# AN ABSTRACT OF THE THESIS OF

Andrew N. Gray for the degree of Doctor of Philosophy in Forest Science presented on March 17, 1995. Title: Tree Seedling Establishment on Heterogenous Microsites in Douglas-fir Forest Canopy Gaps

Signature redacted for privacy.

Abstract approved: ______________________________

Thomas A. Spies

Tree seedling establishment and growth were studied in experimental canopy gaps to determine the effect of structural and environmental heterogeneity on species dynamics within mature and old-growth Douglas-fir forests in the Cascades of central Oregon and southern Washington. Factors examined included forest age, gap size, within-gap position, substrate, year of germination, density of understory vegetation, shading by woody debris, light, moisture, and surface temperature. Four gap sizes, with gap diameter to tree height ratios ranging from 0.2 to 1.0, were created in the fall of 1990. Seeds of *Abies amabilis*, *Pseudotsuga menziesii*, and *Tsuga heterophylla* were sown in controlled microsites and germination, survival, and growth were monitored for two growing seasons. Seedlings established from natural seed rain were also monitored in natural microsites.

Seedling establishment was greater in gaps than in closed-canopy areas, but was relatively low in portions of large gaps exposed to direct solar radiation, particularly for *Tsuga*. Shade from woody debris facilitated establishment in exposed areas, while shade from understory vegetation aided establishment of *Pseudotsuga* but not of *Tsuga*. Establishment in shaded portions of gaps declined with vegetation cover, with a greater effect from herbs than from shrubs. Seedling establishment was greatest on decayed wood in closed-canopy areas and small gaps, was similar on mineral soil, litter, and wood in shaded portions of largest gaps, and was lowest on litter in exposed portions of large gaps. Species establishment patterns differed between years, apparently due to differences in weather. Seedling growth increased with gap size, and was greatest in gap centers. The growth response to increasing light was greatest for *Tsuga*.

Some evidence for gap partitioning by seedlings was found, although all species were most abundant in similarly shaded portions of gaps. Establishment and growth of the different species was related to seed size and interacting gradients of above- and below-ground resource levels. Heterogeneity at the seedling scale often over-rode environmental gradients associated with gap size and within-gap position. While gaps may accelerate development of old-growth characteristics in these forests, establishment of *Tsuga heterophylla* is particularly sensitive to microsite quality.

# Tree Seedling Establishment on Heterogenous Microsites in Douglas-fir Forest Canopy Gaps

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Andrew N. Gray

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# TREE SEEDLING ESTABLISHMENT ON HETEROGENEOUS MICROSITES IN DOUGLAS-FIR FOREST CANOPY GAPS

## CHAPTER 1: GENERAL INTRODUCTION

### Introduction

"Forest dynamics are driven by disruption, with heterogeneity in disturbances hypothesized to produce forests that are inherently heterogeneous and ever-changing" (Platt and Strong 1989, p. 535). By removing some or all of the biomass present on a site, disturbances provide opportunities for new tree establishment and the growth of surviving individuals. Many factors affect this process, including site availability, differential species availability, and differential species success (Table 1.1, Pickett *et al.* 1987). These factors span a range of spatial and temporal scales, and interactions between them can profoundly affect the composition of vegetation colonizing a disturbed area. Controls on the colonization process can largely determine community composition, but may not be discernible through observation of established plants (Watt 1947, Grubb 1977, Harper 1977).

Canopy gaps are relatively small disturbances (involving the death of one to several trees in a group) that create patches of younger vegetation within older forests. These patches may be foci for compositional change of entire forest stands, or for maintenance of existing composition in a dynamic steady state (Veblen 1992). Canopy gaps are important sites for plant establishment and growth because of the greater abundance of resources (*e.g.* light and moisture) relative to the surrounding closed-canopy forest (Canham and Marks 1985). Resource levels can vary greatly within and among gaps, however, potentially affecting species dominance patterns (Orians 1982, Denslow 1987). Tree seedling germination and survival occurs on understory microsites at the scale of a few $cm^2$. Microsite quality in most plant communities is extremely heterogenous, and the number of microsites that are 'habitable' and the speed with which they are colonized determines the population size

**Table 1.1:** A hierarchy of successional causes (from Table 3 in Pickett *et al.* 1987)

| General causes of succession | Contributing processes | Modifying factors or conditions |
|---|---|---|
| Site availability | Coarse-scale disturbance | Size, severity, time, dispersion |
| Differential species availability | Dispersal | Landscape configuration, dispersal agents |
| | Propagule pool | Time since last disturbance, land use treatment |
| Differential species performance | Resource availability | Soil conditions, topography, microclimate, site history |
| | Ecophysiology | Germination requirements, assimilation rates, growth rates, population differentiation |
| | Life history strategy | Allocation pattern, reproductive timing, reproductive mode, |
| | Environmental stress | Climate cycles, site history, prior occupants |
| | Competition | Hierarchy, presence of competitors, identity of competitors, within-community disturbance, predators and herbivores, resource base |
| | Allelopathy | Soil chemistry, soil structure, microbes, neighboring species |
| | Herbivory, predation, and disease | Climate cycles, predator cycles, plant vigor, plant defenses, community composition, patchiness |

of plants (Harper 1977). Thus understanding the nature and abundance of different microsites, and their "habitability" for different species, is crucial to understanding forest dynamics following disturbance. Seed dispersal and microsite environments can be affected by factors operating at scales much larger than the microsite itself, however. The multiple factors affecting tree seedling establishment in microsites can be profitably arranged into a hierarchy of higher-level constraints on lower-level processes (after Allen and Hoekstra 1992) (Figure 1.1). Using light intensity at a microsite as an example:

-- latitude and cloud cover at the landscape scale determine light intensity above the canopy

-- the structure and composition of tree crowns at the stand scale determine light intensity penetrating through the canopy

-- the size, shape, and orientation of gaps determine the intensity of direct and indirect light falling within gaps

-- the density of understory vegetation and coarse woody debris within a gap determine light intensity at different microsites.

The heterogeneity of environments and resources within and among gaps may control species diversity in forests (Orians 1982). Gap size and position within gaps are important determinants of tree composition in gaps in many forests (Runkle 1982, Poulson and Platt 1989, Minckler and Woerhide 1965, Brandani *et al.* 1988). Other factors may override the effects of gap size and position, however. In some forests, the density of understory plants and presence of specific substrates for seedling establishment are more important to tree species' success than gap size (Veblen 1985, Ehrenfeld 1980, Nakashizuka 1989). Some tropical forests with high temporal and spatial variation in seed rain and gap events also show few species-specific patterns with gap size and within-gap location (Denslow 1987, Uhl *et al.* 1988).

Several different ideas have been advanced concerning the importance of gaps in forest dynamics, which are not necessarily mutually exclusive. The "gap partitioning hypothesis" proposes that the resource gradient from intact canopy areas into large gaps is too broad to be dominated by any one species; in other words, a

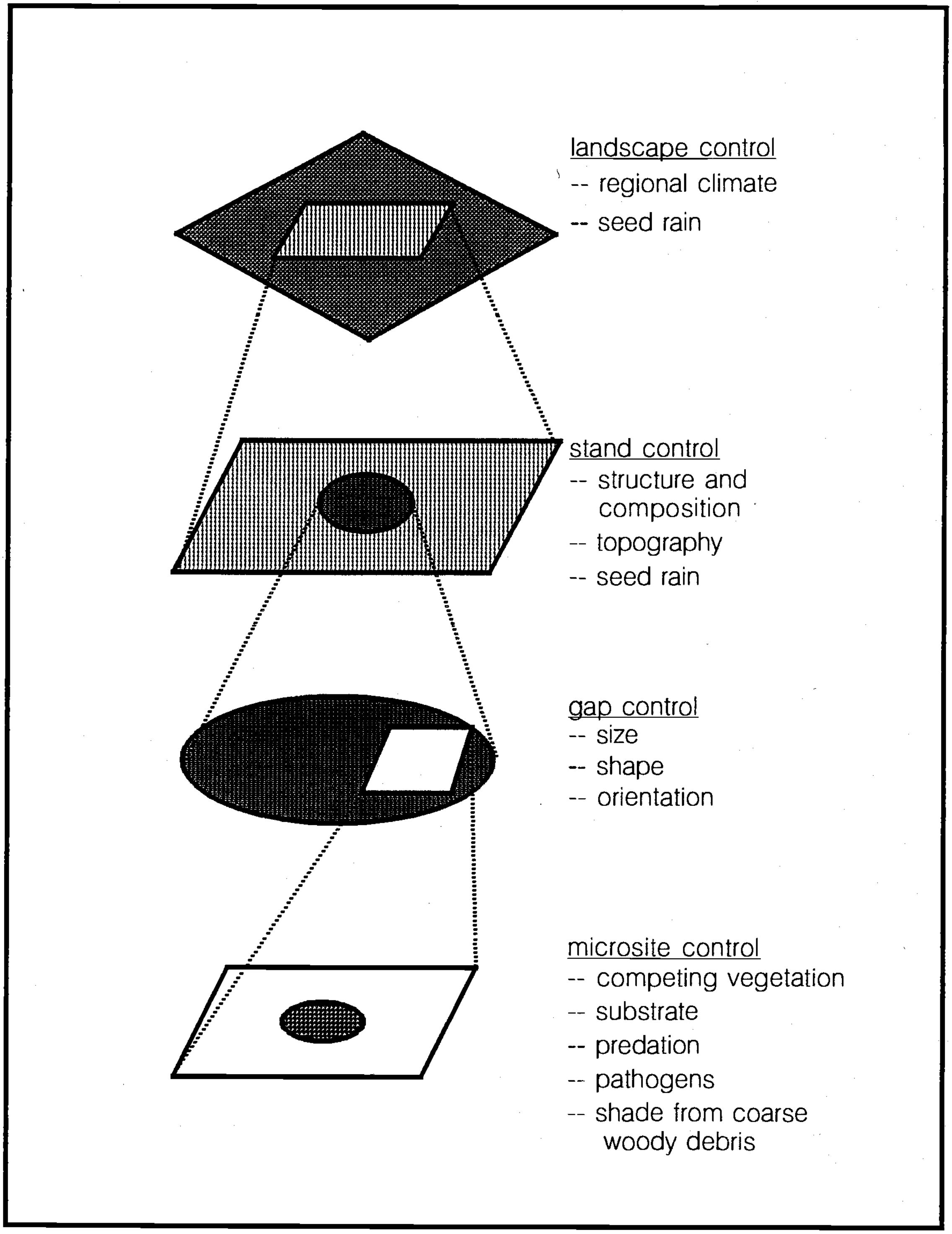

**Figure 1.1:** Hierarchy of controls on seedling establishment in forest canopy gaps

given species' autecology (e.g. shade-tolerant or -intolerant) should make it most successful in environments characteristic of a given gap size or within-gap location (Ricklefs 1977, Denslow 1980). An alternative hypothesis is that development in gaps is entirely a function of chance (*e.g.* individuals happen to be present when and where a gap forms, or early colonists succeed regardless of species) (Denslow 1987). Another contrasting idea is that vegetation response to gaps is largely determined by vegetation patterns that were established in the understory of the closed-canopy forest (Brokaw and Scheiner 1989).

All green plants require the same basic resources (light, water, mineral nutrients) for survival and growth. Most canopy gap research on plant dynamics, however, examines readily identifiable patches of vegetation that are usually designated structurally and/or compositionally (*e.g.* gap/non-gap, mineral soil/litter). Gap research has been criticized for testing the importance of the gap paradigm by only working within the gap/non-gap classification, instead of examining the variation in structure and resources to which plants actually respond (Lieberman *et al.* 1989). Some studies quantify resource levels in the various patch types studied (Minckler and Woerhide 1965, Denslow 1987, Uhl *et al.* 1988) while many others do not (*e.g.* Runkle 1982, Brandani *et al.* 1988, Nakashizuka 1989, Veblen 1985). The patch classifications are generally assumed to represent important environmental differences, but the relative accuracy of patch-based versus resource-based models of plant performance beneath heterogenous forest canopies has not been evaluated.

The role of gaps in the conifer forests of the Pacific Northwest has received little attention (but see Stewart 1986a, Spies *et al.* 1990). Large and high-intensity disturbances like wildfire and clear-cutting have been studied extensively (*e.g.* Hemstrom and Franklin 1982, Morrison and Swanson 1990, Halpern 1989), yet gap formation appears to have similar point return intervals as fire in these forests (Spies and Franklin 1989) and may therefore have an equally important impact on community development. It is not known how the change in species dominance with succession from mature to old-growth forest in the region is influenced by patch-scale changes via canopy gaps. The most typical successional sequence in the "Douglas-fir forests" of the region (*Tsuga heterophylla* Zone in Franklin and Dyrness 1973) is of young, generally even-aged forests dominated by relatively shade-intolerant *Pseudotsuga menziesii* ((Mirb.) Franco) (Douglas-fir) in a single tree canopy layer developing into multi-layer old-growth forests containing increasing amounts of shade-tolerant *Tsuga heterophylla* ((Raf.) Sarg.) (western hemlock) and *Abies amabilis* (Dougl. Forbes) (Pacific silver fir) (Munger 1940, Franklin *et al.* 1981). Foresters have generally assumed that initial dominants gradually lose control on a site as they grow older, allowing the invasion and development of understory plants, but the mechanisms of this late-successional development are not well understood (Oliver and Larson 1990). Causal mechanisms of species abundance can rarely be ascertained by examining mature vegetation, and studies must focus instead on the processes of seedling establishment and early growth (Harper 1977, Grubb 1977).

Several non-exclusive hypotheses concerning the importance of canopy gaps for succession in mature Douglas-fir forests are possible:

1. Gaps are not important for tree establishment; shade-tolerant trees can establish under intact canopies of mature shade-intolerant trees.
2. Widespread thinning of canopy dominants and/or abrasion of overlapping crowns as stands age create many tiny gaps which increase light levels across the entire stand; shade-tolerant trees establish throughout the stand in response to these changes.
3. Establishment of shade-tolerant trees is limited to the environments present within discrete canopy gaps.

The overall objective of this dissertation is to examine the role of canopy gaps on tree seedling establishment in mature, mesic Douglas-fir forests of the western Cascade Range. The process of seedling establishment in experimentally-created gaps was studied in terms of stand structure, gap size, within-gap position, substrate, understory shade, understory competition, and interactions between these factors. Resource levels under a variety of conditions were quantified and related to seedling survival and growth. Results provide new information on the mechanisms and nature of compositional change in mature forests of the Pacific Northwest.

The role of gaps in mature forests has important implications for forest management in the Pacific Northwest. The loss and fragmentation of late-successional forests has been a contentious issue for decades. Recent proposals for management of federal lands emphasize moving young stands within reserve areas toward greater structural and compositional diversity (FEMAT 1993). While passively allowing stands to age may accomplish this goal, selective harvest has been proposed as a way to achieve structural complexity more rapidly and allow some commodity extraction as well (McComb *et al.* 1993, FEMAT 1993). For either strategy, it is important to know how canopy gaps influence development of old-growth forests, how long it would take for old-growth structure to develop naturally, and whether patch selection harvesting can mimic this process. A related silvicultural question is whether the commercially valuable *Pseudotsuga* can be grown in small patches in multi-aged, multi-structured stands. If the occurrence of gaps is increasing on a global scale, as is suggested for the tropics by Phillips and Gentry (1994), understanding the nature of species' response to gap events will be increasingly important to forest management in many regions.

## Literature Review

### Role of gaps in forest dynamics

Succession is the process of change in vegetational composition on a given area over time. The primary processes of succession elucidated by Frederick Clements (as presented by Pickett *et al.* 1987) are: *nudation*, the formation of an area wholly or partially devoid of plants by a disturbance, *migration*, the dispersal of organisms to the open site, *ecesis*, the establishment of organisms at the site, *competition*, the interaction between organisms at the site, and *reaction*, the modification of the site environment by established organisms which in turn modifies the ability of other organisms to establish and survive. Complementing Clements' scheme, succession in forest communities often follows a predictable sequence of stages (Bormann and Likens 1979, Peet and Christensen 1980, Oliver 1981, Oliver and Larson 1990--using Oliver's terminology): *stand initiation stage*, characterized by the reoccupation of a site following a large disturbance, *stem exclusion stage*, characterized by the occupation of the "growing space" of a site by established individuals until one or more resources becomes limiting, thereby preventing new establishment and often causing mortality of individuals of lesser stature and/or competitive ability, *understory reinitiation stage*, characterized by the establishment and/or growth of understory plants in response to poorly understood environmental changes associated with continued development of overstory trees, and *old-growth stage*, characterized by growth of trees which established after the stem exclusion stage into the overstory, usually in response to mortality of overstory individuals. While mortality of overstory trees can create canopy gaps during any of these stages, vegetation change (i.e. "gap dynamics") is most common in the latter two stages because existing overstory trees are unable to fully occupy the growing space associated with gaps (Oliver and Larson 1990).

