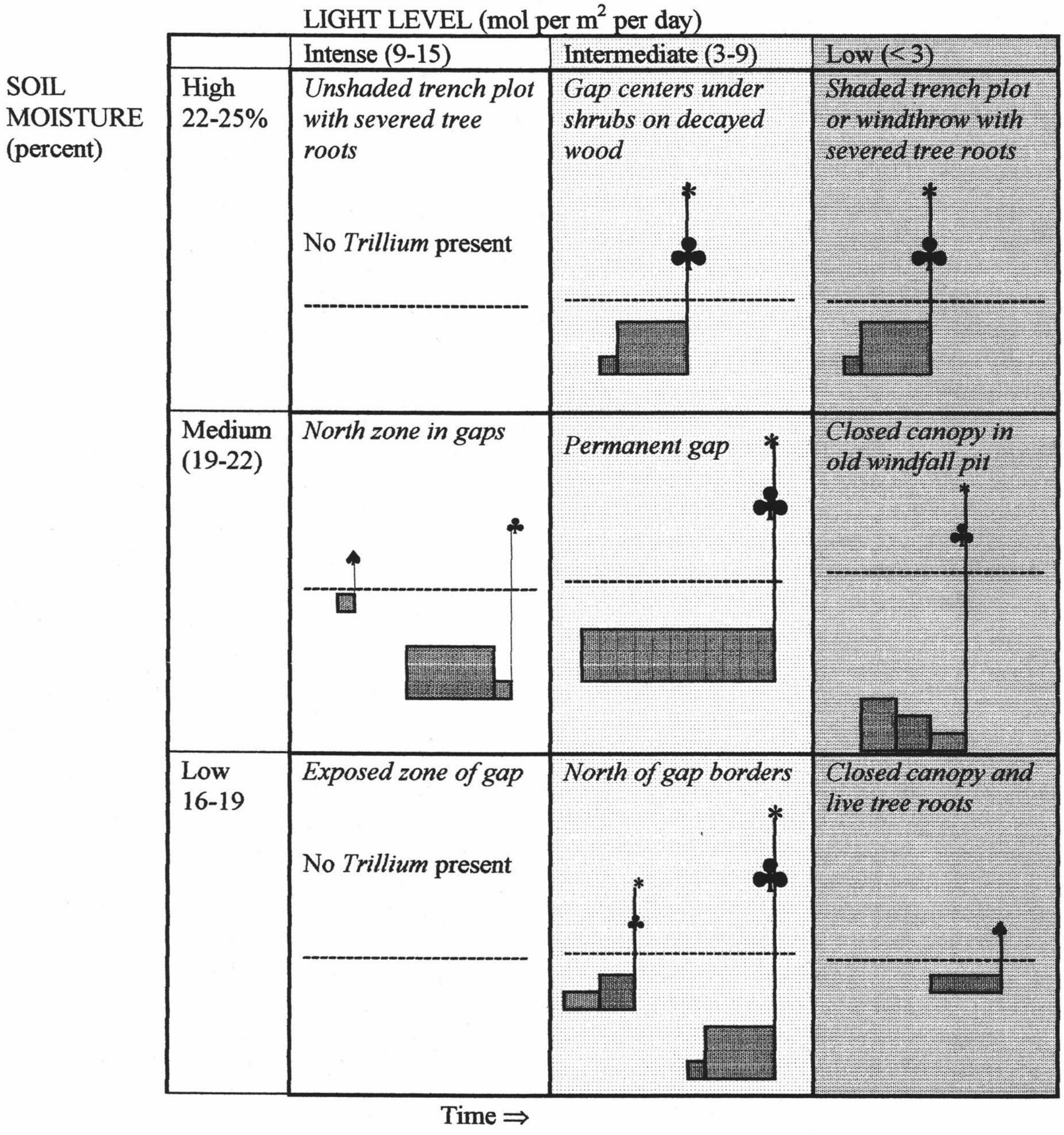


Figure 3.19. Model of fecundity, leaf area, rhizome diameter, and age of *Trillium* at three levels of light intensity and soil moisture measured in this study (maximum light intensity in Oregon can reach 20 mol per m² per day). Text refers to locations where *Trillium* with each growth pattern were found in this study. Depth of rhizomes on single-leafed (♠) and three-leafed (♣) individuals is represented by length of petiole (|). Seed production represented by size of (*). The soil surface is represented by dashed line (---).

3.4.2.1 Intermediate light

Trillium seed production and leaf area (per plant) peaked in intermediate light (e.g., between 2 and 8 mol per m^2 per day) as has been observed with other forest herbs with tall, broad, and horizontal leaves. Locations with such light levels from my study include sites north of borders of all gap sizes, just south of large gap centers under debris and shrubs, and in smaller natural gaps. Pfitsch and Pearcy (1992) similarly found that *Adenocaulon bicolor* produced the most flower heads and seeds and the greatest total dry mass and leaf areas in sunflecks at intermediate levels of diffuse light. Similarly, integrated daily carbon gain was higher and individuals of *Arnica* did not wilt where intermittent shade allowed continuous CO_2 uptake (Knapp et al. 1989). *Uvularia* spp. flowered at greater rates under intermediate light intensities in hardwood forests than either under dark pine canopies or in open fields (Whigham 1974).

In spite of soil moisture being low in some sites with intermediate light (e.g., north of gap borders), some (but not all) individuals there were extremely large and productive. Root depths of large individuals in these sites may have exceeded 35 cm (where rhizomes that were over 10 cm deep had roots that were over 25 cm long).

Seedlings were also found at intermediate light intensities in partial shade cast by canopy and woody debris on gap borders. In these cases, stems were surrounded by at least 4 cm of litter presumably shed by the immediate canopy. This litter layer appeared to protect the rhizomes, which were all within 1 cm of mineral soil surface.

3.4.2.2 Low light

Low leaf area and low seed production were correlated with low light conditions under a dense canopy (e.g., in controls and south of most gap treatments). Soil moisture was also low in such sites. Lower maximum temperatures under the closed canopy suggest that lower heat sums also contribute to low fecundity, because flower formation is generally induced by temperature thresholds; ripening of fruits and seeds requires heat (Larcher 1996). Similarly, *Adenocaulon bicolor* (Pfistch and Pearcy 1989), *Aster acuminatus* (Pitelka et al. 1980), and other herbs (Chadzon and Pearcy 1991) grown in low light are smaller and do not flower in diffuse light without sunflecks.

The variations in leaf area observed in low light may be explained by differences in soil moisture content. For individuals established in low light but where percent moisture exceeds 20 (e.g., in trenched plots where tree roots were severed 8 years earlier), rhizome diameters increased abruptly at 8 annual rings from the base of petioles. The only other large individuals in low light had rhizomes 25 cm below the surface in wet, decayed wood.

Adequate soil moisture allows growth at low light. For example, *Virola* spp. seedlings continue to grow in deep shade, only if water is provided in experimentally irrigated soils (Fisher et al. 1991). Aztet and Waring (1970) similarly found that, although *Pseudostuga* seedlings could establish at 1.85 ly/day where moisture was adequate throughout the growing season, in drier soils they required 6.64 ly/day for establishment. Growth of forest herbs was also described as “luxurious” under canopy where previously severed tree roots increased soil moisture content (Toumey and Kienholz 1931).

3.4.2.3 Intense light

Low fecundity, small leaves, negative rhizome growth rates, and absence of *Trillium* younger than 20 yr were recorded where light intensity was greater than 10 mol per m^2 per day. These conditions may be caused by the heat associated with intense direct light (Gray and Spies 1997), which in turn induces moisture stress. In exposed areas, single-, two-, and small three-leafed individuals that were 20 years old (or older) had negative growth rates for leaves and rhizomes. These responses suggest that these individuals may have continued transpiration without wilting both by reducing specific leaf area (ratio of leaf area to mass) and by reducing the number of leaves. Whether these effects were caused by the intensity of direct or diffuse light was not tested. However, relative growth rates of tropical herbs have shown to be 50% higher in diffuse light than in direct light of equivalent average intensity (Pfitsch and Pearcy 1992).

Elevated leaf temperatures increase evaporative load and create water vapor deficits that lead in turn to excessive transpiration. Although increases in direct light are significantly related to growth of tree seedlings, they are inversely related to leaf size of forest herbs (Pearcy et al. 1994). Pearcy et al. (1994) found that *Adenocaulon bicolor* leaves wilted, curled, and lost turgor after 10 min in direct light and recuperated only in diffuse light. Mortality rates of *A. bicolor* were also highest in direct light and at high levels of diffuse light. These processes may have determined the upper threshold of light intensity associated with seed production which occurred in exposed portions of gaps. Similarly, the number of flowering *Erythronium* per area was significantly greater in single- but not multiple-tree gaps (Collins and Pickett 1987, 1988).