The "gap-phase" concept presented by Watt (1947) suggests that distinct patches within mature forests follow a process of cyclical change with the mortality of dominant trees creating a *gap phase*, to which establishment of many species is restricted. Development of the similar-aged vegetation in these gaps proceeds through the *building* and *mature* phases, the duration of which depends on the longevity of the dominants and whether other species successionally replace them. Most researchers use the term "gap" to refer to openings created by the death of a large branch, a single tree, or a patch of several trees (Runkle 1992), although Watt used the term to refer to large disturbances as well. It is important to recognize, however, that canopy structure of non-gap ("closed-canopy") areas can be quite variable and can experience a wide range of microclimates (Lieberman *et al.* 1989). In addition, closed canopy areas can be affected by light passing through canopy gaps in temperate latitudes: one model indicates that light passing through a single-tree gap can double light levels of closed-canopy forest over an area as much as five times the area of the gap (Canham *et al.* 1990). The characteristics of gaps that appear to be important for tree establishment include gap size, shape, and orientation, time and periodicity of gap creation, influence of gap-creating species, and within-gap environmental heterogeneity (Veblen 1992).

Canopy gaps are important sites for tree development because of the greater abundance of resources relative to closed-canopy areas. Resource levels may vary considerably among and within gaps, however. Light levels within gaps vary with latitude, gap size, shape, and orientation, the height of surrounding trees, and the slope of the site (Geiger 1965, Poulson and Platt 1989, Canham *et al.* 1990). In temperate latitudes, levels of diffuse light increase with gap size, but significant levels of direct solar radiation also reach the understory in northern portions of large gaps (Phillips and Shure 1990, Canham *et al.* 1990). Although different species often have dramatic effects on light levels (Canham *et al.* 1994), the effect of stand composition surrounding gaps on light levels within gaps has not been considered. Soil moisture levels are usually higher in canopy gaps than in closed-canopy areas (but see Collins and Pickett 1988), with little difference associated with gap size, but with decreasing moisture levels near gap edges (Denslow 1987, Minckler and Woerhide 1965, Vitousek and Denslow 1986). This soil moisture response in gaps is commonly attributed to the decrease in transpiring vegetation (Veblen 1992) and a reduction in root density (Wilczynski and Pickett 1993, Vogt *et al.* 1993, Parsons *et al.* 1994) but may be due to increased throughfall of precipitation (Canham 1993). Although rooting patterns differ with tree species and stand age (Hinckley *et al.* 1978, Vogt *et al.* 1983), the effect of stand composition on soil moisture in gaps has not been studied. Differences in soil nutrient levels between gaps and non-gaps have been found in some studies (Mladenoff 1987, Canham 1993, Parsons *et al.* 1994), but not others (Uhl *et al.* 1988, Vitousek and Denslow 1986, Vogt *et al.* 1993). The differing gradients of soil moisture from gap edge to gap center superimposed on north-south light gradients produce an array of resource combinations associated with within-gap position (Oliver and Larson 1990).

Heterogeneity in resources and microsite conditions within and among gaps has been associated with differential species establishment, survival, and growth in temperate deciduous as well as moist tropical ecosystems (Runkle 1985, Denslow

1980, Orians 1982, Lorimer 1989). Whitmore (1989) proposed that tree species fall on a continuum between two basic types: *climax* species which can establish and develop in the shade ("shade-tolerants"), and *pioneer* species which require relatively high light levels for establishment and growth ("shade-intolerants"). Although light levels generally increase with gap size, the importance of gap size on tree seedling composition and density is unclear. Many studies have found that different gap sizes have differing species composition, often in relation to shade tolerance (Runkle 1982, 1990, Phillips and Shure 1990, Poulson and Platt 1989, Huenneke 1983, Lawton and Putz 1988, Minckler and Woerhide 1965, Brokaw and Scheiner 1989). Other studies have found no difference in composition with gap size (Spies *et al.* 1990, Ehrenfeld 1980, Nakashizuka 1989). Seedling and sapling density tends to increase with gap size (Runkle 1982, Alaback and Tappeiner 1991), but Veblen (1985) found the reverse to be true. Growth rates usually increase with gap size (Phillips and Shure 1990, Minckler *et al.* 1973, Stewart 1986a); Hibbs (1982) found that different species attained their highest growth rates in different gap sizes. Contradictory results may be due to differing species life histories and gap characteristics among forest types, although differences in the range of gap sizes studied or in sample sizes by gap size could also be important. Comparisons between studies are often hindered by description of gap size in terms of area, with no information on height of surrounding trees, which is a primary determinant of gap light environments.

The heterogeneity of environments within gaps may be the most important characteristic of gaps with regards to species diversity (Orians 1982). Many studies have found differences in species composition associated with within-gap position (Brandani *et al.* 1988, Stewart 1986a, Poulson and Platt 1989, Lorimer 1989), although Uhl *et al.* (1988) did not. Vegetation growth rates also vary by position, often being greatest in gap centers (Alaback and Tappeiner 1991, Denslow *et al.* 1990, Minckler *et al.* 1973, Uhl *et al.* 1988). An experimental study comparing positions that primarily receive morning or afternoon light (west or east sides, respectively) found no consistent effects on seedling growth (Wayne and Bazzaz 1993). The availability of substrates like mineral soil have been found to be important even in forests where they represent less than 0.1% of the area

(Nakashizuka 1989, Putz 1983). Similarly, logs can be important for establishment of both shade-tolerant and -intolerant trees (Lawton and Putz 1988, Veblen 1989, Stewart 1986a, White *et al.* 1985). Competition from understory vegetation in gaps may limit tree establishment, particularly for shade-intolerant species (Veblen 1982, 1989, Nakashizuka 1989). For some tropical forests in particular, Denslow (1987) found that species seemed to be arrayed along a continuum of light requirement, but little of the variation in composition was related to gap size and position factors because high species diversity, low predictability of gap events, and temporal and spatial variation in seed rain contributed to high sampling error.

Canopy gaps are important sites for tree development; it is unclear, however, whether all trees require canopy gaps for survival in the understory or growth into the canopy. Knowledge is incomplete about whether trees which dominate gaps establish in response to the gap environment or were present before gap formation (Connell 1989). Many shade-tolerant species can establish and maintain minimal growth rates under low light levels (as "advance regeneration") until they are released from suppression by overstory mortality (Oliver and Larson 1990). The patchiness of advance regeneration present before gap formation may lead to differences in species composition between gaps (Brokaw and Scheiner 1989). Some studies indicate that most gap dominants develop from advance regeneration (Runkle 1990, Uhl *et al.* 1988). Response of advance regeneration to increased resources can be quite slow, however, and growth can be exceeded by germinants of the same, or less shade-tolerant, species (Burton and Mueller-Dombois 1984, Runkle 1989, Poulson and Platt 1989). While shade-tolerants may not need gaps to become established, in many cases they appear to require multiple gap events in order to grow into the canopy (Uhl *et al.* 1988, Runkle and Yetter 1987, White *et al.* 1985). It may be that the success of advance regeneration depends less on actual gap size or light levels than on disturbance frequency and the duration of periods of release vs. periods of suppression (Canham 1989). It is important to note, however, that if the overstory canopy is not too dense, some shade-tolerant species may grow directly into it (Canham 1989).

Most of the work on gap dynamics has focused on old-growth forests (*e.g.* Denslow 1980, Runkle 1981) and little is known about the importance of gaps in earelier phases of forest development. Gap-phase replacement of canopy trees appears to maintain species composition in old-growth temperate hardwoods of the eastern U.S. (Runkle 1990, White *et al.* 1985), although identification of compositional equilibrium is problematic (Veblen 1992). Whether species respond differently to gaps in stands of different age classes is unknown. Older stands with larger trees may lead to larger gaps as those trees die, thus allowing more shade-intolerant trees to establish (Brokaw and Scheiner 1989). On the other hand, the increasing dominance of dense-canopied shade-tolerant species with stand age may limit overall light levels, making gaps more important for establishment of shade-tolerant species and excluding establishment of intolerants (Spies and Franklin 1989). Variation in stand composition can also affect the distribution of advance regeneration, which may lead to filling of similar gaps by different species (White *et al.* 1985, Stewart 1986a).

This brief review of gap dynamics indicates that there appear to be few general patterns describing species response to forest gaps; all of the variables important for understanding succession (Table 1.1) appear to be important for gap dynamics as well. This suggests that the gap paradigm must be broadened to include forest structure, the nature and severity of disturbance, within-gap heterogeneity, and the interaction between large catastrophic and small disturbances (Spies and Franklin 1989).

## Canopy gaps in the Pacific Northwest

Canopy gaps in the Pacific Northwest are created by a variety of agents, including fire, windthrow, wind-snap, landslides, avalanches, insects, root rot, butt rot, and other pathogens, or a combination of these (Meyer 1930, Agee 1991, DeBell and Franklin 1987, Spies *et al.* 1990, Franklin *et al.* 1987, Oliver *et al.* 1984). Standing dead and wind-snap tend to be the most common conditions of dead trees in intact forest stands (58-87%), followed by wind-throw (9-23%) (Franklin *et al.* 1987, Franklin and DeBell 1988, Spies *et al.* 1990). Thus most gaps cause relatively little disturbance to soil or understory plants, although large amounts of coarse woody debris are often present on the forest floor. Moderate intensity fire created patchy openings in these forests in the past (Teensma 1987, Morrison and Swanson 1990), however, leaving standing dead trees and a variety of substrates ranging from intact forest floor to mineral soil. Gaps within stands are not always a result of recent tree mortality, however; Meyer (1930) estimated that 12% of the total area in a survey of mature forests had remained open since stand initiation. Rates of gap formation appear to vary with stand age, with mortality of overstory trees being twice as frequent in mature stands than in old-growth stands (Spies *et al.* 1990).

The most common size of canopy gap in the only surveyed old-growth Douglas-fir stand in the Pacific Northwest was 85 $m^2$, typically caused by the death of two or more trees. The same study found a median gap size of 19 $m^2$ in a mature stand, typically caused by the death of one tree (Spies *et al.* 1990). A survey by Meyer (1930) of 63 mature stands (average age around 80 yrs) found that 71% of the canopy gaps were less than 200 $m^2$ in size (this calculation excludes his "veterans" and "hardwoods" classes, but includes "gullies and creeks"). Although not as common, gaps greater than 300 $m^2$ in size do occur (Spies *et al.* 1990, Meyer 1930). Vegetation response within canopy gaps appears to be much slower than that found in other forests, generally with a lack of canopy closure within gaps even 25 yrs after gap formation (Spies *et al.* 1990).

## Establishment of *Pseudotsuga menziesii*

The establishment of *Pseudotsuga menziesii* from seed has been studied primarily in open areas such as clearcuts. Seed production by *Pseudotsuga* is erratic, with years of abundant production occurring at intervals of 2 to 10 years; most seed is shed between October and December (Isaac 1943, Reukema 1982). Seed predation is an important factor in clearcuts: in one study, birds and mammals consumed 69%

of the seed before germination, and cutworms (*Noctuidae*) and mammals consumed 19% of the seedlings during germination (Gashwiler 1967). In another study, germination of seeds protected from predation was twenty-four times greater than that of unprotected seed in clearcuts (Minore 1986). Deer mice (*Peromyscus maniculatus*) appear to be an important predator, with populations often increasing sharply following large seed crops (Halvorson 1982). The primary abiotic cause of mortality in open sites is related to high soil surface temperatures, with temperatures greater than 52° C being lethal in the first weeks after germination (Silen 1960). Seedlings are often able to withstand higher temperatures (up to 71° C) by the end of the first growing season (Isaac 1943, Hermann 1963). Substrate material and duration of exposure can affect lethal temperatures over a range of 28° C (81° C for 5 minutes to 53° C for two hours) (Silen 1960). The effects of substrate on temperature has been the primary focus of many investigations; blackened soil is hottest (Isaac 1943), and unburned mineral soil tends to be cooler and drier than soil with a covering of litter (Hermann 1963). Survival and growth of *Pseudotsuga* seedlings was similar on mineral soil and forest floor seedbeds in one study, however (Hermann and Chilcote 1965). Seedling survival in exposed areas appears to benefit from understory shade (Minore 1972), with shade from logs and stumps being better than that from live plants (Isaac 1938). Degree of shade appears to have no effect on the germination of *Pseudotsuga* seed, although damping-off fungi (several species--Russell 1990) and predation appear to be important agents of mortality in shaded microsites (Hermann and Chilcote 1965).

Little work has focused on establishment of *Pseudotsuga menziesii* within stands, although Franklin (1963) described increased seedling survival in a shelterwood cut, attributed to intermittent shading by standing tree boles. *Pseudotsuga* saplings occur in small gaps in dry forest areas (Franklin and Dyrness 1973, Means 1982), but is rare in mesic forests of the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973, Isaac 1943). In Sierran mixed-conifer forests, mortality from predation, fungi, and over-winter litter burial were more important in shaded than unshaded portions of stands (Tappeiner and Helms 1971). Survival of *Pseudotsuga* germinants within coastal Sitka spruce (*Picea sitchensis* (Bong.) Carr.)

forests was low and inconsistent on substrate and competition treatments (Harmon and Franklin 1989). Of 100 *Pseudotsuga* seedlings examined within closed-canopy areas of Cascade forests, virtually all were rooted into mats of mycorrhizal fungi (Griffiths *et al.* 1991). It has generally been assumed that *Pseudotsuga* is limited by insufficient light within forests, but the thresholds of resource limitation have not been established.

## Establishment of *Tsuga heterophylla*

In contrast to *Pseudotsuga menziesii*, relatively few studies of *Tsuga heterophylla* seedling establishment have been conducted in open areas. Seed production of *Tsuga* is frequent and abundant, with heavy cone crops occurring every 3 to 4 yrs, and rarely a year occurring without some seed production (Ruth 1976). Most seed is shed between October and January, but up to 5% may be shed during summer months (Williamson 1976). Seed predation in one clearcut consumed approximately 40% of *Tsuga* seed fall, while 29% of the seedlings were consumed during germination (Gashwiler 1967). In another study, germination of seeds protected from predation was eight times greater than that of unprotected seed in clearcuts (Minore 1986). Lethal temperatures have not been established for *Tsuga*, but it appears to be more sensitive to exposure than *Pseudotsuga* (Livingston and Black 1987a). No seedlings established in recent clearcuts in one study in the Oregon Coast Range, although good regeneration can occur when microsites are shaded or during a wet spring (Ruth 1976). Damping-off fungi may be important causes of mortality to germinants in cool and moist conditions. Within forests, most established *Tsuga* seedlings are found on decayed *Pseudotsuga* logs (Christy and Mack 1984). Survival of planted *Tsuga* seed was greater on logs than on the forest floor, but less so when competing vegetation was removed from the forest floor (Harmon and Franklin 1989). Survival on the forest floor in intact forests seems to be limited by the inability of seedlings to establish extensive root systems (due to relatively small seed size) before the forest floor is dried out by the roots of established vegetation

(Haig *et al.* 1941, Scott *et al.* 1976). Williamson (1976) stated that *Tsuga* could establish on any substrate as long as moisture was adequate. Greater early survival on logs as opposed to forest floor may be at least partially offset by increased mortality as logs fragment and topple seedlings and saplings (Harmon and Franklin 1989).