The low fecundity, leaf area, and rhizome growth rates observed at light intensities over 12 mol per m^2 per day suggest that *Trillium ovatum* may be less photosynthetically plastic than *Trillium grandiflorum* and unable to grow over the range of light intensities observed for that species by Sparling (1967). If *Trillium ovatum* is unable to increase concentration of carboxylating enzymes (Boardman 1977), the declines in performance rates in intense light could be caused by photoinhibitory damage to photosystem II reaction centers. Exposed leaves of *Trillium ovatum* do experience photoinhibitory damage to photosystem II reaction centers after exposure to direct light (Powles et al. 1981).

Low performance rates could also be caused by low moisture during summer drought. Exposed sites where *Trillium* was established were characterized by dry soil and a thin litter layer (Figure 3.15). These conditions, in addition to effects of bright light on leaf temperature and photolability (Larcher 1996), may contribute to the lack of individuals younger than 20 yr in exposed sites and to the low fecundity, small size, and negative growth rates of rhizomes of existing individuals. Leaves of some individuals in such exposed sites also curled and turned brown. In such sites, the small (< 0.1 cm^3) and shallow (< 5 cm) rhizomes of individuals younger than 10 yr may desiccate because they are not protected by litter. In contrast, the larger and deeper rhizomes of older individuals may store enough resources or be at depths with sufficient moisture to prevent moisture stress. However, the decreasing rhizome size, early withering of leaves, and early senescence recorded in this study suggest that reserves may soon run out for the older individuals as well.

3.4.3 Spatial and temporal patterns of fecundity and growth in canopy gaps

This section will first compare and then explain possible mechanisms for the spatial patterns of performance of *Trillium* with those of *Linnaea* and *Tiarella* among the gap treatments and controls. Maximum seed production and leaf area were greatest north of gaps (of all sizes) than within north or south positions of gaps. Means were also greater in positions north of all gap sizes than in either position within gaps except gap size 1.0. Mean and maximum seed production and leaf area were greater in south than in north positions of all gap sizes. Most *Trillium* in either north or south positions of gaps were almost under the dripline, and were nearly absent from more central locations of especially large gaps (except under debris or dense canopy of young hemlock). Mean and maximum leaf area and fecundity were low in north portions of gap treatments in spite of shade from logs and shrubs. Fecundity was also low under dense canopy except where soil moisture was available. Seedling density was very low but seedlings were present on most gap treatment borders.

The spatial patterns of herbs I observed suggest that *Trillium* differs in response to similar resources and positions gaps from *Linnaea* and *Tiarella*. Such differences are common among species of herbs (Antos and Zobel 1986; Bazazz 1996). On the other hand, the hypothesis that species coexist because of vertical, horizontal, or temporal partitioning of space in gaps has been rejected for canopy trees in some western coniferous forests because of the lack of short-lived, fast-growing "ruderal" trees (Lertzman 1990). Differences in reponses among species of herbs may vary more than among species of trees because of greater variations in stem, leaf, and root morphology among species of herbs (Chapter 1).

In spite of its patchy distribution, the spatial patterns and rates of *Trillium*'s response to gaps can be at least coarsely compared with those of *Tiarella* and *Linnaea* because all three species were measured in the same conditions at the same time. Before creation of experimental gaps, the abundance of all herbs, including *Trillium, Tiarella,* and *Linnaea* was low (Chapter 2). Cover is generally low for herbs with low annual germination rates, infrequent germination, delayed flowering, or low fecundity and growth rates (Tamm 1956; Bierzychudek 1982; Deno 1993), especially where resources are scarce. However, by 1998 the abundance of *Linnaea* (and all other vegetatively-spreading herbs) and *Tiarella* had increased dramatically in gap treatments and seed production and growth rates of these two species also increased there (Chapter 2). Cover of *Trillium* may have remained low (according to the 1997 data) within gaps because of lack of recruitment, mortality, and/or low leaf area of individuals that survived gap creation. No *Trillium* younger than the gaps were found within the gaps, and leaf and rhizome growth rates were negative in some exposed areas of the gaps.

On the other hand, by 1998 the mean and maximum seed production and leaf area, and seedling density of *Trillium* were generally higher on gap borders than within gaps. Within gaps, seedlings were absent and seed produciton and leaf area were higher in south than north positions. Unlike *Linnaea*, seed production was lowest not highest in north portions of gaps probably because temperatures that induce flowering for *Linnaea* induce excessive moisture stress for *Trillium* and because soil moisture remains low even under coarse woody debris in such positions (Gray 1995). Seed production occurred in more southerly positions for *Trillium* than for *Tiarella*. Seed production was generally quite low (e.g. one to two seeds per individual) for exposed indivduals established on south rims of gaps. One individual established just south of the center of gap size 1.0 (under dense hemlock canopy) was almost as large and productive as individuals outside of the treatment. Maximum temperatures in the shade cast by three layers of structure present on gap borders (canopy, litter, and debris) were probably lower than in shade only cast by coarse woody debris or shrubs in north portions of gaps with less canopy shade. Gap borders appeared to provide habitats for two types of responses by *Trillium*. Size and seed production per individual were greatest just north of gaps where a few individuals produced the majority of seeds counted in the entire study. South borders, on the other hand, were covered by a greater number of smaller *Trillium* which may persist at lower rates of seed production until light or soil moisture levels change.

Trillium may have been less abundant within gaps than *Linnaea* and *Tiarella* because flexibility of response for *Trillium* was lower than for *Tiarella* and *Linnaea* (Chapter 2) and varied along a narrower range and lower intensities of light than for the other species. Bazazz (1996) defines response flexibility as the ability of a particular genotype to function in a variety of environments either because of the "plasticity" (variety) of phenotypes that it can express in different environments or because of its ability to acclimate previously established modules to new conditions. Early-successional species respond more flexibly and rapidly to a wider range of resource levels than do late-successional species (Bazzaz 1996). Late successional species are less plastic in physiological processes and morphological characteristics such as leaf height and orientation and in branching of flowering stalks or rhizomes. They can persist as seedlings or at negative growth rates as mature individuals in low light, but are sensitive to decreases in soil moisture and intense light. Thus, (relatively) early successional species occur in larger gaps and different positions of gaps and at lower percent soil moisture and at higher light intensities than later successional species. Frequent herbivory or other types of disturbance may be detrimental to *Trillium* (Anderson 1994) because of its low flexibility. Species with more rapid and flexible response of seed production or growth respond more rapidly to removal of taller herbs and shrubs (Denslow 1985).

The low flexibility of *Trillium* compared to the other two species in my study is consistent with other studies. For example, *Trillium*'s seed production varied by about one hundred seeds per plant (2 per m^2 plant cover) because each rhizome generally produced one unbranching stem that only supported one capsule. In contrast, rapid growth of numerous, branching vegetative structures of *Linnaea* and *Tiarella* conferred immediate support of hundreds of seeds per m^2 plant cover. Horizontal growth rates and architectural flexibility also varied less for *Trillium* than for *Tiarella* or *Linnaea*. Maximum growth of *Linnaea* stolons reached more than 60 cm in length per season, far exceeding the increases of less than

1 cm per year per *Trillium* rhizome. *Linnaea* stolons branch frequently (Antos and Zobel 1984a), but there was no evidence of branches on any *Trillium* rhizome in this study. Other studies show that *Trillium* has a low range of photosynthetic response to light (Powles et al. 1981), dies back in response to burial (Antos and Zobel 1984b) and has inflexible leaf architecture (Givinish 1982).

3.4.4 Implications for management

Trillium's ability to persist in forests despite either intense or low light conditions implies the species is adapted to some level of disturbance and changes in available resources. For example, patterns of rhizome age and growth within gaps and controls suggest that some *Trillium* can persist for at least a decade following this scale of disturbance. Spies (1988) confirms that *Trillium* can occur in young Douglas-fir forests 30 to 40 years after wildfire. On the other hand, negative growth rates of leaves and rhizomes also suggest that populations of *Trillium* could fluctuate and become locally extirpated where ever light and soil moisture remain unfavorable for long enough periods.

Survival of established individuals alone does not ensure a thriving population. Although some established individuals may survive environmental variations, populations will not persist in the long term without new establishment. Seedlings were present on most gap treatment borders (of all sizes) but absent from north positions (which have less shade from tree canopy than any other gap position as gap sizes increase) and rare under dense canopy. Seedlings were absent in sites with intense light. Such sites are also dry and unshaded by litter. Absence in south positions may be caused by dense herb canopy. A similar lack of seedlings even in proximity to potential parents was documented for plantations and clearcuts in a study conducted in the Siskiyou Mountains of southwestern Oregon (Jules 1996).

The structure of the of the majority of Pacific Northwest forest has been altered since Euro-american settlement began (Spies et al. 1994). The size distribution of openings in the forest canopy, as well as the types and amounts of internal structure historically produced by wildfire, are generally homogenized by logging and development (Perry 1995). Young, dense plantations that now dominate many landscapes (Spies et al. 1990) can have less available light, moisture and exposed mineral soil for herbs and shrubs because small trees are less likely to uproot and create gaps, tip-up mounds, and large woody debris (Spies et al. 1991).

Although this species of *Trillium* may not currently be threatened over its entire range by such changes, Jules (1996) concludes that it is probable that the distribution and abundance of *Trillium ovatum* and other understory herbs have been significantly altered by structural changes to forests. Jules (1996) also concludes that the likelihood of maintaining *Trillium* populations in some forests can be increased by protecting areas that have never been harvested and by managing plantations in such a way that they can be colonized by these species. Forest managers are now required to leave 15% of the trees in managed stands (ROD 1994). Fortunately, these guidelines allow flexibility in the distribution of the remaining trees which can range from grouped to dispersed. This range of options can be compatible with conservation management plans for *Trillium*.

Two approaches could contribute to the conservation and restoration of *Trillium* populations. First, a "group leave" approach could be used to maintain the availability of propagules from patches of established individuals. In this approach, managers could first locate large and productive *Trillium*, then protect them from mechanical damage and other disturbances by maintaining forest canopy and adding other forest structures. Piles of coarse woody debris adjacent to trails and roads may deter trampling and prevent herbivory by deer, which prefer large *Trillium*. Continuous protection of large, productive individuals is more efficient than labor-intensive planting programs for maintaining the genetic diversity of herbs with low germination and growth rates, infrequent years of germination, and extended lag times before reproduction (Primack and Mao 1992). Protection of productive parts avoids the lag time before reproduction. *Trillium* younger than 10 yr do not reproduce, and this species produces the most seeds after 15 to 20 yr even in the best resource conditions. Lack of protection from frequent disturbances (by herbivory, trampling, environmental extremes) may prolong growth to reproductive size and result in smaller individuals with few or no seeds in year(s) following destruction of aboveground plant parts (Anderson 1994). In addition, plant protection allows existing plants to produce genetically different seeds each year which increases the likelihood the seeds will be adapted to year-to-year changes in microsites and climates.

The group leave approach could also be used to protect potential germination sites as well as sites for young *Trillium* to grow. Mineral soil exposed by root-throw, emerging *Monotropa*, fungi, and pocket gophers may provide germination sites within these areas, especially during wet years. Partial shade from the forest canopy and tops of downed trees from adjacent harvests could increase germination and survival rates in moderately dry sites. Protection of such areas for at least 10 yr can allow seedlings to grow to reproductive size and for small, flowering *Trillium* to increase size and rates of seed production.

A second approach could be to manage directly for *Trillium* while forest stands are being thinned. For example, gaps in the forest canopy could be located to provide light and soil moisture conditions in sites with previously established *Trillium*, even if they are young or non-flowering. If the primary objective is to manage for *Trillium*, all woody debris could be left at the site to provide the levels of partial shade that are associated with maximum performance of this species. If boles are removed for commercial purposes and only tops remain, then at least the tops of downed trees could be moved to sites where standing and downed trees and litter together partially shade individuals north of gaps. Within gaps, shade from shrubs, trees, and debris left in south and centers of logged gaps (e.g. where soil moisture and some shade from the forest canopy are also available) would more likely result in large productive *Trillium* than in north portions of gaps. Managers could also increase seed production and growth of previously established *Trillium* by increasing the availability of soil moisture to their roots. Soil moisture content can be increased by completely uprooting trees or by leaving boles intact and severing roots, as in the trench plot experiment. Management of *Trillium* by thinning trees would be more labor intensive than the group leave approach and risks to the ecosystem are unknown.

The size and age structure of local *Trillium* populations can be used to monitor the success of management of these herbs. For instance, a *Trillium* patch without seedlings in which mean plant size is gradually decreasing from year to year will not be likely to persist as long as a patch containing all age classes and where growth rates of leaves are positive.

3.4.5 Limitations of this study

Although no *Trillium* were observed in sites with dense cover of other herbs and shrubs, his study did not test effects of competition from other species on rates of growth and fecundity of *Trillium.* Competition with other understory species that intercept light and deplete soil moisture has been hypothesized as the reason *Trillium* are absent from forest edges adjacent to clearcuts (Luoma and Thies 1997) which have different environmental conditions than on borders of smaller openings in the forest canopy (Chen and Spies 1990; Gray and Spies 1996). Another shade-tolerant herb, *Cimicifuga elata*, suffers low fecundity

(Kaye and Kirkland 1994), and tree seedlings suffer low growth and survival rates (Gray and Spies 1997) where other species of herbs are dense.

Resources and plant performance in this study were directly measured over a period of only 2 years and only in one site in old-growth stands. The resource levels measured in experimentally logged old (but not young) forests could only generally be applied to *Trillium*'s performance between 1990 and 1996. Soil moisture could only be measured from depths of 0 to 15 cm because of difficulties inserting probes into rocky soils. These near-surface soil moisture measurements may not be relevant to older *Trillium* with deeper rhizomes. Likewise, sizes of leaves and rates of seed production before 1997 could only be inferred from diameters of intact rhizomes. Whether seed production over the lifetime of these shade-tolerant herbs is greater in small permanent gaps formed by topography than in sites adjacent to large but more temporary gaps was not tested. *Trillium*'s patchy distribution was patchier where herbivory from slugs and deer eliminated some individuals. Treatment boundaries were not always where the forest canopy dripline actually was.

3.5 Conclusions

Seed production, leaf area, and seedling density were generally greatest on gap borders. Leaf area and seed production were greater in south positions than in north positoons, controls or positions south of gaps and and were quite high for one individual under shrubs and debris in a near-central position of one replicate of gap size 1.0. Within gaps, seed production and leaf area, but not seedling density, thus increase in positions shaded by canopy. Performance in north positions of large gaps remains lower than on gap borders or in south positions in spite of shade from coarse woody debris or shrubs. Performance increases under dense canopy where soil moisture is available.

Fecundity was a function of both plant development and resources. Flower construction is delayed for about 10 years, even in sites where resource levels are associated with growth and reproduction of older individuals. Both seed production and leaf area show a non-linear, somewhat bell-shaped response to light with mean leaf area and seed production being greatest at intermediate light. Variations of leaf area and seed production are also greatest at intermediate light because large, productive individuals and seedlings occur together at these light intensities. Although large individuals are present in sites with low light, none were found in intense light. Thus, gaps in the conifer forest canopy can provide spatial and temporal resource heterogeneity that allow *Trillium* to grow and reproduce.

CHAPTER 4. SUMMARY AND CONCLUSIONS

4.1 Introduction

The overall goals of this study were to evaluate how small-scale disturbances in old growth forests affect the fecundity and growth of forest herbs and to determine whether species of herbs differ in their responses to resource variation associated with canopy gaps. The first objective was to determine whether fecundity and growth rates of *Tiarella*, *Linnaea* (both in Chapter 2) and *Trillium* (Chapter 3) increased in gaps and, if so, whether performance varies among gap size and position. The second objective was to compare fecundity and growth of the three species along gradients of soil moisture, light, and time.

A quasi-experimental approach was used to monitor performance of herbs along spatial and resource gradients. However, because no treatments were specifically applied to herbs, the approach of this study is observational. Because *Trillium* distribution is patchy, it was monitored over larger areas than the two more common species which were studied in and around gaps. Unlike *Linnaea* and *Tiarella*, individuals of *Trillium* are distinct and can be aged by counting annual constrictions on their rhizomes. Thus growth rates and volume of rhizomes as well as relationships of flower and seed production, leaf area and other plant characteristics could be related to age.