The establishment of *Tsuga heterophylla* in relation to overstory canopy structure has received considerable attention. In the *Tsuga heterophylla/Abies amabilis* transition zone (after Franklin and Dyrness 1973), *Tsuga* survival was highest in gaps, as well as on logs and wind-throw mounds, presumably due to earlier snow-melt and less burial of young seedlings by litter mats (Thornburgh 1969). In similar forests in British Columbia, most *Tsuga* saplings in gaps were found on logs, and those on the forest floor were not judged to be potential gap-fillers (Lertzman and Krebs 1992). In mesic forests, *Tsuga* appeared to be more abundant in gaps than in closed-canopy areas, although most established prior to gap formation (Stewart 1986a). In similar forest types, the difference in *Tsuga* abundance between gaps and closed-canopy areas was greater in an old-growth forest than in a mature forest (8 vs. 3 times as much, respectively) (Spies *et al.* 1990). No significant relationship was found between seedling survival or density and light levels between 10 to 70% of open under coastal shelterwood treatments (Ruth 1976). Minore (1972) found that most seedlings in coastal forests were on logs at light levels less than 40% of open, on both logs and forest floor at 40-60% light, and few on either substrate at higher light levels. In coastal *Picea sitchensis* stands, survival of planted *Tsuga* seeds on logs was highest at 90-60% canopy cover, but growth increased with decreasing canopy cover (Harmon 1987). Seedling growth was greater in trenched plots, although no difference in soil moisture was detected (Christy 1986). The process of *Tsuga* seedling establishment in relation to gap characteristics has not been studied directly. The relationship between successful gap capture and tree origin (i.e. advance regeneration or new establishment) is also unknown.

## Establishment of *Abies amabilis*

Most studies of *Abies amabilis* seedlings have described seedling densities in relation to stand characteristics. Seed production by *Abies* is erratic, with abundant crops occurring every 3 to 6 yrs, and dispersal occurring from September to November (Franklin 1974). Post-dispersal seed predation appears to be important. In one study, germination of seeds protected from predation was twelve times greater than that of unprotected seed in clearcuts (Minore 1986). Thornburgh (1969) noted that seedling consumption by rodents and insects does occur, although *Peromyscus* apparently prefer *Pseudotsuga* and *Tsuga* seed over those of *Abies* (Moore 1940). Density of *Abies* tends to be greater in gaps than in closed-canopy areas (Thornburgh 1969, Long 1976, and Stewart 1986a). The density of *Abies* seedlings younger than 50 yrs of age was negatively correlated with a wide range of tree canopy and understory herb cover in one study (Wilson 1991). Another study, however, found no relationship between the distribution of saplings (30-60 cm tall) and canopy cover (Lertzman 1992). Survival of *Abies* in exposed areas may depend on whether germinants have sufficient time to develop deep roots before summer drying of upper soil layers (Kotar 1972). Seedling survival may be better on mineral soil than on forest floor, but the effect is not consistent (Kotar 1972, Thornburgh 1969). Regeneration of *Abies* has been found to be irregular in space and time, possibly due to transient canopy gaps or climatic variation (Wilson 1991). The effect of gap size, substrates, and resource availability on *Abies* establishment has not been determined.

## Methodology of seedling studies

Studies of seedling establishment can be observational or manipulative. The simplest type of study is a survey in which inferences are made concerning the types of environments in which seedlings are found and the potential causal mechanisms of establishment (Long 1976, Maguire and Forman 1983). Specific conclusions based on observations made at one point in time may be tenuous, however, since sites favorable to early survival may be detrimental to later survival, and sites in which older seedlings are found may have been much different during early phases of establishment. Thus it is preferable to track populations of seedlings over time to describe both emergence and survival of seedlings.

Studies of seedling establishment based on natural seed rain (Gashwiler 1967, 1970) do not involve manipulation of seed dispersal mechanisms, but must rely on annually erratic seed production. This type of study is necessarily long-term (5 or more years to get large seed crops of the species of interest) to adequately characterize emergence and survival, and comparisons between species may be affected by different population sizes or emergence of different species in years with differing climate.

Most seedling establishment studies entail sowing seed under desired conditions and following emergence and growth over one or more growing seasons (*e.g.* Harmon and Franklin 1989, Fried *et al.* 1988, Christy and Mack 1984, Thornburgh 1969, Kotar 1972, deSteven 1991, Minore 1986). Seeds were protected from small mammal and bird predators with wire cages in all of these studies. In some studies, the exclosures were removed soon after germination was completed, while in others they were left for the duration of the study. Paired plots of protected and unprotected seed may be included to assess predation effects, although predation can vary greatly from year to year due to fluctuating populations of small mammals or fluctuating food supply (Gashwiler 1967). In addition, experimenters often sow seed at unnaturally high densities; the likelihood of predators consuming most of the seed in concentrated, unprotected patches of food is high (Minore 1986). One solution to this problem is to sow unprotected seed on dispersed transects (Fried *et al.* 1988), but this makes application of specific manipulations (e.g. weeding, trenching, substrates) problematic. Few studies have attempted to account for non-predation effects of exclosures by adding treatments using wire cages open to predation in addition to uncaged areas (but see Gashwiler 1967). Even this approach depends on sufficient unconsumed seedlings in unprotected treatments to establish exclosure effect. Other studies have used seed coated with rodenticide instead of exclosures (Hermann 1963).

Treatments are usually assessed in terms of the number of planted (or naturally dispersed) seed which emerge, and the number of those which survive for successive growing seasons. Although following the fate of individuals is preferable (Harper 1977), most studies have tracked numbers of individuals in a treatment (*i.e.* population size) over time. Survival percentages can be rather small and variable, ranging from 15-90% for *Pseudotsuga menziesii* (Hermann and Chilcote 1965) to 0.2-5% for *Tsuga heterophylla* (Harmon and Franklin 1989). Most studies plant at least 50, and up to 500, seeds per treatment to ensure a reasonable population size to track over time. Environmental measurements of light, surface temperature, and soil moisture are often made on a subset of treatments for descriptive or correlative assessment of potential causes of differences in survival.

Most of the studies I examined which monitored early seedling establishment did not plant seeds in successive years (Kotar 1972, Thornburgh 1969, Christy and Mack 1984, Hermann and Chilcote 1965, Fried *et al.* 1988, Harmon and Franklin 1989, Gill and Marks 1991, Minore 1986). Other studies planted successively over 2 or 3 years (Tappeiner and Alaback 1989, Burton and Bazzaz 1991, DeSteven 1991). The main emphasis of most studies was on survival over the first growing season, although some (*e.g.* Harmon and Franklin 1989) tracked survival into the second year.

## Study Design and Objectives

### Gap Study

To examine the role of gaps in Douglas-fir forests in the Pacific Northwest, an interdisciplinary study was established which created experimental gaps of various sizes by cutting patches of trees. A primary objective of this research was to determine whether below-ground resources and processes are affected by the presence and size of canopy gaps. The study was designed to test the role of above- and below-ground resource abundance on plant community response to gaps, specifically as they related to forest successional stage, gap size, and within-gap heterogeneity. A long-term experimental approach was chosen by documenting initial conditions and controlling differences in topography, gap shape, and plant communities among gaps. Prior to gap creation, permanent sample grids were established in each plot and trees were tagged, measured, and mapped. Variables measured before and after gap creation include: vegetation cover and biomass, microclimate (light and air and soil temperature), soil moisture, tree seedling establishment, litterfall, soil leachate, root density, nitrogen mineralization, and foliage decomposition.

The experimental gaps were created in four forest stands of natural origin on relatively flat sites (less than 20% slope) within the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973) of the west side of the Cascade Mountains. Two stands were in old-growth forests (approximately 500 yrs in age) dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla* in multiple canopy layers, and two stands were in mature forests (90-140 yrs. in age) dominated by *Pseudotsuga* in a single canopy layer (Table 1.2). One old-growth stand was located in the H.J. Andrews Experimental Forest northeast of the town of Blue River in the central Oregon Cascades, and the other three stands were located in the Wind River Experimental Forest north of the town of Carson in the southern Washington Cascades (Figure 1.2).

Experimental gaps were located in areas with relatively dense tree canopies to minimize interactions with recent natural gap events. Four sizes of gaps were created, with two replicates of each size and two control sites in each stand. Gap diameter (measured between tree crown edges) was scaled to the average height of trees in the stand and were as circular as possible. The gap diameter to tree height ratios for the 4 gap sizes were 0.2, 0.4, 0.6, and 1.0. The control plots were equal in area to the 1.0 gap size. The 0.2 gap size corresponded to the crown width of a single canopy dominant tree, which appears to be the most common gap size in the Cascades (Spies *et al.* 1990). Gaps were created in the fall of 1990 by cutting all trees (except *Acer circinatum*) over 2 m tall within the gap perimeter. Trees were stage-felled into specific locations (usually in the northeast and/or northwest quadrants

**Table 1.2:** Characteristics of the four stands in the experimental gap study. Gap size ratios are described in the text. *Pseudotsuga* refers to *Pseudotsuga menziessii*, "tolerants" includes *Tsuga heterophylla*, *Thuja plicata*, *Abies amabilis*, and *Abies grandis*. Covers are sums of individual species' cover estimates, with "understory" generally referring to vegetation less than 1 m in height, and mid-story to vegetation 1-5 m in height (Cover by species in Appendix). Soil texture from Gray and Spies (*in press*).

| Age class: | old-growth | | mature | |
|---|---|---|---|---|
| Stand name: | HJA | TCO | MCY | PCM |
| Location | 44°15'N, 122°15'W | 45°49'N, 122°00'W | 45°47'N, 121°57'W | 45°50'N, 121°49'W |
| Elevation (m) | 900 | 550 | 550 | 850 |
| Soil texture | Loam | Loam | Clay loam | Sandy loam |
| *Pseudotsuga* age (yrs) | 350-500 | 350-500 | 90 | 140 |
| Mean canopy height (m) | 50 | 50 | 35 | 50 |
| Gap Size and Area (m2) | | | | |
| 0.2 | 79 | 79 | 38 | 79 |
| 0.4 | 314 | 314 | 154 | 314 |
| 0.6 | 707 | 707 | 346 | 707 |
| 1.0 | 1960 | 1960 | 960 | 1960 |
| Tree Basal Area ($m^2$/ha) | | | | |
| *Pseudotsuga* | 73.5 | 39.2 | 58.5 | 83.3 |
| Tolerants | 62.0 | 58.0 | 0.2 | 0.6 |
| Vegetation Mean cover (%) | | | | |
| Understory bryophytes | 7.3 | 8.1 | 9.6 | 5.0 |
| Understory herbs | 4.9 | 9.3 | 0.8 | 26.7 |
| Understory shrubs | 9.4 | 26.8 | 46.9 | 35.6 |
| Mid-canopy trees | 4.2 | 5.8 | 43.4 | 34.6 |

to avoid damage to southern trees which defined the gap shade pattern), and skidders situated outside of the gaps winched the fallen tree boles from the gaps with cables. Some of the abundant *Acer circinatum* in the midstory of the mature stands was cut to facilitate cutting and removal of tree boles.

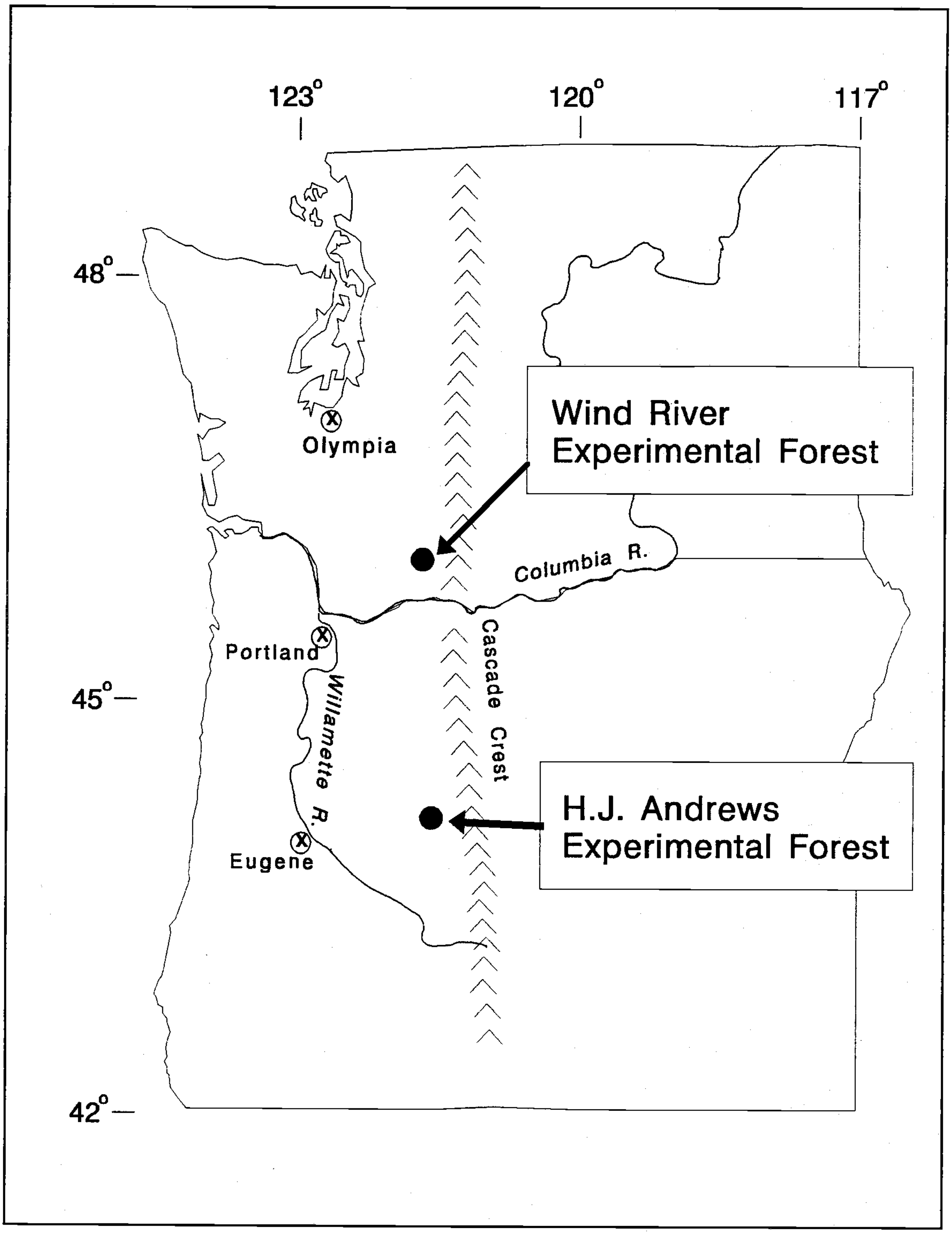

**Figure 1.2:** Map of Oregon and Washington showing locations of study areas.

### Tree seedling establishment study

The objective of the tree seedling establishment study was to determine the extent to which structural and environmental heterogeneity within and among canopy gaps affect tree seedling establishment in mature Douglas-fir forests. The focus of the study was on the variety of microsites present within and among gaps and closed-canopy areas, and the effect of resource abundance associated with those microsites on tree seedling establishment and growth. Research was designed to test four basic hypotheses:

Hypothesis 1: Survival and growth of seedlings of different tree species will differ across the environmental gradient represented by gap size and within-gap position. This is a restatement of the gap partitioning hypothesis, limited to the seedling establishment phase. It suggests that there are fundamental differences in the autecology of different species that will lead to differentiation along strong environmental gradients. Specifically, I hypothesize that shade-intolerant trees will only become established in large gaps, while shade-tolerant trees will become established primarily in small gaps. This hypothesis is addressed in Chapter 2.

Hypothesis 2: Survival and growth of seedlings of different tree species in gaps will differ in forests of different successional stages. Forest composition, structure, and tree age vary with successional stage and affect the abundance of above- and below-ground resources in closed-canopy areas and potentially in gaps as well. These environmental differences are hypothesized to create differing patterns of seedling survival in gaps and closed-canopy areas. This hypothesis is addressed in Chapter 2.

Hypothesis 3: Survival and growth of seedlings of different tree species will vary on different microsites within gaps and intact forest. Specifically, it is hypothesized that differing seedbed substrates, understory vegetation densities, and shading by coarse woody debris substantially alter microsite environments, thereby altering seedling survival patterns expected based on gap size and within-gap position alone. This hypothesis is addressed in Chapter 3.