4.2 Summary and synthesis of results

Growth and fecundity of all three species increased in response to canopy gaps. Fecundity and growth of *Linnaea* and *Tiarella* were greater within gaps than in controls where canopies were dense. Fecundity, growth rates, and size of *Trillium* under dense canopy were also low except where individuals were established in areas of relatively high

The low number of replicates of each treatment made it difficult to state conclusively that gap size generally has no effect on herbs. The data did suggest, however, that differences in *Linnaea*'s performance among sizes of gaps, were generally small and not linear, especially when border positions were included. The fecundity of *Tiarella* increased somewhat consistently with gap size until gap size 0.6. Minimum gap size threshold for increases in fecundity appeared to be larger for *Linnaea* than for *Tiarella.* On the other hand, growth rates of both species increased even in small gaps.

When fecundity and growth were compared among the largest gaps (which have wider resource gradients than small gaps), performance varied more with gap position and resources than with gap size (Figure 4.1). Within gaps, fecundity was greatest in northern positions for *Linnaea* and in southern positions for *Tiarella*. Growth rates of both *Linnaea* and *Tiarella* were greater in southern than in northern positions. On the other hand, fecundity and leaf area of *Trillium* were greatest in positions north of gaps. *Trillium* seedlings were present on borders of gaps and within controls, but no *Trillium* younger than gaps were present in positions within gaps.

Exceptions to these spatial trends of performance in gaps occurred where canopy and fallen trees varied among equivalent positions among replicate treatments. All three species are sensitive to the microsite heterogeneity within gaps and controls.

Before creation of experimental gaps, the abundance of all herbs, including, *Linnaea Tiarella,* and *Trillium* was low. By 1998 the abundance of *Linnaea* and *Tiarella* had increased dramatically within gap size 1.0. However, while long-term data indicated slight increases in frequency and cover on gap borders, abundance of *Trillium* did not increase within gaps. Frequency of *Linnaea* declined in controls from 1990 to 1997. Cover of *Tiarella* increased slightly in controls.

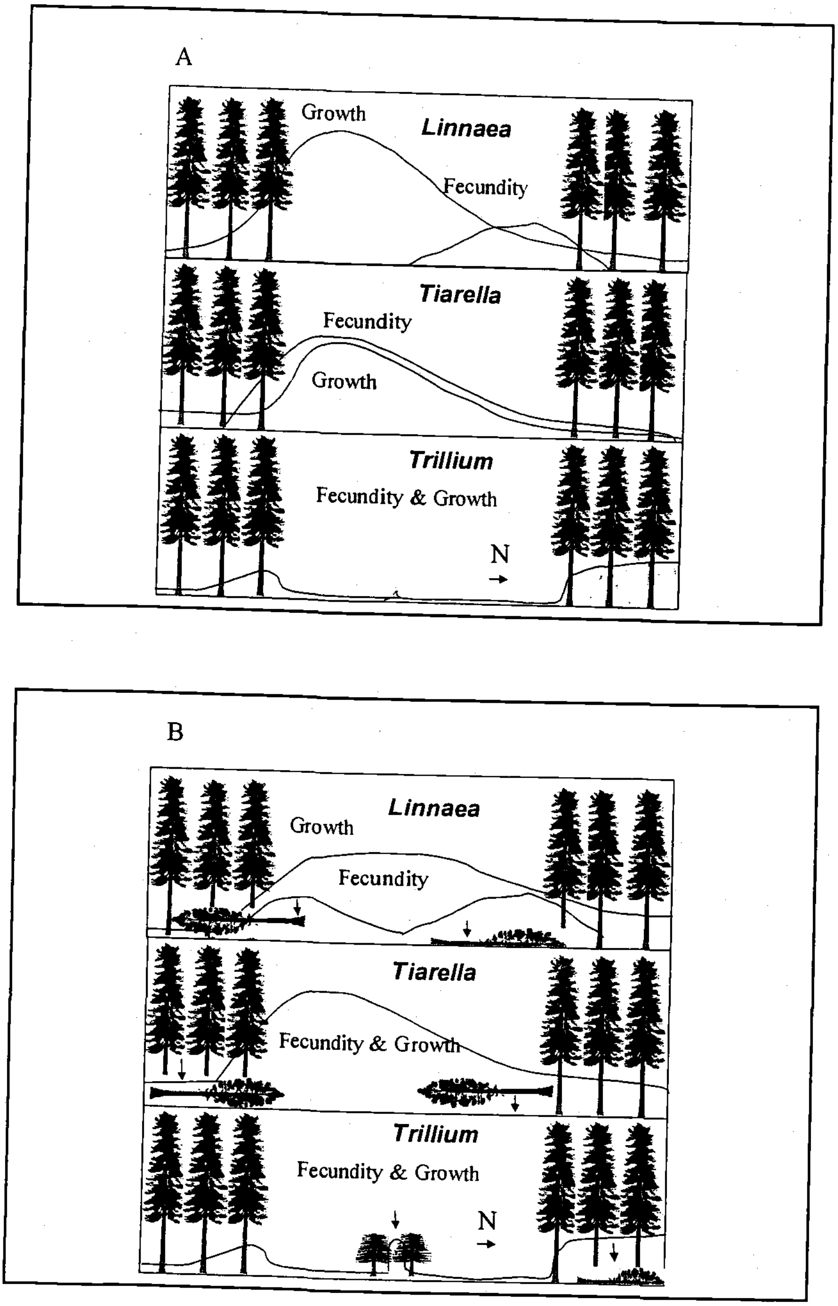


Figure 4.1. Idealized distributions of fecundity and growth for *Linnaea*, *Tiarella*, and *Trillium* across large gaps (sizes 0.4, 0.6 and 1.0) (A) without coarse woody debris, shrubs, or variations in topography within or bordering gaps and (B) with coarse woody debris (arrows indicate locations where fecundity or growth may have been greater because of standing or fallen trees).

Resource availability may explain why fecundity, growth rates and abundance increased for all three species in response to gaps. Fecundity increased with an interaction of light and soil moisture for *Linnaea* and soil moisture for *Tiarella*. Similarly, growth rates increased with soil moisture for both of these species.

Fecundity of *Trillium* was a function of both resources and plant development and was most directly related to leaf area. A sequence of growth beginning with increases in rhizome depth, then increases in rhizome volume, and finally increases in leaf area may explain the apparent 10-yr lag before flower production. Leaf area is mainly a function of rhizome volume, light intensity, and soil moisture. Although responses to soil moisture (measured at shallow depths) and light were relatively weak when analyzed along with effects of plant size, age, and other environmental factors, seed production and leaf showed a non-linear distribution along gradients of light. Greatest rates of performance for *Trillium* occurred at intermediate light intensities characteristic of gap borders.

Resources varied by position and species response varied along resource gradients. Differential performance of the three species among similar gap size and positions and analysis of resource gradients suggests that the three species are adapted to different levels of available light and soil moisture. Patterns of performance among gap locations suggest that fecundity and growth of the three species increases with light intensity until high surface temperatures, low soil moisture, or both induce moisture stress. Different tolerances for moisture stress by each species are probably conferred by morphology and physiology of their leaves, stems, and roots (Chapter 1).

Gaps may increase abundance of these herbs as long as individuals are located in microsites or positions where rates of their major mode of reproduction increase. For example, despite the large number of capsules produced, *Linnaea*'s germination rates are low (Clark 1990). No seedlings were observed for *Linnaea* anywhere in this study. On the other hand, growth rates of 60 cm in length of stolons per year were recorded for individuals in unoccupied space of gap fringes. Therefore, horizontal growth of *Linnaea*'s stems, not fecundity and sexual reproduction, may explain increases in frequency for *Linnaea* from 1990 to 1997. However, growth rates of stolons in 1997 were lower in areas where density of herb canopy was high. *Linnaea* may quickly reach new sites by changing the length, growth rate and angle of spacers as levels of resources change if it has "guerilla" growth patterns (Lovett-Doust 1981). Whether rates of branching and total length varied in gaps vs. controls was not measured in this study.

Rhizome growth patterns may partially explain why relative increases of frequency in gap size 1.0 by 1997 were so much lower for *Tiarella* than for *Linnaea.* Unlike *Linnaea*'s stolons, annual additions to the length of *Tiarella* rhizomes rarely exeed *ca* 2 cm and branches are rare (Antos and Zobel 1984a,b). *Tiarella* may persist within or near areas of original establishment because of short and equal spacers that increase in density rather than length in response to resource availability. Such a "phalanx" lifeform (Lovett-Doust 1994) may allow *Tiarella* to compete with other herbs as resources become available in gaps. *Tiarella*'s passively-dispersed seeds also would not likely travel far.

On the other hand, vertical growth of *Tiarella* stalks may explain why relative increases cover (from 1990 to 1997) of *Tiarella* were slightly greater than those of *Linnaea.* Rapid growth of *Tiarella* in gaps resulted in tall stalks that produced more and longer branches (and branchlets) that covered more area and supported more capsules (per m^2 cover) than did the shorter shoots of *Linnaea*. Such growth patterns of new individuals may result in increased cover in just a few years.

In contrast, *Trillium* responded to gaps at different locations, with lower rates of fecundity and growth and at narrower or lower light intensities than did *Linnaea* and *Tiarella*. Cover of *Trillium* may have remained low within gaps (Chapter 3) because of lack of recruitment, mortality, and/or low leaf area of individuals that survived gap creation. No *Trillium* younger than the gaps (e.g. 8 yr) were found within the gaps and those that persisted in the gaps were 10 to at least 20 yr. *Trillium* that were between 20 and 45 yr were found in various other locations. Mean fecundity and growth were lowest in north portions of gaps regardless of coarse woody debris and shrubs. Leaf and rhizome growth rates were negative in some exposed areas of the gaps. On the other hand, by 1998, seed production and leaf area, and seedling density of *Trillium* were higher on gap borders than within gaps. Gap borders appeared to provide two types of ecological optima that increase fitness of *Trillium*. Size and seed production per individual were greatest just north of gaps where a few individuals produced the majority of seeds counted in the entire study. A greater number of smaller *Trillium* on the southern edges the gaps appeared to cover more area, and these may persist at lower rates of seed production until light or soil moisture levels change.

Among the three species in this study, *Trillium* may be the most adapted to relatively low levels of disturbance or as Bazazz (1996) terms, is most "late-successional" because it (1) responds to a narrower range of environmental factors and at lower light intensities and because it (2) responds with less allocational flexibility than *Linnaea* or *Tiarella*. (Response flexibility is defined as the ability of a particular genotype to function in a variety of environments either because of the "plasticity"(variety) of phenotypes that can be expressed in different environments or because of its ability to acclimate previously established modules to new conditions). In contrast, *Linnaea* may have traits that allow it to be more "early-successional" (e.g., to colonize unoccupied and thus exposed, resource-rich sites) in gaps than *Tiarella* or *Trillium*.

Response to resources. *Linnaea* produces the most capsules (per cover) at 12 to 14 mol per m^2 per day than *Trillium* or *Tiarella* but fecundity appears to decrease in sites after canopy of taller herbs intercept light from this low-growing species. Fecundity of *Tiarella* peaked at greater soil moisture and lower light than did *Linnaea* and, unlike *Linnaea*, in the shade of other vegetation. Rates of capsule production are are greater for *Tiarella* than for *Linnaea*, but only in intermediate light (e.g. 3 to 12 mol per m^2 per day), and are lower at light intensities where fecundity is greatest for *Linnaea.* Response for *Trillium* varied along a narrower range and at lower intensities of light than did the other two species in this study. *Trillium* persists at negative growth rates as mature individuals and is sensitive to decreases in soil moisture and high light. *Trillium* seed production peaked in the lowest light (e.g at 2 to 8 mol per m2 per day). *Trillium* persists in low light as seedlings. *Tiarella*'s seedlings were, in contrast, found within more exposed areas of gaps.

Flexibility of response of the three species. *Trillium* is less plastic in leaf height and orientation, branching of flowering stalks, and in horizontal rhizome growth rates and thus responds more slowly, and/or negatively to disturbance than *Linnaea* or *Tiarella*. From minimum to maximum, *Trillium*'s seed production varied by less than a hundred seeds per plant. Most *Trillium* produced one stem per rhizome which varied by no more than 100 cm^2 of leaf area per plant and 10 cm in height. In contrast, rapid growth of the more variable vegetative structures (e.g. height and number of stalks) of *Linnaea* and especially *Tiarella* conferred immediate support to hundreds of seeds per m^2 in gaps at higher light intensities.

Linnaea's may be able to immediately increase frequency in gaps before the other two species because the maximum rates of stolon growth per season allow the species to rapidly colonize unoccupied space and because *Linnaea* stolons branch frequently (Antos and Zobel 1984a). The average maximum growth of *Linnaea* stolons in gaps of 20 to 35 cm in length per season (and up to 60 cm for some individuals) far exceeded maximum growth rates of *ca* 1 cm per year per *Trillium* rhizome and 4 cm per yr for *Tiarella* rhizomes (documented by other studies) as well as the maximum rates of 10 cm in additional vertical height for *Tiarella* measured in this gap study. *Tiarella* rhizomes rarely branch and there was no evidence of branches on any *Trillium* rhizome in this study. The full range of *Linnaea*'s stolon growth rates among gap and control treatments was diffcult to evaluate because of high growth rates in natural gaps within controls (Figure 2.8) and because only maximum rates were measured in each ring plot. In other words, short stolons were observed under dense canopy and in exposed sites of gaps, but were not measured in this study.

4.3 Conclusions

This study supports the hypotheses that fecundity and growth of *Linnaea* and *Tiarella* will increase within forest canopy gaps and that their performance will vary somewhat with gap size but especially along gradients of gap position and resources. Fecundity of *Tiarella* increased in small gaps but fecundity of *Linnaea* did not. Growth of both species increase in small gaps. On the other hand, differences in the effects of gaps among larger gap sizes (within the range of sizes measured in this study) on species performance can be overridden when plants happen to be located where light, temperature or soil moisture levels are altered by variations in the topography, canopy and internal structure (shrubs and woody debris). For example, fecundity of *Tiarella* was greater in the in the replicate of gap size 1.0 with concave topography and shade from small trees that remained in the gaps.

Response to gaps varied spatially within and adjacent to gaps. *Tiarella* and *Linnaea* increased reproductive rates within gaps but not on gap borders. Fecundity of *Tiarella* was greatest in southern locations while fecundity of *Linnaea* was greatest in northern positions in gaps. Growth rates for both species are lowest in north positions of large gaps. Seedlings were present for *Tiarella* in all but the northern positions of gaps.

Resources affected fecundity and growth of both species. Soil moisture was important for both fecundity and growth of *Tiarella*. Light was important for fecundity of *Linnaea*. Effects of soil moisture and light in center positions varied with gap size unless they were overridden by structural heterogeneity.

Patterns of fecundity and growth, frequency and cover suggest that *Linnaea* can spread quickly into unoccupied space in gaps while *Tiarella* eventually increases in cover as established plants grow in height and canopy density. Although mean growth of *Tiarella* stalks is somewhat greater than for *Linnaea* stolons, maximum growth rates observed in unoccupied locations of gaps for *Linnaea* far exceed growth rates of *Tiarella* stalks in any location. Such growth rates may partially explain why relative increases in frequency of occurrence seven years after gap creation are greater for *Linnaea* than for *Tiarella*. On the other hand, greater mean fecundity and seedling density in gaps for *Tiarella* than for *Linnaea* likely contribute to slightly greater increases in cover for *Tiarella* than for *Linnaea*.

Rates and locations of performance of these two species do not represent behavior of forest herbs (e.g., *Trillium*) with lower potential rates of growth and seed production that increase on gap borders and in root gaps under dense canopy but not within gaps. Fecundity of *Trillium* is a function of plant development and resources. Growth of leaves and flower construction are delayed for about 10 yr, even in sites where light and soil moisture are associated with extremely high rates of seed production and growth of older *Trillium*. Although correlations of soil moisture (at shallow depths) and light with seed production and leaf area were low when analyzed in combination with the size of other plant parts, age and other environmental factors, both seed production and leaf area did show a non-linear response to light. Specifically, fecundity and size were distributed in a bell shaped (skewed-right) pattern along a light gradient with a peak at intermediate light. Relative growth rates of leaves showed a stronger response to soil moisture and light than leaf area. Variations of leaf area and seed production were also greatest at intermediate light because of the presence of both large, productive individuals and small, non-flowering seedlings and small non-flowering plants. Although large individuals were present in some microsites with low light, none occurred in intense light.

My major conclusions are:

1. Gap effect:

- Fecundity and growth rates of *Linnaea*, *Tiarella* increase within gaps in the canopy of Douglas-fir forests.
- *Trillium* respond to gaps, but response rates are greatest on gap borders of all gap sizes, even smallest gaps.

2. Gap size:

- Effects of gap size on mean performance of *Tiarella* and *Linnaea* were relatively weak. Differences in performance in relation to gap size are obsured to some degree by microsite variations in gaps. Effects of gap size are greater when internal structure is absent from north positons of large gaps.
- Minimum gap size associated with increases in fecundity were greater for *Linnaea* than for *Tiarella*.
- Growth of all species increases in small gaps compared to closed canopy areas (with low soil moisture content).