Hypothesis 4: Survival and growth of seedlings of different tree species is significantly correlated with measures of abiotic plant resources. Specifically, it is hypothesized that information on light levels, substrate moisture, and maximum surface temperatures alone can predict tree seedling survival and growth. This hypothesis is addressed in Chapter 4.

These hypotheses required the study of early and late-successional species and their interaction with forest successional stage and gap size. Within this context, the role of within-gap position, seedbed, and understory plant cover was investigated. The study followed two basic approaches: monitoring germination and survival of sown seed on experimental plots where predation, seedbed variation, and understory cover were controlled, and monitoring seed rain and seedling survival and density in the range of microsites naturally occurring in the experimental gaps. Eight distinct experiments were conducted (Table 1.3).

Experiment 1 examined the role of stand age class, gap size, and within-gap position by sowing seed and monitoring germination and survival of *Abies amabilis*, *Pseudotsuga menziesii*, and *Tsuga heterophylla* on seed-plots created at the north ends, centers, and south ends of gap sizes 0.4, 1.0, and controls, and the centers of gap size 0.2. Predation was limited with hardware cloth exclosures and surrounding understory vegetation was removed. To reduce seedbed variability, seed plot substrate was mineral soil. This experiment is described in Chapter 2.

Experiment 2 examined the role of seedbed substrate, stand age class, and gap size by sowing seed and monitoring germination and survival of *Abies amabilis*, *Pseudotsuga menziesii*, and *Tsuga heterophylla* on mineral soil, forest floor, and decayed wood substrates created at the centers of gap sizes 0.2, 0.4, 1.0, and controls. Predation was limited with hardware cloth exclosures and surrounding understory vegetation was removed. This experiment is described in Chapter 3.

Experiment 3 examined the role of understory shade and gap size by sowing seed and monitoring germination and survival of *Abies amabilis*, *Pseudotsuga menziesii*, and *Tsuga heterophylla* under 0%, 40%, and 90% shade levels at the centers of gap sizes 0.4, 1.0, and controls. Predation was limited with hardware

**Table 1.3:** Summary of primary factors examined in the different experiments.

| | | Factors studied | | | | | | | Species studied | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Experiment # | Study material | Stand age | Gap size | Within-gap position | Substrate | Understory shade | Vegetation | Resource levels | *Abies amabilis* | *Pseudotsuga menziesii* | *Tsuga heterophylla* | Chapter # |
| 1 | Sown seed | X | X | X | | | | | X | X | X | 2 |
| 2 | Sown seed | X | X | | X | | | | X | X | X | 3 |
| 3 | Sown seed | | X | | | X | | | X | X | X | 3 |
| 4 | Planted germinants | | | X | | X | | | | X | X | 3 |
| 5 | Natural regeneration | X | X | X | X | | X | | | X | X | 2+3 |
| 6 | Natural regeneration | X | X | X | X | | X | | | X | X | 2+3 |
| 7 | Natural regeneration | X | X | X | X | X | X | | | X | X | 3 |
| 8 | Sown seed | | | | | | | X | X | X | X | 4 |

cloth exclosures and surrounding understory vegetation was removed. This experiment is described in Chapter 3.

Experiment 4 examined the role of shade by coarse woody debris and within-gap position by planting germinants of *Pseudotsuga menziesii* and *Tsuga heterophylla* at varying distance from large logs at the north ends, centers, and south ends of two 1.0 size gaps. Predation was limited with hardware cloth exclosures and surrounding understory vegetation was removed. This experiment is described in Chapter 3.

Experiment 5 examined the pattern of survival of seedlings established from natural seed rain on selected microsites in relation to stand age class, gap size, within-gap position, seedbed substrate, and understory shade within the experimental gaps. This experiment is described in Chapters 2 and 3.

Experiment 6 examined the pattern of density of seedlings established from natural seed rain on systematically placed plots in relation to stand age class, gap size, within-gap position, seedbed substrate, and understory shade within the experimental gaps. This experiment is described in Chapters 2 and 3.

Experiment 7 characterized microsites occupied by seedlings in relation to the availability of microsites by locating seedlings and random points in 1.0 and 0.2 size gaps and characterizing substrate, level and type of southern shade, density and type of vegetation, and seedling size. This experiment is described in Chapter 3.

Experiment 8 examined the role of resource levels and microclimate on seedling survival by measuring light levels, maximum surface temperatures, and soil moisture in or near the experimental seed-plots used in Experiments 1, 2, 3, and 4. This experiment is described in Chapter 4.

# CHAPTER 2: GAP SIZE, WITHIN-GAP POSITION, AND CANOPY STRUCTURE EFFECTS ON SEEDLING ESTABLISHMENT OF CONIFER SPECIES IN FOREST CANOPY GAPS

## Introduction

The size, intensity, and periodicity of natural disturbances profoundly affect the composition, structure, and function of forest ecosystems. Small-scale disturbances in forest communities involving the death of one to several trees create "canopy gaps" which are critical to the community dynamics of many forest types (Pickett and White 1985). The importance of canopy gaps for establishment and growth of different tree species has been documented in deciduous forests of eastern North America and in tropical forests (Runkle 1982, Poulson and Platt 1989, Brokaw 1985, Uhl *et al.* 1988). The importance of canopy gaps for tree species dynamics in coniferous forests has received much less attention (but see Stewart 1986a, Spies *et al.* 1990, White *et al.* 1985). Much of the disturbance research in the conifer forests of the Pacific Northwest has focused on succession following relatively large disturbances like fire or clear-cutting (Isaac and Meagher 1936, Agee and Huff 1981, Dyrness 1973, Halpern and Franklin 1990).

The role of canopy gaps in forest development is poorly studied. Most of the research on gap dynamics has focused on the old-growth phase of development (Denslow 1980, Runkle 1982, Veblen 1989, Canham 1985) and not on the role of gaps in moving forests from one phase to the next. A common developmental sequence in the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973) of Pacific Northwest forests is of young stands dominated by *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) in a single canopy layer developing into multi-layer old-growth forests containing increasing amounts of shade-tolerant *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) (Munger 1940, Franklin et al. 1981, Spies and Franklin 1991). The invasion of shade-tolerant species appears to be associated with an increase in size and reduction in density of overstory *Pseudotsuga* with forest age (Oliver and Larson 1990), but it is not clear whether it is a response to widespread thinning in canopy density or to localized environments present in canopy gaps created by mortality of dominant trees. Alternative, but not exclusive, hypotheses concerning the importance of canopy gaps for succession in mature Douglas-fir forests include: 1) shade-tolerant trees become established under intact canopies, 2) shade-tolerant trees invade throughout stands in response to many tiny gaps caused by widespread thinning of canopy dominants and/or abrasion of overlapping crowns as dominants age, and 3) establishment of shade-tolerant trees is limited to specific environments present within canopy gaps.

The developmental processes of old-growth forests have important implications for ecosystem management in the Pacific Northwest. The loss and fragmentation of late-successional forests has been a contentious issue in the region for decades. Recent proposals for management of federal lands emphasize moving young stands within reserve areas toward greater structural and compositional diversity (FEMAT 1993). While passively allowing stands to age may accomplish this goal, heavy thinning and selective harvest have been proposed as ways to achieve structural complexity more rapidly and allow some commodity extraction as well (FEMAT 1993, McComb *et al.* 1993, Spies *et al.* 1991). For either strategy, it is important to know how canopy gaps influence development of old-growth forests, how long it would take for old-growth structure to develop naturally, and whether patch selection harvesting can mimic this process. A related silvicultural question is whether the commercially valuable *Pseudotsuga* can be grown in small patches in multi-aged, multi-structured stands. If the occurrence of gaps is increasing on a global scale, as is suggested for the tropics by Phillips and Gentry (1994), understanding the nature of species' response to gap events will be increasingly important to forest management in many regions.

Canopy gaps are important sites for establishment and growth of plant species because of the greater abundance of resources (*e.g.* light and moisture) relative to the surrounding forest (Veblen 1992). Resource levels can vary greatly within and among gaps, however, potentially affecting species dominance patterns (Denslow 1987, Poulson and Platt 1989). Resource levels within forests also vary with annual climate, potentially modifying species' response in any given year. The heterogeneity of environments and resources within gaps may in fact determine the diversity of species in forests (Orians 1982). This idea has been referred to as the "gap partitioning hypothesis" and proposes that the resource gradients from intact canopy areas into large gaps is too broad to be dominated by any one species, so that a species should be most successful in environments characteristic of a particular gap size or within-gap location (Ricklefs 1977, Denslow 1980). Patterns of resource abundance associated with gap size and location within gaps result in a potentially wide range of micro-environments for tree seedling establishment and growth. In northern latitudes, for example, the northern sides of large gaps receive several hours of direct solar radiation, while the southern sides, or smaller gaps, only receive direct light through sunflecks (Canham *et al.* 1990). In many forests, the establishment and growth of tree species are related to gap size and within-gap location (Runkle 1982, Poulson and Platt 1989, Minckler and Woerhide 1965, Brandani *et al.* 1988). In some forests, however, the density of understory plants and presence of specific substrates (*e.g.* logs or mounds) are more important to tree species success than gap size (Veblen 1985, Ehrenfeld 1980, Nakashizuka 1989). Some studies in tropical forests have found few species-specific patterns with gap size and within-gap position, possibly due to high temporal and spatial variation in seed rain and gap events combined with high species diversity (Denslow 1987, Uhl *et al.* 1988).

The controls on tree seedling establishment in relation to canopy gaps within Pacific Northwest forests are poorly understood. The relatively shade-intolerant *Pseudotsuga menziesii* regenerates in forests on dry sites (Means 1982) but is rarely present in gaps on more mesic sites (Franklin and Dyrness 1973). Whether *Pseudotsuga* establishment is limited by overstory canopies or understory vegetation is not known. While shade-tolerant *Tsuga heterophylla* and *Abies amabilis* seedlings are more abundant in canopy gaps (Harmon 1987, Alaback and Tappeiner 1991, Thornburgh 1969, Long 1976, Stewart 1986a, Spies *et al.* 1990), many gaps are long term features which may take 50 to 100 years to attain canopy closure (Spies *et al.* 1990, Lertzman 1992) (indeed, some gaps may result from lack of establishment during stand initiation rather than from recent overstory mortality). In comparison, canopy closure may take as little as 2 yrs in moist tropical forests (Lorimer 1989) or

5 yrs in temperate deciduous forests (Runkle 1990). Slow filling of gaps in the Pacific Northwest may be caused by the tall, deep crowns of the dominant conifers and the root density of edge trees precluding an abundance of resources in canopy gaps (Canham *et al.* 1990, Oliver and Larson 1990). Alternatively, because over 70% of the gaps in Cascade forests originate from trees which die standing or from snapped boles (Spies *et al.* 1990), the undisturbed forest floor and understory plants may preclude rapid tree establishment and growth.

The importance of differences in stand structure or successional stage on gap-phase replacement is largely unknown. While the death of older, larger trees late in succession may free up more resources within gaps than the death of younger trees early in succession (Brokaw and Scheiner 1989), greater abundance of dense-crowned shade-tolerant trees surrounding gaps in late-successional forests may lead to lower total light levels in gaps (Spies and Franklin 1989). The effect of species like *Tsuga* on understories in intact forests and their association with lower light levels has been documented (Stewart 1986a, Turner and Franz 1986, Maguire and Forman 1983); whether their presence in the forest surrounding gaps is important to within-gap processes is unknown.

I initiated a study of tree seedling establishment in forest canopy gaps as part of a larger study on ecosystem processes within gaps which was started in 1990. The purpose of this paper is to 1) determine whether the establishment and growth of different tree species is affected by gap size and within-gap position, 2) determine whether stand age (with its associated differences in canopy density) affects tree seedling response in gaps, and 3) compare species' response patterns on controlled experimental plots to their response from naturally dispersed seed within the same gaps. Seedling establishment is a continuous process from seed dispersal through germination, emergence, and subsequent survival. Any one of these life-history stages represents a potential bottleneck to establishment. The focus of this study is on survival of emerged seedlings, but data on germination and seed rain are also examined to assess the relative importance of these stages in the process of early seedling establishment. Based on current knowledge of species dynamics in the Pacific Northwest, I hypothesize that: 1) tree species may not require gaps to establish, but establishment and growth will be much more successful in canopy gaps, 2) shade-tolerant *Abies* and *Tsuga* will establish most successfully in small gaps, while establishment of the relatively shade-intolerant *Pseudotsuga* will be limited to high-light areas within the largest gaps, and 3) the relative success of seedling establishment in gaps compared to closed-canopy areas will be greater in dense-canopied old-growth stands than in mature stands.

## Methods

### Site description

Canopy gaps were created by cutting trees in four forest stands in the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973) of the west slope of the Cascade Mountains. Two stands were in old-growth forests (approximately 500 yrs in age) dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla* in multiple canopy layers, and two stands were in mature forests (90-140 yrs in age) dominated by *Pseudotsuga* in a single canopy layer (Table 2.1). One old-growth stand was located in the H.J. Andrews Experimental Forest in the Willamette National Forest of the central Cascades of Oregon; the other three stands were located in the Wind River Experimental Forest in the Gifford-Pinchot National Forest of the southern Cascades of Washington.

Although these stands represent different "age classes" or developmental phases, they differ in developmental history, structure, and composition. Stand HJA (the one stand in the H.J. Andrews Experimental Forest) was in an old-growth forest that experienced a moderate severity fire about 140 yrs ago (Teensma 1987). This disturbance was followed by development of a dense *Tsuga heterophylla* sub-canopy which may have kept understory vegetation sparse. The TCO ("Trout Creek Old-growth") stand was in an old-growth forest and had no obvious signs of disturbance other than small patches of canopy tree mortality, leaving a mosaic of open and

**Table 2.1:** Characteristics of the four stands in the experimental gap study. *Pseudotsuga* refers to *Pseudotsuga menziesii*, "tolerants" includes *Tsuga heterophylla*, *Thuja plicata*, *Abies amabilis*, and *Abies grandis*. Covers are sums of individual species' cover estimates, with "understory" generally referring to vegetation less than 1 m in height, and low-canopy to vegetation 1-5 m in height (cover by species in Appendix).

| Age class: | old-growth | | mature | |
|---|---|---|---|---|
| Stand name: | HJA | TCO | MCY | PCM |
| Location | 44°15'N,<br>122°15'W | 45°49'N,<br>122°00'W | 45°47'N,<br>121°57'W | 45°50'N,<br>121°49'W |
| Elevation (m) | 900 | 550 | 550 | 850 |
| Soil texture | Loam | Loam | Clay loam | Sandy loam |
| *Pseudotsuga* age (yrs) | 350-500 | 350-500 | 90 | 140 |
| Mean canopy height (m) | 50 | 50 | 35 | 50 |
| Tree Basal Area ($m^2$/ha) | | | | |
| *Pseudotsuga* | 73.5 | 39.2 | 58.5 | 83.3 |
| Tolerants | 62.0 | 58.0 | 0.2 | 0.6 |
| Vegetation mean cover (%) | | | | |
| Understory bryophytes | 7.3 | 8.1 | 9.6 | 5.0 |
| Understory herbs | 4.9 | 9.3 | 0.8 | 26.7 |
| Understory shrubs | 9.4 | 26.8 | 46.9 | 35.6 |
| Low-canopy trees | 4.2 | 5.8 | 43.4 | 34.6 |
| Total | 25.8 | 50.0 | 100.7 | 101.9 |

closed canopy areas with a variety of understory density. The MCY ("Martha Creek Young") stand was in a mature forest that established after the Yacolt fire of 1902 (Hofmann 1917). The stand was dominated by a fairly dense *Pseudotsuga* overstory, yet also had abundant *Acer circinatum* Pursh. (vine maple) in the mid-story and a high density of woody shrubs in the understory. Most of the large snags from the previous stand appear to have been cut in the 1930's, probably to discourage the spread of a subsequent fire. The PCM ("Panther Creek Mature") stand was in a mature forest that experienced at least one severe *Dendroctonus pseudotsugae* (Douglas-fir beetle) outbreak and was salvage-logged in the 1950's; the tree canopy was fairly open-grown with a high density of vine maple, herbs, and shrubs.

Soil characteristics also differed among stands. The soil in stand HJA is a deep (depth to C horizon 1 m), well-drained, dark brown gravelly loam over a cobbly silt-loam C horizon. It was formed in colluvium from basic igneous rock and volcanic ash, and is classified as a loamy-skeletal, mixed, frigid Fluventic Dystrochrept (Brown 1975). The soil for stand TCO is a deep (typically 2 m to bedrock), well-drained, dark brown sandy loam. It was formed in relatively young deposits of volcanic tephra over basaltic lava flows and is classified as an Andic Haplumbrept belonging to the Stabler series (Franklin and DeBell 1988). Soil classifications are unavailable for the mature stands, but textural classes were derived from particle size analyses using the hydrometer method on two soil samples from the upper 30 cm of soil from each stand (Table 2.1).

Climatic regimes from meteorological stations in or near the two Experimental Forests are similar, with summer drought and high temperatures common from June through September, a pattern characteristic of the Pacific Northwest (Figure 2.1). Winter snowpacks are often transient at 500-1000 m in the Cascades, with temporary accumulations occasionally exceeding 1 m in depth. Wind River received more precipitation in the winter, and less in the spring, than the H.J. Andrews station. Wind River also experienced a greater temperature range throughout the year than did the H.J. Andrews. Some of the differences between stations may be due to local topography (*e.g.* the Wind River station is in a much larger valley bottom than the H.J. Andrews station); the actual climates of the stands near these stations probably vary with elevation and topography. Climate varied over the duration of the study, with higher precipitation, and lower maximum and minimum temperatures, from March through August of 1993 than in the same period in 1992.

Within each stand, experimental gaps were located in areas with slopes less than 20% and with relatively dense tree canopies (to minimize interactions with recent gap events). Four sizes of circular gaps were created in each stand with two replicates of each size and two control plots (replicates are identified as "1" or "2"). Gap diameter (measured between tree crown edges) was scaled to the average height

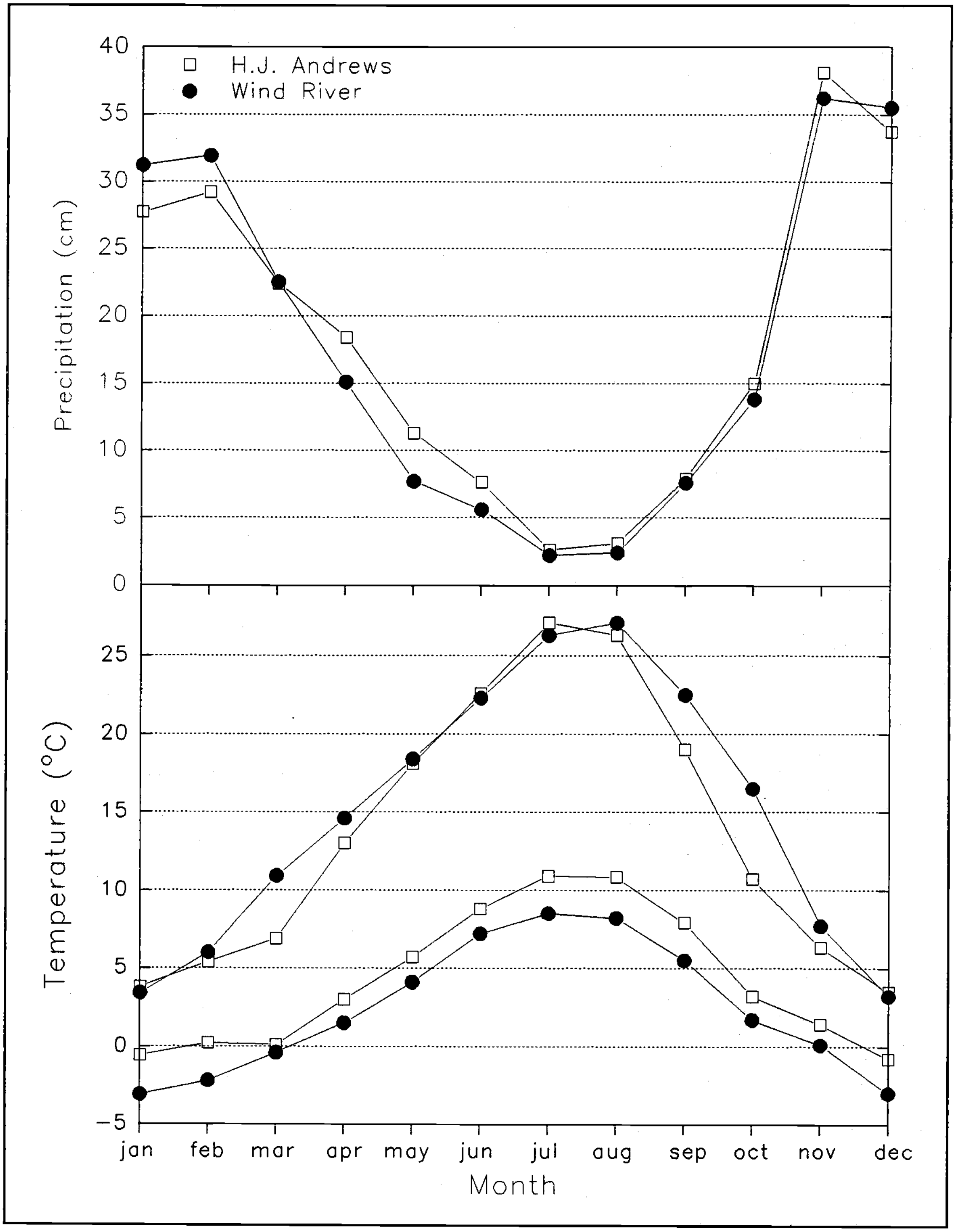

**Figure 2.1:** Climate of study areas by month. Monthly sums of precipitation and monthly means of daily temperature maxima and minima were averaged for the same 15 yr period (1977-1992). Data for H.J. Andrews are from the Watershed 2 meteorological station (elevation 460 m), data for Wind River are from the Carson Fish Hatchery NOAA station (elevation 330 m).

of trees in the stand. The gap diameter to tree height ratios for the four gap sizes were 0.2, 0.4, 0.6, and 1.0. The control plots were equal in area to the 1.0 gap size. The 0.2 gap size corresponded to the crown width of a single canopy dominant tree, and appears to be the most common gap size in the Cascades (Spies *et al.* 1990). Gaps were created in the fall of 1990 by cutting all trees over two m tall (except *Acer circinatum*) within the gap perimeter. Trees were stage-felled into specific locations (usually in the northeast and/or northwest quadrants to avoid damage to southern trees which defined the gap shade pattern), and skidders situated outside of the gaps (to minimize disturbance to soils and understory vegetation) winched the fallen tree boles from the gaps with cables. The piles of branches and foliage trimmed from the felled trees were moved outside the gap perimeter to avoid localized differences in nutrient input and shading within the gaps. Some of the abundant *Acer circinatum* in the mid-story of the mature stands was cut to facilitate cutting and removal of tree boles.

Microclimate within the experimental gaps was monitored for up to two years following gap creation (Chapter 4). General results are described here to provide context for the seedling establishment studies (Table 2.2). Quantum levels of photosynthetically active radiation (PAR) increased with gap size, although levels in the 0.2 gap size were only slightly higher than those in controls. A pattern of increasing light levels from the southern to the northern edge of gaps was evident in all gaps larger than the 0.2 size. Light levels varied among stands, with a ranking of PCM > TCO ≈ HJA > MCY in controls and 0.2 gap sizes. Rankings in the larger gaps were more variable, probably due to differences in crown outlines at southern edges of gaps. Temperatures at the surface of the forest floor in the northern portions of the 0.4 and 1.0 gap sizes often exceeded 60°C on warm, sunny days. Although trends varied among stands, volumetric soil moisture levels in the upper 15 cm tended to be higher in most gap locations than in controls, although gap edges (particularly on the north side of the larger gaps) were often drier than gap centers (Table 2.2, Gray and Spies 1993). Soil moisture levels also tended to be higher in old-growth stands, which may be due to differences in soil texture, density of understory vegetation, or topographic position.

**Table 2.2:** Photosynthetically active radiation (PAR) and volumetric water content (H2O) by stand, gap size, and within-gap position (N,C,S = north, center, and south, respectively), for replicate 1 gaps. Light measurements were taken over the summer of 1991, soil moisture data is from August 1992.

| | | Age class: | old-growth | | mature | |
|---|---|---|---|---|---|---|
| Gap | Pos | Stand name: | HJA | TCO | MCY | PCM |
| *PAR (mol/$m^2$/day)* | | | | | | |
| ctl | N | | 1.37 | 1.65 | 0.82 | 0.61 |
| ctl | C | | 0.98 | 1.13 | 1.09 | 2.03 |
| ctl | S | | 2.14[1] | 0.87 | 1.17 | 1.78 |
| 0.2 | C | | 2.33 | 2.29 | 2.03 | 3.91 |
| 0.4 | N | | 11.44 | 12.79 | 5.40 | 6.24 |
| 0.4 | C | | 3.50 | 14.00[2] | 4.07 | 3.91 |
| 0.4 | S | | 2.28 | 3.09 | 1.81 | 4.64 |
| 1.0 | N | | 15.05 | 18.74 | 20.03 | 20.19 |
| 1.0 | C | | 12.49 | 14.68 | 11.95 | 24.01 |
| 1.0 | S | | 2.37 | 2.26 | 2.52 | 7.22 |
| *H2O (% vol.)* | | | | | | |
| ctl | N | | 19.9 | 17.0 | 15.1 | 12.7 |
| ctl | C | | 22.2 | 17.6 | 16.3 | 9.9 |
| ctl | S | | 23.2 | 17.2 | 12.1 | 12.4 |
| 0.2 | C | | 23.5 | 21.5 | 21.9 | 13.2 |
| 0.4 | N | | 22.4 | 15.7 | 18.8 | 12.2 |
| 0.4 | C | | 24.6 | 22.3 | 29.6 | 16.6 |
| 0.4 | S | | 26.0 | 22.0 | 23.1 | 14.5 |
| 1.0 | N | | 21.0 | 21.9 | 13.2 | 11.0 |
| 1.0 | C | | 24.9 | 19.9 | 16.6 | 11.8 |
| 1.0 | S | | 24.8 | 20.0 | 20.1 | 13.6 |

[1] Anomolously high measurement due to gap south of plot edge

[2] High measurement due to low canopy height at portion of south edge of gap

## Seed-sowing experiment

The first of the three experiments on seedling establishment in relation to gap size and within-gap position was a manipulative approach using known quantities of sown seed and attempting to control variation from seedbed and understory vegetation. This manipulative study was conducted on a standardized substrate in three of the four gap sizes and in controls, using both replicates (Figure 2.2); the 0.6 gap size was not used to reduce effort, and because a pilot study indicated conditions within this gap size were similar to those found in portions of the 0.4 and 1.0 gap sizes. Three within-gap positions (north, center, and south) were identified in each gap and control, except for the 0.2 gap size, in which only one position (center) was used. The north and south positions were close to gap edges but not beneath the canopy. For each position, three 60 * 60 cm seed-plots were created. To minimize variation due to forest floor type and depth and the amount of coarse fragments in the soil, the forest floor and much of the A1 soil horizon was removed and the upper 10 cm of soil churned, removing coarse fragments and roots over 1 cm in diameter in the process. This soil disturbance was believed to have little effect on the availability of mycorrhizal inocula (Randy Molina, *personal communication*). Mycorrhizal mats (Griffiths *et al.* 1991) were avoided if possible or removed. A uniform layer of B1 horizon soil was tilled at a road-side in the TCO stand and spread in a surface layer 2.5 cm deep across the seed-plots at all of the stands to further reduce effects of substrate variation on the experiment.

Exclosures were placed over each seed-plot to deter seed and seedling predation by rodents and birds, which can deplete seedling populations by more than 60% (Gashwiler 1967). Exclosures were made of galvanized metal hardware cloth (12 mm mesh) and consisted of a 15 cm tall cylinder sunk 7-10 cm into the soil, covered with a removable cone about 40 cm tall at the peak. The cylinder was 56 cm in diameter, enclosing an area of 0.25 $m^2$. Exclosures reduced PAR quantum levels at an exposed site in a gap by 17.5%, but had no detectable effect on surface temperatures. Potentially competing understory vegetation in and around the seed-plots (growing above a 45° line projecting from the base of the exclosures) was clipped or uprooted at regular intervals throughout the course of the study. Seed-plots were either located away from the potential shade of mid-story trees, or trees were tied back to minimize shading. Seed-plots were created during the summer and fall of 1991 and seed was sown in the late fall of 1991 (one year after gap creation). Seed-

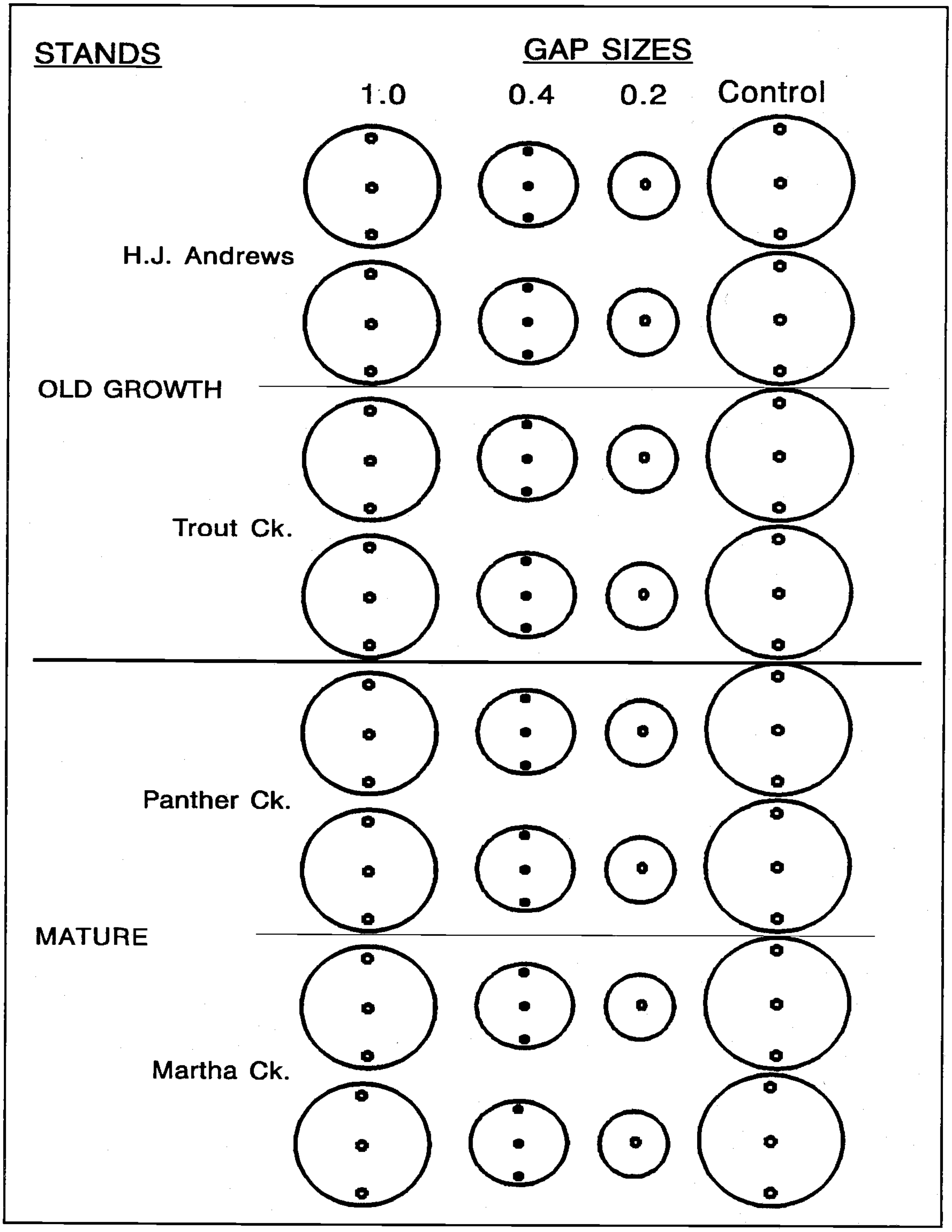

**Figure 2.2:** Schematic of experimental design for seed-sowing experiment, showing age classes, stands, replicates, gap sizes, and within-gap positions. Each within-gap dot represents three seed-plots.

plot surfaces were roughened slightly with a hand rake to discourage seed movement by raindrops (Lawrence and Rediske 1962).