3. Gap position:

- Herbaceous response to gaps is non-uniformly distributed within and adjacent to gaps. *Linnaea* and *Tiarella* respond to different positions within gaps and *Trillium* performs best on gap borders.

4. Resource gradients:

- Herbs can persist in low light environments but need increases in light and soil moisture to increase growth and reproduction.
- *Linnaea, Tiarella,* and *Trillium* increase rates of fecundity and growth where light and moisture are available. *Trillium* can increase rates of performance at lower light intensities where percent soil moisture is relatively high.

5. Species differences

- Fecundity and growth vary among species located in similar resource levels and positions. Fecundity increases at higher light intensity for *Linnaea* than for *Tiarella* and at the lowest light intensity for *Trillium.*
- Increases in frequency of occurrence within large gaps were greatest for *Linnaea*. Increases in cover within large gaps were about the same *Linnaea* and *Tiarella*. Both measures of abundance within large gaps were lowest for *Trillium*.
- Growth of established plants not new establishment explain changes in the abundance of *Linnaea* within gaps. Presence of seedlings indicate that fecundity may contribute to increased abundance of *Tiarella* in gaps and *Trillium* on gap borders.
- Maximum rates of seed production per m^2 cover were greatest for *Tiarella,* intermediate for *Linnaea,* and lowest for *Trillium*.
- Horizontal growth rates (per growing season) were greater for *Linnaea* than for the other

two species in all treatments.

6. Effects of time and plant size on *Trillium.*

- Seed production and leaf area of *Trillium* are functions of plant development and resources.
- Maximum seed production and leaf area occurs north of gaps. Seedlings occur on all gap borders but not within gaps. Productive *Trillium* occur within gaps only if shaded by tree canopy on south border and by shrubs and debris within gaps.
- Although fecundity is most directly related to leaf area and is greatest in intermediate light, large belowground parts allow persistence in low and intense light.
- *Trillium* live to at least 40 yr and do not produce seeds before 10 yr.
- Depth of *Trillium* rhizomes consistently increase in depth with time.

7. Implications to ecological science

- Rates of performance of all three species vary among gap position. Thus species of herbs partition horizontal space in gaps.
- Patterns of performance of herbs along horizontal gradients in gaps are altered over time as vertical space becomes occupied by taller species.
- Differences in autecology among herbs (e.g., the morphological and physiological differences of leaves, stems, and roots) partially explain spatial and temporal patterns of performance of herbs in gaps.
- Variations of spatial and temporal trends of performance of each species in gaps are imposed by structure in gaps that alter light and soil moisture.
- Performance of herbs in the shade of forest canopy is relatively predictable. Performance of herbs in areas of gaps not shaded by the forest canopy is less predictable

because of random locations of both herbs and internal structure (debris, shrubs, and topography.

8. Implications to management of forests

- Structural diversity in plantations can benefit herbs.
- Effects of gaps vary among herbs. Therefore, the choice of gap size, location and frequency depend on which species and which responses for each species are prioritized. For example:
    - Gap size. Large gaps provide more variable microsites and contrasting resource levels than small gaps. Positions within large gaps may substantially increase seed production of *Tiarella* and *Linnaea* but not *Trillium* while, concurrently, positions bordering large gaps increase performance of *Trillium* but not *Tiarella* and *Linnaea*. Structural heterogeneity within large gaps increases perfomance rates of all three species. Small gaps will increase (1) growth of established *Linnaea*, *Tiarella*, and *Trillium* and (2) fecundity of established *Tiarella* and *Trillium*, but not *Linnaea*.
    - Gap location. The location of new gaps will affect performance of established herbs. *Linnaea* established within or near new gaps will increase in frequency and growth rates of stolons. Rates of performance and cover of *Tiarella* will increase when this species is located in the south half of new gaps. *Trillium* may increase rates of growth, seed production and seedling density when gaps are locatedjust south of established individuals.
    - Gap frequency. Frequent removal of herb, shrub and forest canopy layers will increase fecundity and growth rates of *Linnaea*. Repeated removal or damage of *Trillium* leaves will reduce size of this species in the following season.

LITERATURE CITED

Alaback, P. B. 1982. Dynamics of understory biomass in Sitka Spruce-Western Hemlock forests of Southeast Alaska. Ecology 63(6): 1932-1948.

Allen, M. F. 1993. The ecology of mycorrhizae. Cambridge University Press, Cambridge.

Alpert, P. 1996. Nutrient sharing in natural clonal fragments of *Fragaria chiloensis*. Journal of Ecology 84:395-406.

Anderson, R. C. 1994. Height of white-flowered Trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. Ecological Applications 4(1):104-109.

Anderson, R. C., O. L. Loucks, and A. M. Swain. 1968. Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. Ecology 50(2):255-262.

Antos, J. A. 1988. Underground morphology and habitat relationships of three pairs of forest herbs. Amer. J. Bot. 75:106-113.

Antos, J. A. and D.B. Zobel. 1984a. Ecological implications of belowground morphology of nine coniferous forest herbs. Bot. Gazette. 145(4)508-517.

Antos, J. A. and D. B. Zobel. 1984b. Plant form, developmental plasticity and survival following burial by volcanic tephra. Can. J. Bot. 63:2083-2090.

Antos, J. A. and D. B. Zobel. 1984c. Upward movement of underground plant parts into deposits of tephra from Mount St. Helens. Can. J. Bot. 63:2091-2096.

Antos, J. A. and D. B. Zobel. 1986. Seedling establishment in forests affected by tephra from Mount St. Helens. Amer. J. Bot. 73(4):495-499.

Atzet, T. and R. H. Waring. 1972. Selective filtering of light by coniferous forests and minimum light energy requirements for regeneration. Canadian Journal of Botany 48: 2163-2167.

Bailey, J.D., C. Mayrsohn, P.S. Doescher, E. St. Pierre, J.C. Tappeiner. 1998. Understory vegetation in old and young Douglas-fir forests of western Oregon. Forest Ecology and Management 112:289-302.

Bazzaz, F. A. 1996. Plants in changing environments: Linking physiological, population and community ecology. Cambridge University Press.

Beaty, S. W. 1988. Influence of microtopography and canopy gaps on spatial pattern of forest understory plots. Ecology 65(5):1406-1419.

Bell, A. D. and P.B. Tomlinson. 1980. Adaptive architecture in rhizomatous plants. Botanical Journal of the Linnaean Society 80:125-160.

Bell, A.D., D. Roberts, and A. Smith. 1979. Branching patterns: the simulation of plant architecture. Journal of Theoretical Biology 81:351-375.

Bierzychudek, P. 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. New Phytologist 90:757-776.

Boardman, N. K. 1977. Comparative photosynthesis of sun and shade plants. Ann. Rev. Plant Physiol. 28:355-377 1977.

Brokaw, N.V.L. 1985. Treefalls, regrowth, and community structure in tropical forests. pp. 53-69 *In* The ecology of natural disturbances and patch dynamics (Eds., S. T. A. Pickett and P. S. White) Academic Press.

Cain, M. L., H. Damman, and A. Muir. 1998. Seed dispersal and the Holocene migration of woodland herbs. Ecological monographs 68(3):325-347.

Canham, C. D. and J.S. Denslow, W.J. Platt, J.R. Runkle, T. A. Spies, and Peter S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20: 620-631.

Chazdon, R. L. and R. W. Pearcy. 1991. The importance of sunflecks for forest understory plants. Bioscience 41 (11):760-766.

Chen, J.; J.F. Franklin, and T.A. Spies. 1993. Contrasting microclimates among clearcut, edge and interior of old-growth Douglas-fir forests. Agric. and For. Meteorology. 63: 219-237.

Christian, P. 1961. Trilliums: Propagation and Cultivation, part 4. p.339-342.

Clark, D. 1990. Factors determining species composition of post-disturbance vegetation following logging and burning of old growth Douglas-fir forest. Oregon State University. M. S. Thesis.

Collins, B. S., K. P. Dunne, and S. T. A. Pickett. 1985. Responses of forest herbs to canopy gaps. *In* The ecology of natural disturbances and patch dynamics (Eds., S. T. A. Pickett and P. S. White) Academic Press.

Collins, B.S. and S.T.A. Pickett. 1987. Influence of canopy opening on the environment and herb layer in a northern hardwoods forest. Vegetatio 70:3-10.

Collins, B.S. and S.T.A. Pickett. 1988. Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. Journal of Ecology 76:437-450.

Crawley, M. J. 1986. Plant ecology. Blackwell Scientific Publications.