One hundred *Abies amabilis*, 100 *Pseudotsuga menziesii*, and 500 *Tsuga heterophylla* seeds were divided evenly between the three seed-plots of each gap position. All seed were sown during the first three weeks of November 1991. The seeds used at the HJA stand were from a local seed zone, and those used at the other three stands were from a Wind River seed zone (all seedlots were from the Wind River Nursery). Germination tests conducted by the Wind River nursery estimated seedlot viability for *Abies* at 95 and 93%, *Pseudotsuga* at 94 and 70%, and *Tsuga* at 76 and 76% for the Wind River and H.J. Andrews seed zones, respectively. Natural seed rain also added large numbers of seed in the fall of 1991, primarily *Pseudotsuga* in the mature stands (MCY and PCM), and both *Pseudotsuga* and *Tsuga* in the old-growth stands (HJA and TCO). Seed rain was monitored with seed traps placed along north-south transects in replicate 1 of each gap size and control in each stand. Since seed sowing and placement of exclosure tops occurred after natural seed dispersal had started, seed which had already been shed was more exposed to predation than seed which was shed after sowing.

Seedlings were counted in the seed-plots once each month from late April to October of 1992 and in June and October of 1993. Due to time constraints associated with establishing and maintaining other experiments, two of the counts (April and August 1992) were only made in replicate 1 of each gap size and control in each stand. Seedlings were considered "germinants" if there was any above-ground evidence of a radicle emerging from the seeds. Seedlings were considered "emergent" and counted if they were erect and rooted and had mostly shed their seed coats (dead seedlings were also counted). Seedlings were considered dead when they were missing, cut at the stem, or entirely lacking green color. If the total number of live and dead seedlings on a plot exceeded the previous month's count of live seedlings, the number of dead seedlings in excess (*i.e.* which had never been counted as live) was recorded as "new mortality" (*e.g.* if there were 20 live seedlings @ $t_1$, and 18 live and 6 dead seedlings at $t_2$, then 4 seedlings were recorded as "new mortality"). Similarly, if the total number of germinants and emergents on a plot in one month exceeded the subsequent month's count, the number of seedlings in excess was recorded as "un-emerged germination" (*e.g.* if there were 10 germinants and 2 emergents @ $t_1$, and 0 germinants and 5 emergents at $t_2$, then 7 seedlings were recorded as "un-emerged germination"). The types of damage and mortality seen were noted. The fate of individual seedlings was monitored on center seed-plots in one control and one 1.0 size gap in stands PCM and TCO and on north and south seed-plots of the 1.0 gap size in stand TCO by marking all seedlings as they emerged (by inserting toothpicks into the soil on the north side of each seedling). At the end of the 1992 and 1993 growing seasons, basal diameter and height were measured on up to 5 randomly selected seedlings of each species from each replicate 1 seed-plot. The time of year at which most seedlings' terminal bud scales hardened (bud "set") was noted for the different gap size by within gap position locations during the seedling counts. Seedling growth began to be restricted by exclosure tops in 1993, so the tops were removed from all seed-plots in July 1993. Measurements from seedlings which had clipped or browsed tops was noted.

Annual variation in seedling establishment was investigated by repeating the study the following year in the TCO stand. Unoccupied portions of plots were roughened with a hand rake and sown in the fall of 1992 with the same numbers of seed used the previous year. Density of *Tsuga* seedlings was so high in 20 of the 60 TCO seed-plots that patches of seedlings were removed (and individuals counted) to create space for the newly-sown seed. Seedlings were counted monthly from early June to mid-October 1993. The fate of individual seedlings was monitored with toothpicks in all plots for *Abies* and *Pseudotsuga*, while *Tsuga* was monitored only in north and center plots of 0.4 and 1.0 size gaps (*Tsuga* density was too high on other plots to reliably associate toothpicks with individuals). Causes of seedling mortality were identified and counted at each visit. Seedlings were measured in October 1993 using the procedure used for the 1992 cohort (seedling populations will be referred to by year of emergence, *i.e.* those which emerged in 1992 will be referred to as the "1992 cohort").

## Survival of natural regeneration

This study was designed to follow the fate of seedlings originating from natural seed rain in different natural microenvironments within each gap size by within-gap position combination. In late May or early June of 1992, within two weeks of emergence of many of the seedlings in the gaps, replicate 1 of each gap size (except 0.6) and control in each stand was searched and individuals or clumps of first-year *Pseudotsuga* and *Tsuga* were marked with small pin flags. A concerted effort was made to locate up to 15 seedlings in each treatment combination of gap size (0, 0.2, 0.4, and 1.0), position (north, center, south-- center only in 0.2's), understory cover level (0, 50, and 90 percent), and substrate (forest floor and decayed wood). Nevertheless, sample sizes varied considerably between treatment combinations, and *Tsuga* seedlings were rare in the mature stands (MCY and PCM). To avoid edge and east-west effects, most seedlings located were within 4-6 m of the north-south transect bisecting the gaps. Gap positions were delineated by dividing this north-south belt into three zones of similar area (*e.g.* for a 50 m diameter gap, south positions were 0-17 m, center positions were 17-34 m, and north positions were 34-50 m from the southern gap edge). Marked seedlings were revisited in September 1992, and July and October 1993 to assess survival.

## Density of natural regeneration

This study was designed to assess the size and density of tree seedlings originating from natural seed rain within the gaps and controls. Permanent vegetation sample plots were established prior to gap creation at a 2 m spacing on the north-south and east-west axes of all gaps, and at a 4 m spacing throughout the remainder of the gap area. Understory cover by species and density of tree seedlings was estimated annually (beginning the summer prior to gap creation) in most of the 0.25 $m^2$ vegetation plots. Seedlings were classified as less than 1 yr old or older and their basal diameters were measured in 0.1 mm increments. Plots on the cardinal and diagonal transects were sampled in all gaps in the summer of 1993. In addition to the gaps and control plots sampled for the two seedling previous studies, the 0.6 gap size was sampled for this study.

## Statistical Analyses

The null hypothesis that tree seedling establishment was not affected by the fixed factors of stand age, gap size, within-gap position, tree species, or interactions between them was evaluated with a four factor split-split plot Analysis of Variance (ANOVA) for each experiment. The experimental design for all experiments was unbalanced (missing cells due to only one position in gap size 0.2) and was analyzed with a Type IV Sums of Squares ANOVA (GLM procedure in SAS 6.10 [SAS Institute Inc. 1987]). The Type IV method on unbalanced designs, however, selects a subset of the full range of testable linear contrasts in a somewhat arbitrary fashion, requiring careful examination of the contrasts generated by the program and possibly further analyses using selected cell means (Milliken and Johnson 1984, Shaw and Mitchell-Olds 1993). Examination of the linear contrasts generated by SAS indicated they were appropriate. In addition, balanced Type III ANOVA runs on the data-set with the 0.2 gap size omitted changed the mean squares of factors and interactions very little, suggesting the Type IV analyses were valid. Within-gap position was technically a repeated measure of gap size, and could be treated as a split-plot level only if the covariance matrices satisfied the Huynh-Feldt condition (Huynh and Feldt 1970). The Huynh-Feldt condition was assessed by conducting sphericity tests on position for each species in repeated-measures ANOVAs (GLM procedure in SAS 6.10 [SAS Institute Inc. 1987]); none of the datasets violated this condition. Initial ANOVA tests for the seed-sowing and density of natural regeneration experiments included two terms for sub-plot error: a term for the variation of gaps within stands, and a term for the variation of gap-size replicates within stands. If the Mean Squares for both terms were similar, additional ANOVAs were calculated with both terms combined in the sub-plot error (as the variation of gap-size replicates within stands);

if the Mean Squares for the variation of gaps within stands was larger, then it was used as the sub-plot error. If Mean Squares for whole-plot error terms were smaller than Mean Squares for sub-plot error terms (which would require a negative variance --an impossibility-- under the ANOVA model [Milliken and Johnson 1992]), the whole-plot term was left out of the model and whole plot effects were tested with the larger sub-plot error terms. Results of the analyses were considered significant if the probability of a Type I error was less than 0.05. Determination of significant differences among treatment means was conducted for terms which were significant in the ANOVAs (analogous to Fisher's protected Least Significant Difference) using least-squared means and 95% confidence intervals calculated with the MIXED procedure in SAS 6.10 [SAS Institute Inc. 1987]). Although the latest version of the MIXED procedure only uses Type III Sums of Squares analyses, ANOVA results were very similar to the Type IV analyses calculated using the GLM procedure, so separation of means tests were considered reliable. Means of interactions of interest which were not significant in the ANOVAs were graphed, and the degree of overlap of the standard errors of the means was used as an indication of potential differences which might be biologically significant.

### Seed-sowing experiment

The response variable for the analysis of establishment in the seed-sowing experiment was the fraction of the maximum number of emerged seedlings counted on a treatment (maximum live plus all "new mortality" counts) that were still alive at the end of the experiment (termed "establishment"). This measure could potentially under-estimate seedling "survival" by missing seedlings that died and were replaced by new emergents; this turnover effect was evaluated by comparing survival of individually marked seedlings with establishment calculated from counts on the same seed-plots and is shown in the results. It is still possible that seedlings germinated and died without a trace between counts or before the first count; the frequency of this occurrence is unknown.

Since seedlings were not counted on replicate 2 seed-plots during the first sample period in 1992, establishment on these plots may have been over-estimated if the greatest number of emerged seedlings were present at that time. This was evaluated by examining changes between the first and second counts on replicate 1 plots of the same treatments: a decline in seedling numbers occurred on 8 out of 30 species by gap size by within-gap treatment combinations (Table 2.3). Some of this decline may have been captured on replicate 2 seed-plots with the dead seedling counts, which were included in the seed-plot maxima. Ignoring the first count on the replicate 1 plots would simplify interpretation of results, but would further over-estimate establishment by not including early mortality. Instead, the maximum number of emerged seedlings (live and dead) counted on a seed-plot was used to estimate establishment; implications of potential over-estimation of establishment on replicate 2 seed-plots is discussed with the results.

Since *Tsuga* seedlings were removed from 20 of the 60 TCO seed-plots to make room for the second-year sowing of seed, final seedling counts were adjusted under the assumption that the original number of seedlings would have followed the same survival trajectory as those that were left after thinning did (*i.e.* final count/post-thin count = adjusted/pre-thin count). Final counts on the thinned plots were adjusted with the formula: adjusted count = (pre-thin count * final count)/post-thin count.

**Table 2.3:** Percent change in seedling numbers by gap size, position, and species for summed replicate 1 locations for which counts declined from April to May 1992.

| Species | Gap size | Position | Percent decline |
|---|---|---|---|
| *Abies* | control | South | 38 |
| *Abies* | 0.4 | North | 10 |
| *Abies* | 1.0 | North | 20 |
| *Pseudotsuga* | 1.0 | North | 4 |
| *Tsuga* | 0.4 | North | 67 |
| *Tsuga* | 0.4 | Center | 6 |
| *Tsuga* | 1.0 | North | 76 |
| *Tsuga* | 1.0 | Center | 31 |

The experimental unit ("treatment") for this study was position within a particular gap. All seedling counts were summed across the three seed-plots (as experimental sub-plots) comprising a position treatment within a gap, and establishment calculated on those sums. As is common with binomial data, establishment percentages exhibited non-uniform variance and non-normality, and were transformed with an arcsin-square root equation specifically designed for data with several values close to zero (Zar 1984, eq. 14.5):

$$p' = 0.5 * \{\arcsin([N_f / (\max + 1)]^{½}) + \arcsin([(N_f + 1) / (\max + 1)]^{½})\}$$

where:
$p'$ = transformed value
$N_f$ = number of seedlings alive at final count
max = maximum number of seedlings found on a treatment

Since establishment estimates were more precise for treatments with greater maximum numbers (*e.g.* establishment of 50 out of 100 seedlings is more precise than 5 out of 10), the ANOVA was weighted by the square root of the denominator ("max") values (square root of "max" reduced the weighting bias towards *Tsuga* in the old-growth stands, which had high emergence values due to natural seed rain). There were no missing values (*i.e.* treatments where max = 0) in this analysis.

The analysis of stand effects on seedling establishment in closed canopy areas was conducted as a separate single-factor ANOVA (balanced, Type III Sums of Squares) for each species, using the transformation and weighting described above on the position treatments in both replicate control areas per stand (six treatments/stand). An initial ANOVA model was run to calculate the variance associated with treatments within control replicates and the variance associated with control replicates within stands. Non-significant *F*—tests (*p* values > .30) indicated that the two variances were not significantly different for any species, so treatments were modelled as independent samples within stands.

The comparison of measures of establishment used data from replicate 1 gaps in each stand, since seed rain and germination in April 1992 was only measured in these gaps. (Seed rain was monitored in a few seed replicate 2 gaps in the old-growth stands, and seed rain varied by as much as 200% between replicates.) Establishment as a fraction of seed was calculated by converting seed rain measurements to an area basis and dividing into the density of established seedlings on each treatment. Establishment as a fraction of germination was calculated by adding the maximum number of emerged seedlings and un-emerged germination and dividing into the number of established seedlings on each treatment. Trends in emergence and mortality over time were investigated for replicate 1 gaps only, due to missing sample periods in replicate 2 gaps.

The analysis of annual effects on seedling establishment in stand TCO was similar to the full analysis described above for the 1992 cohort, except that establishment for the first cohort was calculated using the last count of 1992 (before thinning of *Tsuga* from plots). Establishment for the second cohort was calculated using the last count of 1993. Stand age was not a factor for the ANOVA of annual effects (only one stand), and the cohort year factor was split within the gap and position factors. The same transformation and weighting was done for this ANOVA as is described above for the analysis of second-year establishment. Due to missing values, only 109 observations of the 120 possible treatment combinations were used in this analysis.

The analysis of seedling size for the 1992 cohort was similar to the analysis of establishment for the same cohort. The response variable for the ANOVA was the mean size of the seedlings measured in a treatment (*i.e.* three seed-plots), where size was calculated as seedling height multiplied by basal area. This volume-related measure of size was chosen as a better measure of seedling growth in a given environment than height, because many plants increase height growth relative to biomass in low light conditions (etiolation--observed in *Pseudotsuga*), and height of small seedlings can be sensitive to the depth in the soil at which seeds germinate (observed for all species). Measured seedlings with damaged tops (from animal browsing) were included in the analysis (their presence had no effect on ANOVA results). The size data were log-transformed ($\log(y+1)$) before analysis, and the ANOVA was weighted by the number of seedlings measured. Due to missing values (*i.e.* treatments without surviving seedlings) only 96 observations of the 120 possible treatment combinations were used in the analysis.

### Survival of natural regeneration

The response variable for the analysis of survival of natural regeneration was the percentage of the initial number of emerged seedlings counted for a treatment that were still alive at the end of the second growing season. Seedling counts were summed for each within-gap position before calculating survival. The data were transformed for the ANOVA with the same arcsin-square root transformation as used for the seed-sowing experiment. Due to the very low number of *Tsuga* seedlings in the mature stands, separate analyses were done for *Pseudotsuga* (using all four stands) and *Tsuga* (using the two old-growth stands). Each analysis was weighted by the denominator used to calculate survival (*i.e.* initial number of emergents). There were no missing values in this analysis.

### Density of natural regeneration

The tree seedling density data was allocated to three within-gap positions by dividing the north-south transect of each gap into three equal lengths (identical to the procedure used in gathering data for the survival of natural regeneration study) and only including plots within four m of the transect. Only two-year old seedlings (*i.e.* 1992 cohort) were considered in the analysis, by subtracting the number of 0.1 mm diameter seedlings present on a plot in 1993 by the number present in 1992 (new emergents were given a basal diameter of 0, so did not confuse this calculation). The response variable for the ANOVA was the combined seedling density on all the vegetation plots in a position within a gap. This density value was log-transformed ($\log(y+1)$) and weighted by the number of vegetation plots in each treatment. Due to the very low number of *Tsuga* seedlings in the mature stands, separate analyses were done for *Pseudotsuga* (using all four stands) and *Tsuga* (using the two old-growth stands).