Davis, M. B. 1986. Climatic instability, time lags, and community disequilibrium. *In:* Community Ecology (Eds. J. Diamond and T. J. Case). Harper and Row.

Denslow, J. S. 1985. Disturbance-mediated coexistence of species. pp 307-323 *In* The ecology of natural disturbances and patch dynamics (Eds., S. T. A. Pickett and P. S. White) Academic Press.

Easter, M.J. and T.A. Spies. 1994. Using hemispherical photography for estimating photosynthetic photon flux density under canopies and in gaps in Douglas-fir forests of the Pacific Northwest. Can. J. For. Res. 24: 2050-2058.

Erikkson, O. 1988. Variation in growth rate in shoot populations of the clonal dwarf shrub *Linnaea borealis.* Holarct. Ecol. 11:259-266.

Esau, K. 1960. Anatomy of Seed Plants. Wiley, New York.

Fisher, B. L., H. F. Howe, and S. J. Wright. 1991. Survival and growth of *Virola surinamensis* yearlings: water augmentation in gap and understory. Oceologia 86: 292-297.

Fisher, R. A. 1966. The design of experiments, Hafner, New York.

Franklin, J. F. and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press.

Gadgil, M. and O. T. Solbrig. 1972 The concept of *r*- and *K*-selection: evidence from wild flowers and some theoretical considerations. The American Naturalisht:106(947): 14-31.

Gill, D. E. 1986. Individual plants as genetic mosaics: ecological organisms versus evolutionary individuals. *In* Plant Ecology (Ed. M. J. Crawley) Blackwell Scientific Publications.

Givinish,T. J. 1982. On the adaptive significance of leaf height in forest herbs. The American Naturalist 120(3):353-381.

Givinish, T. J. 1987. Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. New Phytol. 106:131-160.

Gray, A. N. 1996. Tree seedling establishment on heterogenous microsites in Douglas-fir canopy gaps. Oregon State University. Ph.D. Thesis.

Gray, A. N. and T. A. Spies. 1996. Gap size, within-gap position and canopy structure effects on conifer seedling establishment. Journal of Ecol. 84: 635-645.

Gray, A. N. and T. A. Spies. 1997. Microsite controls on tree seedling establishment in conifer forest canopy gaps. Ecology 78(8): 2458-2473.

Gray, A. N. and T. A. Spies. 1995. Water content measurement in forest soils and decayed wood using time domain reflectometry. Can. J. For. Res. 25:376-385.

Grime, J.P. 1979. Plant strategies and vegetation processes. Wiley. Great Britain. 222 pp.

Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52:107-145.

Habeck, J. R. 1968. Impact of fire suppression on forest succession and fuel accumulations in long-fire-interval wilderness habitat types. *In* Proceedings--Symposium and Workshop on Wilderness Fire. Missoula, Montana, Nov. 15-18, 1983 USDA For. Ser. Gen. Tech. Rep. INT-182 1985.

Halpern, C.B. and T.A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5(4):913-934.

Hanley, T. A. and W. W. Brady. Understory species composition and production in old-growth western hemlock - Sitka spruce forests of southeastern Alaska. Can. J. Bot. 75: 574-580.

Hansen, A. J., T.A. Spies., F. J. Swanson, and J. L. Ohmann. 1991. Conserving Biodiversity in Managed Forests. Lessons from natural forests. BioScience 41(6): 382-392.

Hanzawa, F. and S. Kalisz. 1993. The relationship between age, size, and reproduction in *Trillium grandifolium* (Liliaceae). American Journal of Botany 80(4): 405-410.

Hanzawa, F. M., A. J. Beattie, D. C. Culver. 1988. Directed dispersal: demographic analysis of an ant-seed mutualism. The American Naturalist: 131: 1-13.

Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, S.P. Cline, N.G. Auman, J.R. Sedell, G.W. Lienkaemper, K. Cromack Jr., and K.W. Cummings. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15:133-302.

Harper, J. P. 1979. Population biology of plants. Academic Press.

Harvey, A. E., Jurgensen, M. F., Larsen, M. J., Graham, R. T. 1987. Relationships among soil microsite, ectomycorrhizae, and natural conifer regeneration of old-growth forests in western Montana. Canadian Journal of Forest Research: 17-58-62.

Henry, H. A.L. and L. W. Aarssen. 1997. On the relationship between shade tolerance and shade avoidance strategies in woodland plants. Oikos 80(3): 575-582.

Hitchcock, C. L. and A. C. Cronquist. 1973. Flora of the Pacific Northwest. University of Washington Press. Seattle and London.

Hobbs, R. J. and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6:(3): 324-337.

Hopkins, W. 1994. Introduction to plant physiology. Wiley.

Hubbell, S. P. and R. B Foster. 1986. Canopy gaps and the dynamics of a neotropical forest. *In* Plant Ecology (Ed. M. J. Crawley) Blackwell Scientific Publications. London.

Hubbell, S. P. and R. B. Foster, S. T. O'Brien, K.E. Harms, R. Condit, B. Weschler, S. J. Wright, S. Loo de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283:554-557.

Huenneke, L. F. 1983. Understory response to gaps caused by the death of *Ulmus americana* in central New York. Bull. of the Torrey Bot. Club 110(2):170-175.

Huston, M. and T. Smith. 1987. Plant succession: life history and competition. American Naturalist 130:168-198.

Hutchings, M. 1986. The structure of plant populations. *In* Plant Ecology (Ed. M. J. Crawley) Blackwell Scientific Publications. London.

Jules, E. S. 1995. Consequences of forest fragmentation for the understory plant, *Trillium ovatum*: changes in demography and biotic interactions. Abstract. Conservation and management of Oregon's native flora. Native Plant Society. November 15-17, 1995.

Jules, E. S. 1996. Yellow jackets (*Vespula vulgaris)* as a second seed disperser for the myrmecochorous plant, *Trillium ovatum*. The Amer. Mid. Nat. 135:367-9.

Jules, E. S. 1998. Habitat fragmentation and demographic change for a common plant: Trillium in old-growth forest. Ecology 79(5):1645-1656.

Kaye, T. and M. Kirkland. 1994. *Cimicifuga elata:* Status, habitat analysis, monitoring, inventory and effects of timber management. Oregon Department of Agriculture, USDI Bureau of Land Management and USDA Forest Service.

Klinka, K, and V. J. Krajina, A. Ceska, and A. M. Scagel. 1989. Indicator plants of British Columbia. Vancover: University of British Columbia Press.

Knapp, A. K., W.K. Smith and D. R. Young. 1989. Importance of intermittent shade to the ecophysiology of subalpine herbs. Functional ecology 3:753-758.

Kotanan, P. M. 1997. Effects of gap area and shape on recolonization by grassland plants with differing reproductive strategies. Can. J. Bot. 75L352-361.

Kuchler, A. W. 1964. Potential natural vegetation of the conterminguous United States. American Geographical Society, Special Publichation 36.

Larcher, W. L. 1995. Physiological plant ecology, 3rd ed. Springer.

Linderman, R. G., R. N. Ames, and T. C. Allen. 1975. Studies on Lily Mycorrhizae. The Lily Yearbook, No 28. Technical Paper No. 4070. Oregon State Unversity.

Lertzman, K. P. 1992. Patterns of gap-phase replacement in a subalpine, old-growth forest. Ecology 73(2):657-669.

Lieberman, M., D. Lieberman, and R. Peralta. 1989. Forests are not just swiss cheese: canopy stereogeometry of non-gaps in tropical forests. Ecology 70(3): 550-552.

Luoma, D. L. and W. G. Thies. 1997 Stumps fumigated with chloropicrin: effects on surrounding plants. Can. J. For. Res. 27: 1737-1745.

Lovett-Doust, L. 1981. Population dynamics and local specialization in a clonal perennial (*Rannunculus repens*). I. The dynamics of ramets in contrasting habitats. Journal of Ecology 69:741-750.

Lyford, W. H. and D. W. MacClean. 1966 .Mound and pit microrelief in relation to soil disturbance and tree distribution in New Brunswick Canada. Harvard For. Pap 15. Harvard Univ., Cambridge Massachusetts.

Matlack, G.R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology 75(5)1491-1502.

McConnaughay, K.D.M and F.A. Bazzaz 1990. Interactions among colonizing annuals: is there an effect of gap size? Ecology 71:1941-1951.

McIntyre, S., S. Lavorel, and R. M. Tremont. 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. Journal of Ecology 83:31-34.

Meier, A. J., S. P. Bratton, and D. C. Duffy. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. Ecological Applications 5 (4): 935-946.