## Results

### Seed-sowing experiment

#### Trends in emergence and mortality

The timing of emergence and mortality differed among gap locations for the three species studied. (For simplicity, a gap size by within-gap position interaction is referred to as a "location", and identified as follows: 1.0 North, 0.4 Center, etc.) Most of the seedlings emerged between late April and early June. Seedlings of all species emerged earlier in more exposed locations (*e.g.* maximum numbers of live seedlings occurred in early May at 1.0 North locations for *Abies* and *Pseudotsuga*, and 1.0 North and Center and 0.4 North and Center locations for *Tsuga*) than in less exposed locations (maximum numbers of live seedlings occurred in June in controls and gap size 0.2 for all species) (Figure 2.3). Mortality in exposed locations was rapid and substantial for *Tsuga*, with most of the mortality at the 1.0 North, 1.0 Center, and 0.4 North locations having occurred by July of the first year. Mortality in exposed locations was slower and less severe for *Abies*, with mortality slowing after July at 1.0 Center and 0.4 North locations but continuing steadily until September at 1.0 N locations. Mortality in exposed locations was relatively minor for *Pseudotsuga*. Mortality in open, shaded locations (1.0 South, 0.4 Center and South) was relatively minor for all species. *Abies*, and to a lesser extent *Tsuga*, suffered relatively high mortality over winter in gap size 0.2, while mortality was gradual through the first year for all species in controls.

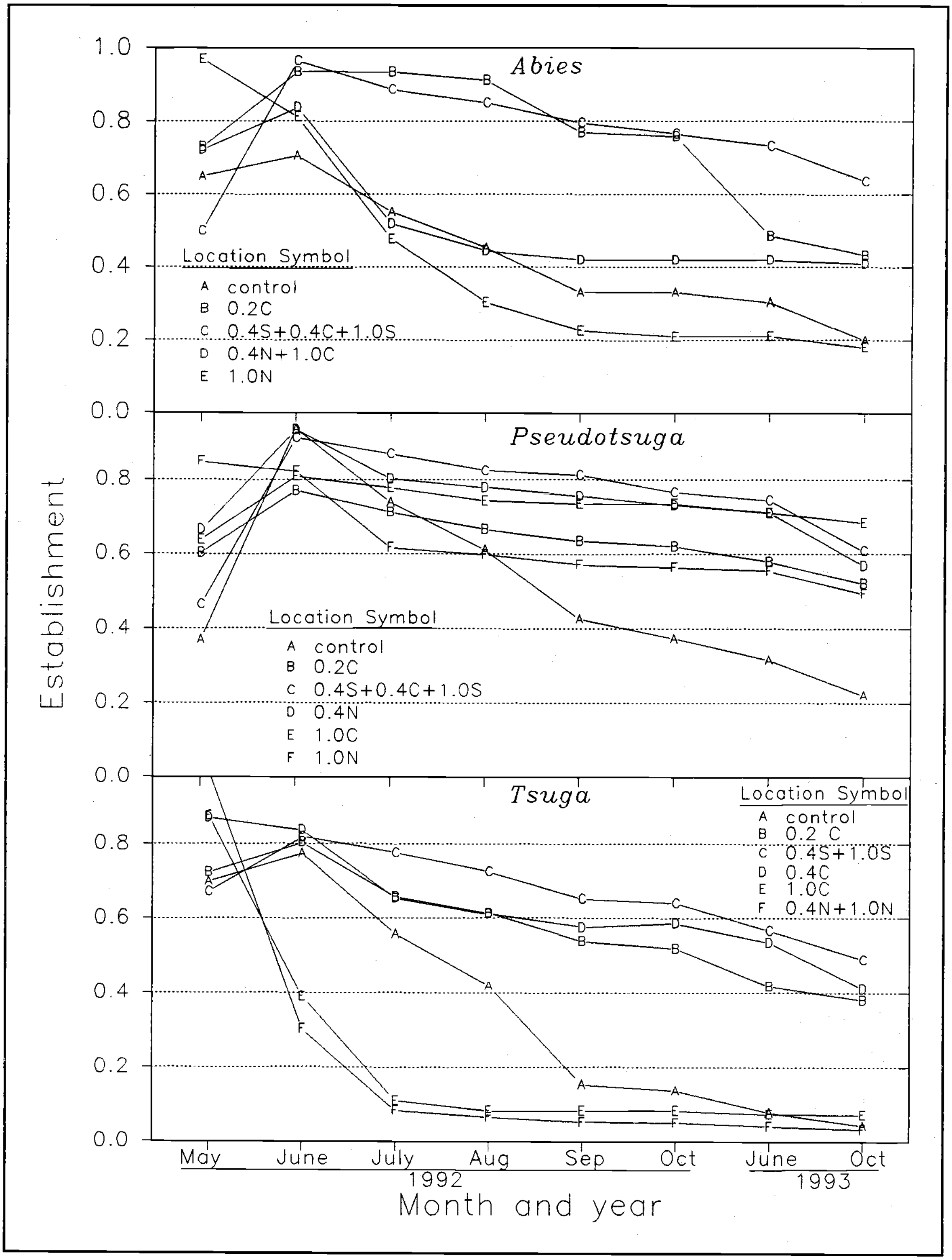

**Figure 2.3:** Seedling establishment trends (% of maximum emerged) over two growing seasons for the 1992 cohort in controlled seed-plot study by location and species. Locations with similar trends were grouped to simplify illustration. Data are from replicate 1 locations from each stand (n=4).

### Establishment of 1992 cohort

Establishment at the end of two growing seasons differed significantly among species and location. Effects on seedling establishment of gap size, within-gap position, species, their two-way interactions, and their three-way interaction, were all significant (Table 2.4). The gap size by position by species interaction reflected the suitability of different locations for the three species. While establishment in controls was relatively low for all species, establishment was low in 1.0 North locations for

**Table 2.4:** Results of split-split plot ANOVA on seedling establishment (% of maximum count) for seed-sowing experiment. Factor abbreviations are: age= age class, gap= gap size, pos= position, spp= species. Significant effects (p < .05) are marked with asterisks (*).

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| age | 1 | 0.94215 | 0.19 | 0.7021 |
| Error: stand(age) | 2 | 4.83595 | | |
| gap | 3 | 14.12650 | 9.33 | 0.0112 * |
| age*gap | 3 | 0.23122 | 0.15 | 0.9242 |
| Error: stand*gap(age) | 6 | 1.51450 | | |
| rep(age*stand*gap) | 16 | 0.81252 | | |
| pos | 2 | 3.80470 | 21.52 | 0.0001 * |
| age*pos | 2 | 0.95353 | 5.39 | 0.0054 * |
| gap*pos | 4 | 2.47179 | 13.98 | 0.0001 * |
| age*gap*pos | 4 | 0.44173 | 2.50 | 0.0449 * |
| spp | 2 | 22.85567 | 129.26 | 0.0001 * |
| age*spp | 2 | 0.25778 | 1.46 | 0.2359 |
| gap*spp | 6 | 0.76780 | 4.34 | 0.0004 * |
| pos*spp | 4 | 1.64965 | 9.33 | 0.0001 * |
| age*gap*spp | 6 | 0.18955 | 1.07 | 0.3817 |
| age*pos*spp | 4 | 0.21538 | 1.22 | 0.3054 |
| gap*pos*spp | 8 | 0.67909 | 3.84 | 0.0004 * |
| age*gap*pos*spp | 8 | 0.11224 | 0.63 | 0.7476 |
| Error: rep(age*stand *gap*pos*spp) | 156 | 0.17682 | | |
| Total | 239 | | | |

*Abies* and *Tsuga*, and in 0.4 North and 1.0 Center locations for *Tsuga* (Figure 2.4). Establishment was high for all species in 1.0 South, 0.4 Center, and 0.4 South locations. Despite their relatively small size, establishment in 0.2 gaps was significantly greater than in controls, and comparable to establishment in less exposed locations of larger gaps. Although light levels were similar in small gaps and controls, soil moisture was higher in 0.2 gaps than in controls. Within 1.0 gaps, there was a significant gradient of increased establishment from North to South positions for *Abies* and *Tsuga*. This corresponds to decreasing levels of light and surface temperature and increasing soil moisture content within these gaps. *Pseudotsuga* is generally considered the least shade-tolerant of the three species (Minore 1979), but its establishment after two growing seasons in controls and 0.2 gaps was greater than that of *Tsuga*, and similar to that of *Abies*. Considering the effect of missed initial counts in replicate 2 seed-plots (Table 2.3) suggests that within-gap establishment gradients for *Abies* and *Tsuga* in large gaps were steeper than shown, but that differences among locations or species would not change significantly.

Seedling establishment did not differ significantly by forest age class, but the age class effect was significant in interaction with position and with gap size and position (Table 2.4). Means tests detected no significant differences at the p=.05 level among age class by gap size by position means, probably due to the marginal significance of the interaction, and north and south age class by position means were not estimable due to missing cells in the design. The following trends may account for the significance of the age class interactions, however. Establishment of *Abies* and *Tsuga* in North positions tended to be greater in old-growth stands than in mature stands, but establishment of these species in South positions tended to be greater in mature stands than in old-growth stands (Figure 2.5a). The greatest differences between age classes at the gap size and within-gap position level were greater establishment in control North positions, and lower establishment in 1.0 South positions in old-growth than in mature stands. There was also a tendency towards greater establishment in exposed locations (1.0 North and Center, 0.4 North), lower establishment in open shaded locations (1.0 South, 0.4 Center and South), and greater

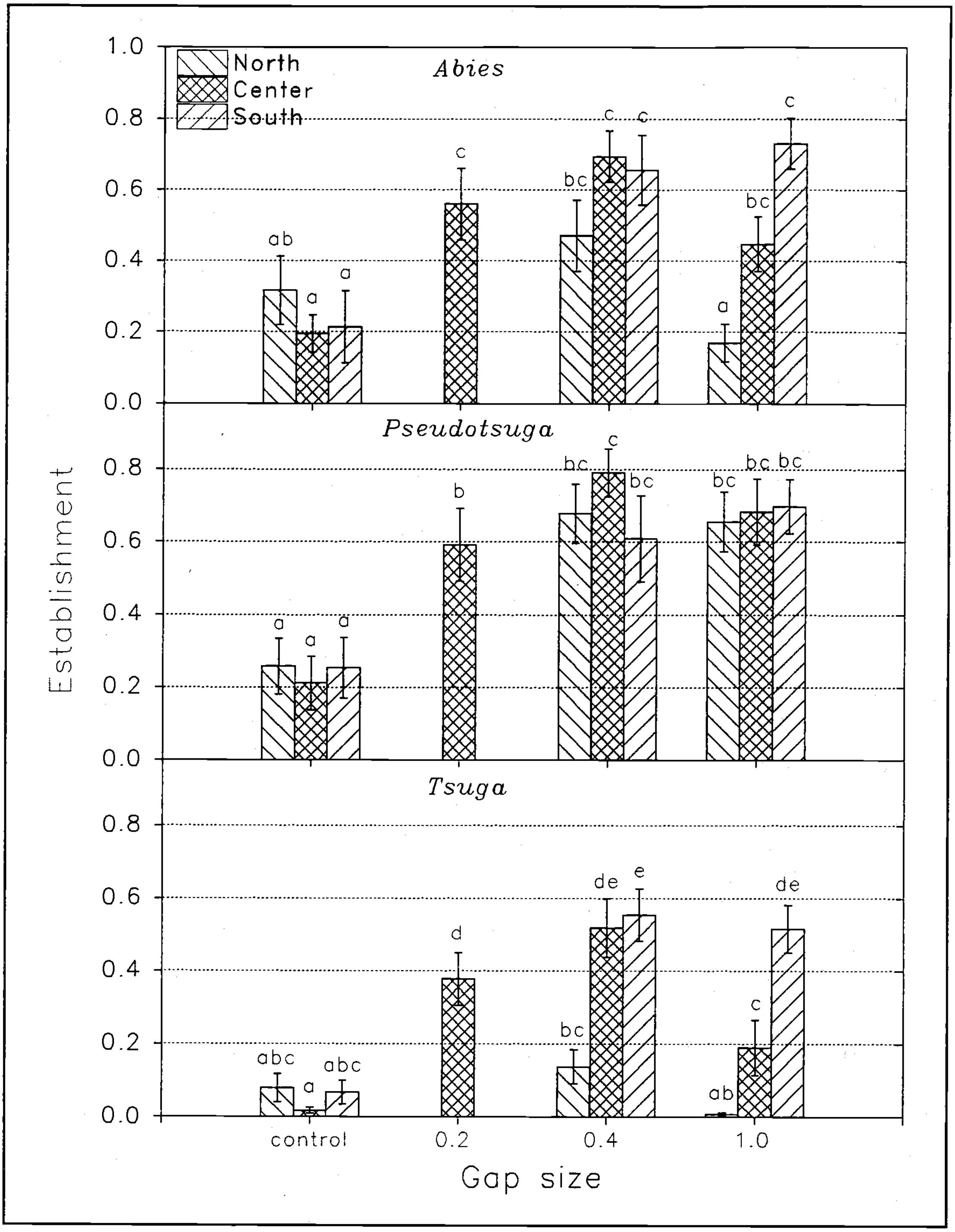

**Figure 2.4:** Seedling establishment (% of maximum emerged) by gap size, within-gap position, and species after two growing seasons for the 1992 cohort in seed-sowing experiment. Data are means and standard errors of all replicates(n=8). Means within a species with different letters were significantly different according to analysis of least-square means in ANOVA at p=.05.

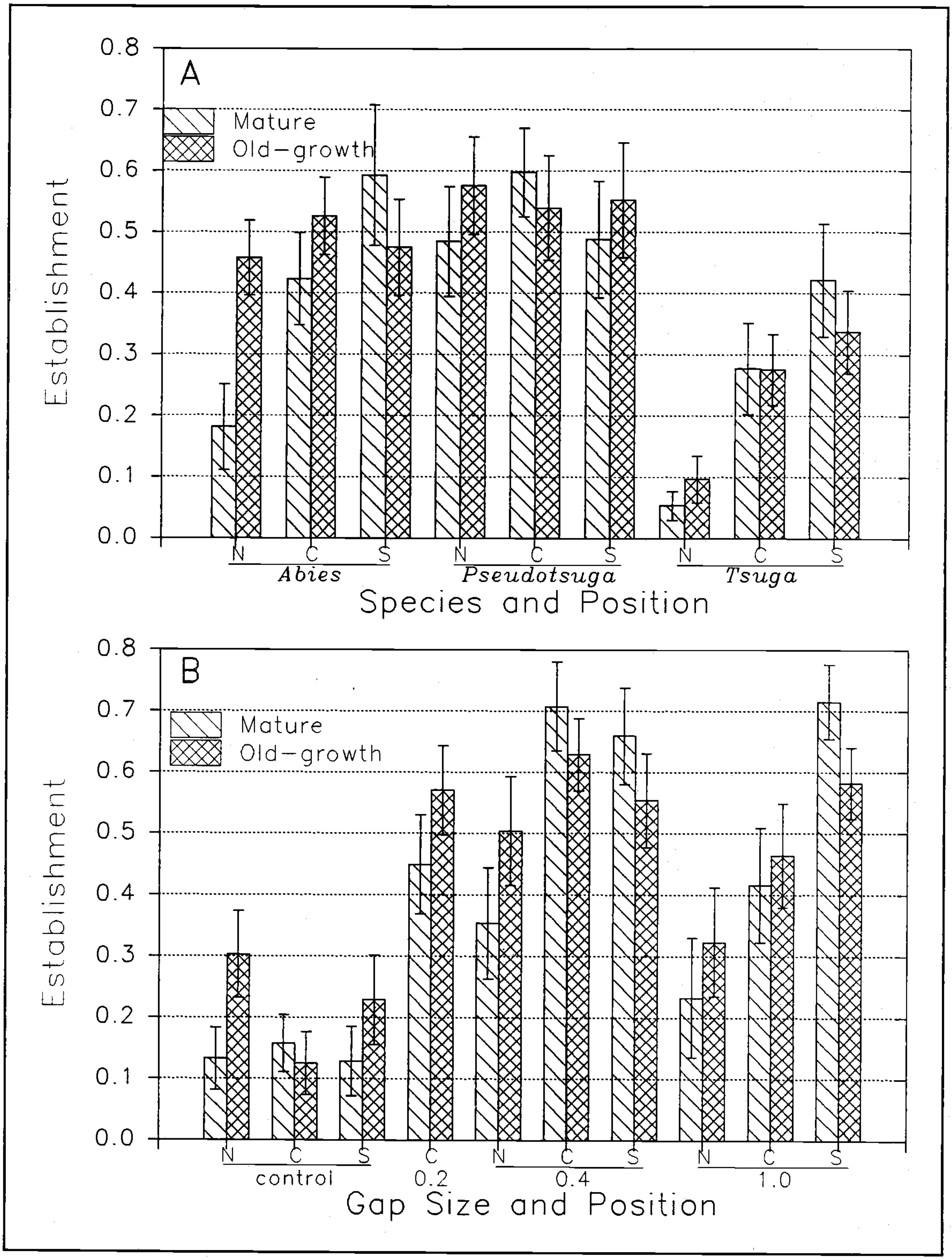

**Figure 2.5:** Age-class effects on seedling establishment (% of maximum emerged) after two growing seasons for the 1992 cohort in seed-sowing experiment by (a) within-gap position and species, and (b) gap size and within-gap position. Data are means and standard errors of all replicates within an age class (n=4).

establishment in more shaded locations (controls and 0.2 gaps) in the old-growth age class than in the mature age class (Figure 2.5b).