Mesler, M. R. and K. L. Lu 1983. Seed dispersal of *Trillium ovatum* (Liliaceae) in second-growth redwood forests Amer. J. Bot. 70(10):1460-1467.

Noble, I. R. and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio 43:5-21.

Pearcy, R. W., H. A. Mooney, J. E. Ehleringer, and P. W. Rundel, eds. 1991. Plant physiological ecology. Chapman and Hall.

Perry, D.A. 1988. Landscape pattern and forest pests. Northwest Environmental Journal. 4:213-228.

Perry, D. A. 1995. Forest ecosystems. Baltimore: The Johns Hopkins University Press.

Pfitsch, W. A. and R. W. Pearcy. 1992. Growth and reproductive allocation of *Adenocaulon bicolor* following experimental removal of sunflecks. Ecology 73:2109-2117.

Pickett, S. T. A. and P. S. White. 1985. The ecology of natural disturbances and patch dynamics. Academic Press.

Pickett, S. T. A., S. L. Collins and J. J. Armestro. 1987. Models, mechanisms and pathways of succession. The Botanical Review53(3):335-371.

Pitelka, L. F. and J. W. Ashmun. 1985. The physiology and ecology of connections between ramets in clonal plants. *In* The Population Biology and Evolution of Clonal Organisms (Eds. J. Jackson, L. Buss and R. Cook). Yale University Press.

Pitelka, L. F., Stanton, D. S. and Peckerman, M. O. 1980. Effects of light and density on resource allocation in a forest herb, *Aster acuminatus* (Compositate). Amer. J. Bot. 67: 942-948.

Pojar, J. and A. MacKinnon. 1994. Plants of the Pacific Northwest Coast. Lone Pine Publishing. Vancouver, Canada.

Powles, S. B., and O. Bjorkmann. 1981. Leaf movement in the shade species *Oxalis oregana:* Role in protection against injury by intense light. Carnegie Institute. Washington Yearbook 80: 63-66.

Primack, R.B. and S.L. Miao. 1992. Dispersal can limit local plant distribution. Conservation Biology 6 (4):513-519.

Rich, P.M. 1989. A manual for analysis of hemispherical canopy photography. Manual LA-11733-M. Los Alamos National Laboratory, Los Alsamos, N. M.

Rogers, R. S. 1985. Local coexistance of deciduous-forest groundlayer species growing in different seasons. Ecology 66:1041-1051.

Rose, R., C. Chachulski, and D. L. Haase. 1997. Propagation of Pacific Northwest native plants: a manual, volume 3. Unpublished.

Rothwell, F. M. and W. G. Vogel. 1982. Mycorrhizae of planted and volunteer vegetation on surface mined areas. USDA For. Serv. Gen. Tech. Rep. NE-66, 12 pp.

Runkle, J. R. 1985. Responses of forest herbs to canopy gaps. *In* The ecology of natural disturbances and patch dynamics (Eds., S. T. A. Pickett and P. S. White) Academic Press.

Runkle, J. R. 1992. Guidelines and sample protocol for sampling forest gaps. Gen. Tech. Rep. PNW-GTR-283. Portland, OR: US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Ryser, P. 1996 The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. Functional Ecology 10:717-723.

SAS Institute Inc. 1987. SAS/STAT Guide for personal Computers, version 6 edn. Cary, NC. 1028 p.

Silvertown, J .W. and J. Lovett Doust. 1993. Introduction to plant population biology. Blackwell Science.

Schultz, K. E. and M. S. Adams. 1995. Effect of canopy gap light environment on evaporative load and stomatal conductance in the temperate forest understory herb *Aster macrophyllus* (Asteraceae). Amer. Journ. Bot. 82(5):630-657.

Smith, W. K. , D. T. Bell, and K. A. Shepherd. 1998. Associations between leaf structure, orientation, and sunlight exposure in five Western Austrailian communities. American Journal of Botany 85(1): 56-63.

Smith, D. 1986. The practice of silviculture. New York: John Wiley and Sons.

Sobey, D.G. and P. Barkhouse. 1977. The structure and rate of growth of the rhizomes of some forest herbs and dwarf shrubs of the New Brunswick-Nova Scotia border region. Canadian Field Naturalist 91:377-383.

Sparling, J. H. 1967. Assimilation rates of some woodland herbs in Ontario. Botanical Gazette 128: 160-168.

Spies, T. A. 1991. Plant species diversity and occurrence in young, mature and old-growth Douglas-fir stands in Western Oregon and Washington. Pages 91-109 in L. F. Ruggiero, K.B. Aubry, A.B. kCArey, and M.H. Huff, technical coordinat ors. Wildlife and Vegetation of Unmanaged douglas-fir Forestes. USDA Forest Service Pacific Northwest Research Station, Portland, OR.

Spies, T. A. and W. J. Ripple, and G. A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications 4(3):555-568.

Spies, T. A., J. F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Canadian Journal of Forest Research 16:558-568.

Spies, T. A. and J. F. Franklin. 1989. Gap characteristic and vegetation response in coniferous forests of the Pacific Northwest. Ecology. 70(3):543-545.

Spies, T. A. 1991. Response of coniferous ecosystems to tree-fall gaps. Belowground Ecology. 2(1):13-14.

Spies, T. A.; J. F. Franklin, T. B. Thomas. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology. 69(6): 1689-1702.

Stewart, G.H. 1986. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. Canadian Journal of Forest Research, 16:558-568.

Steel, R.G.D. and J.H. Torrie. 1980. Principles and procedures of statistics. McGraw Hill, New York.

Sydes, C.. and J. P. Grime. 1981. Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. II. An Experimental Investigation. Journal of Ecology 69:249-262.

Tappeiner, J. C. and P. B. Alaback. 1989. Early establishment and vegetative growth of understory species in the western hemlock--Sitka spruce forests of southeast Alaska. Can. J. Bot. 67:318-325.

Teensma, P.D. A. 1987. Fire history and fire regimes of the central western Cascades of Oregon. Ph.D. thesis, University of Oregon, Eugene, OR.

Thompson, J. N. 1985. Patch dynamics, interactions and evolution. IN: The ecology of natural disturbances and patch dynamics (Eds., S. T. A. Pickett and P. S. White) Academic Press.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press.

Toumey J. W. and R. Kienholz. 1931. Trenched plots under canopies. Yale University School of Forestry Bulletin Number 30.

USDA Forest Service. 1994. Record of Decision for ammendments to Forest Service and Bureau of Land Management Planning Documents within the Range of the Northern Spotted Owl. Standards and Guidelines.

Valverde, T. and J. Silvertown. 1998. Variation in the demography of a woodland understory herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis. Journal of Ecology 86:545-562.

van der Pijl, L. 1969. Principles of Dispersal in Higher Plants. Springer-Verlag.

Van Pelt, R. and M. P. North. 1996. Analyzing canopy structure in Pacific Northwest old-growth forests with a stand-scale model. Northwest Science 70:15-30.

van der Heijden, M.G. A., J.N. Kilronomos, M. Ursic, P. Moutoglis, R. Stretwolf-Engle, T. Boller, A. Wiemken, and I. R. Sanders. 1998. Mycorrhizal fungal diversity determine plant biodiversity, ecosystem variability and productivity. Nature 396: 69-72.

Waring, R. H. and W. H. Schlesinger. 1985. Forest Ecosystems. Academic Press.

Watt, A. S. 1947. Pattern and process in the plant community. Journal of Ecology 35:1-22.

Wesselingh, R. A.,P.G.L. Klinkhamer, T. J. De Jong, and L. A. Boorman. 1997. Threshold size for flowering in different habitats: Effects of size-dependent growth and survival. Ecology 78(7): 2118-2132.

Whigham, D. 1974. An ecological life history study of *Uvularia perfoliata* L. The American Midland Natuarlist 91(2):343-359.

Wijesinghe, D. K. and S. N. Handel. 1994. Advantages of clonal growth in heterogeneous habitats: an experiment with *Potentilla simplex*. Journal of Ecology 82: 492-502.

Wijesinghe, D. K. and M. J. Hutchings. 1999. The effects of environmental heterogeneity on the performance of *Glechoma hederacea*: the interactions between patch contrast and scale. Journal of Ecology 87:860-872.

Zobel, D. B. and J. A. Antos, J. A. 1997. A decade of recovery of understory vegetation buried by volcanic tephra from Mount St. Helens. Ecological Monographs 67(3):317-344.

Zobel, D. B., A. McKee, G. M. Hawk, and C. T. Dyrness. 1976. Relationships of environment to composition, structure and diversity of forest communities of the Central Western Cascades of Oregon. Ecological Monographs 46:135-156.