Seedling establishment in closed-canopy control areas differed significantly by stand in single-factor ANOVAs for each species ($F_{[3,23]}$=.030, .014, and .0005 for *Abies*, *Pseudotsuga*, and *Tsuga*, respectively). The rankings of stand establishment means were similar for all species, with MCY < HJA < PCM < TCO (Table 2.5). Low establishment in stand MCY may be associated with low light levels (Table 2.2), while the tendency towards greater establishment in TCO than PCM may be related to greater moisture levels and in spite of lower light levels. Although canopy density tended to be more patchily distributed in PCM and TCO than in MCY and HJA, there appeared to be no resource difference related to the significant differences in establishment between HJA and TCO.

## Annual effects on establishment

First-year seedling establishment in stand TCO differed significantly between 1992 and 1993 (Table 2.6). The year effect was significant alone and in interaction with gap and position, species, and gap and species. Due to low initial emergence in 1993, establishment percentages for *Pseudotsuga* in all gap sizes, and for *Abies* in 1.0

**Table 2.5:** Means and standard errors of seedling establishment (% of maximum count) by stand and species for 1992 cohort on seed-plots in controls (n=6). Stand means with different letters differed significantly (p < .05) in the analysis of least-square means in the ANOVA on arcsin of square-root transformed establishment values.

| | *Abies* | | *Pseudotsuga* | | *Tsuga* | |
|---|---|---|---|---|---|---|
| MCY | 0.104 ± 0.047 | a | 0.106 ± 0.053 | a | 0.006 ± 0.004 | a |
| HJA | 0.173 ± 0.085 | a | 0.124 ± 0.072 | a | 0.013 ± 0.010 | a |
| PCM | 0.270 ± 0.096 | ab | 0.320 ± 0.066 | b | 0.032 ± 0.010 | a |
| TCO | 0.424 ± 0.116 | b | 0.413 ± 0.092 | b | 0.168 ± 0.044 | b |

**Table 2.6:** Results of split-split plot ANOVA on first-year seedling establishment (% of maximum count) for 1992 and 1993 on seed-plots in stand TCO. Factor abbreviations are: gap= gap size, rep= replicate, pos= position, yr= year, spp= species. Rep(gap) error term was left out of model because Mean Square was less than that of rep(gap*pos). Significant effects (p <.05) are marked with asterisks (*).

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| gap | 3 | 0.99976 | 1.86 | 0.2003 |
| Error: rep(gap) | | **n.a.** | | |
| pos | 2 | 1.25950 | 2.34 | 0.1464 |
| gap*pos | 4 | 0.80689 | 1.50 | 0.2739 |
| Error: rep(gap*pos) | 10 | 0.53759 | | |
| yr | 1 | 0.75989 | 5.26 | 0.0270 * |
| gap*yr | 3 | 0.20423 | 1.41 | 0.2524 |
| pos*yr | 2 | 0.22123 | 1.53 | 0.2283 |
| gap*pos*yr | 4 | 0.41505 | 2.87 | 0.0346 * |
| spp | 2 | 3.57945 | 24.78 | 0.0001 * |
| gap*spp | 6 | 0.22476 | 1.56 | 0.1846 |
| pos*spp | 4 | 0.63704 | 4.41 | 0.0047 * |
| yr*spp | 2 | 0.50589 | 3.50 | 0.0394 * |
| gap*pos*spp | 8 | 0.32367 | 2.24 | 0.0437 * |
| gap*yr*spp | 6 | 0.40973 | 2.84 | 0.0210 * |
| pos*yr*spp | 4 | 0.20055 | 1.39 | 0.2548 |
| gap*pos*yr*spp | 6 | 0.17948 | 1.24 | 0.3050 |
| Error: rep(gap*pos*yr *spp) | 41 | 0.14443 | | |
| Total | 108 | | | |

gap sizes, were not very reliable. Field observations suggested that seed predation was high before the 1993 cohort emerged, despite identical exclosures for the 1992 and 1993 cohorts. Establishment was significantly lower in control North and 0.4 South locations in 1993 than in 1992 (Table 2.7). Establishment of *Abies* and *Pseudotsuga* in 0.4 gaps was significantly lower in 1993 than in 1992, apparently due to high numbers of clipped seedlings found in that gap size. The greater establishment of *Abies* in controls in 1993 was almost significant. Establishment of *Tsuga* was significantly lower in controls and higher in 0.4 gaps in 1993 than in 1992

**Table 2.7:** Separation of means for significant interactions in ANOVA on first-year seedling establishment (% of maximum count) for 1992 and 1993 on seed-plots in stand TCO. Values are least-square means and standard errors of transformed (arcsin of square-root) establishment data. Means which differed significantly ($p < .05$) between 1992 and 1993 are marked with asterisks (*). Missing values were not estimable due to missing cells in the design or missing data.

| Gap | Pos | Species | 1992 | 1993 | |
|---|---|---|---|---|---|
| Year*gap size*position | | | | | |
| ctl | N | | 0.978±0.101 | 0.692±0.115 | * |
| ctl | C | | 0.654±0.102 | 0.725±0.118 | |
| ctl | S | | 0.859±0.117 | 0.911±0.111 | |
| 0.2 | C | | 1.220±0.100 | 1.079±0.110 | |
| 0.4 | N | | 0.747±0.101 | 0.600±0.110 | |
| 0.4 | C | | 0.997±0.098 | 0.825±0.107 | |
| 0.4 | S | | 1.060±0.103 | 0.706±0.124 | * |
| 1.0 | N | | 0.566±0.106 | . | |
| 1.0 | C | | 0.824±0.102 | . | |
| 1.0 | S | | 1.179±0.098 | 1.012±0.155 | |
| Year*gap size*species | | | | | |
| ctl | | *Abies* | 0.876±0.105 | 1.074±0.095 | |
| 0.2 | | *Abies* | . | . | |
| 0.4 | | *Abies* | 0.970±0.090 | 0.652±0.094 | * |
| 1.0 | | *Abies* | 0.844±0.093 | . | |
| ctl | | *Pseudotsuga* | 0.887±0.090 | 0.713±0.116 | |
| 0.2 | | *Pseudotsuga* | . | . | |
| 0.4 | | *Pseudotsuga* | 1.196±0.084 | 0.677±0.115 | * |
| 1.0 | | *Pseudotsuga* | 1.149±0.084 | 1.112±0.195 | |
| ctl | | *Tsuga* | 0.728±0.059 | 0.541±0.070 | * |
| 0.2 | | *Tsuga* | . | . | |
| 0.4 | | *Tsuga* | 0.638±0.060 | 0.802±0.065 | * |
| 1.0 | | *Tsuga* | 0.575±0.062 | 0.672±0.078 | |

(Table 2.7). At the within-gap level, establishment of *Tsuga* in 1993 tended to be higher in exposed locations (1.0 and 0.4 North and Center) and lower in open, shaded locations (1.0 and 0.4 South) than in 1992 (Figure 2.6). Higher temperatures and greater sunlight in the early summer of 1992 may have promoted early germination and establishment of most of the 1992 cohort in shaded locations but greater mortality

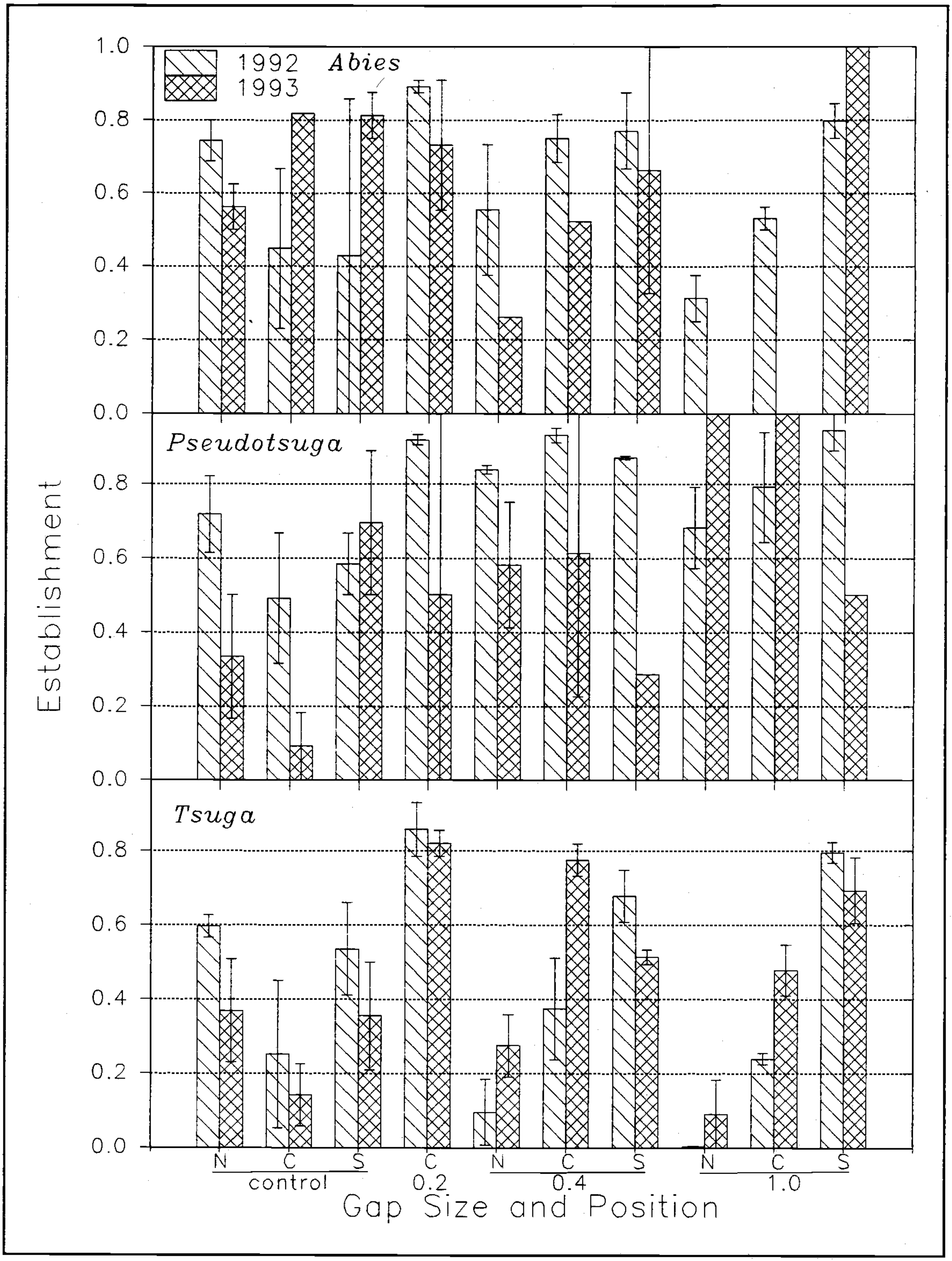

**Figure 2.6:** Comparison of seedling establishment (% of maximum emerged) for 1992 and 1993 cohorts in stand TCO in seed-sowing experiment after one growing season by gap size, within-gap position, and species. Data are means and standard errors of both replicates (n≤2, depending on presence of emergent seedlings).

in exposed locations relative to the 1993 cohort. *Abies*, which can germinate at low temperatures earlier in the year than the other species, apparently benefitted from the cooler, moister conditions in controls in 1993.

### Establishment as a fraction of seed or germination

Some trends in seedling population size were evident with the initial germination of seedlings. Germination of the 1992 cohort (as a fraction of total seed sown plus seed rain) tended to be higher in gaps than in controls for *Abies* and *Tsuga*, but not for *Pseudotsuga* (Table 2.8). Germination rates tended to be greatest for *Abies*, lower for *Tsuga*, and lowest for *Pseudotsuga* (seed lot viability tests [see Methods] indicated *Abies* and *Pseudotsuga* germination rates were similarly greater than those of *Tsuga*). A relatively high proportion of *Abies* germinants did not survive to emergence (*i.e.* died with their cotyledons within the seed coats), while most of the germinants of the other species did emerge. The net effect was that emergence as a fraction of seed was greatest for *Tsuga*, lower for *Abies*, and lowest for *Pseudotsuga*. These measures may be somewhat biased against *Pseudotsuga* due to predator preference of that species (Gashwiler 1967) and the placement of exclosure tops on seed-plots after natural seed dispersal had begun. In addition, the viability of naturally-dispersed seeds is unknown. Trends in establishment by location were similar, however, whether establishment was expressed as a fraction of total seed, germination, or emergence. Establishment as a fraction of total seed rarely exceeded 10% for the 1992 seedling cohort.

Seedling germination was much lower on replicate 1 seed-plots in stand TCO in 1993 than in 1992 (Table 2.9), although germination of *Abies* was actually higher on several replicate 2 seed-plots (not shown). The 1992 pattern of high mortality of *Abies* germinants was not seen on the few locations in 1993 that had enough seedlings to reliably reflect such a pattern. Other annual differences for *Abies* and *Pseudotsuga* were not evident due to low germination rates. Trends in establishment of *Tsuga* by location were similar, whether establishment was expressed as a fraction of total seed,

**Table 2.8:** Measures of establishment for 1992 seed-plot cohort in replicate 1 gaps. Standard errors are in parentheses (n=4).

| | | **% of seed which:** | | | **% establishment as a fraction of:** | | |
|---|---|---|---|---|---|---|---|
| location | # seed | germinated | emerged | # survivors | seed | germinants | emergents |
| *Abies* | | | | | | | |
| ctl N | 100 ( 0) | 15.0 ( 1.5) | 10.3 (1.0) | 4 ( 1.5) | 4.3 (1.5) | 30.6 (10.6) | 41.0 (15.1) |
| ctl C | 100 ( 0) | 13.5 ( 2.2) | 7.2 (1.7) | 1 ( 0.8) | 1.3 (0.8) | 12.1 ( 7.2) | 18.3 (10.7) |
| ctl S | 100 ( 0) | 18.8 ( 4.5) | 9.0 (4.4) | 0 ( 0.0) | 0.0 (0.0) | 0.0 ( 0.0) | 0.0 ( 0.0) |
| 0.2 C | 100 ( 0) | 19.8 ( 7.2) | 12.8 (5.7) | 7 ( 3.9) | 7.0 (3.9) | 26.1 (11.2) | 43.1 (17.8) |
| 0.4 N | 100 ( 0) | 26.0 ( 7.6) | 13.3 (4.5) | 6 ( 3.0) | 5.8 (3.0) | 19.1 ( 6.6) | 43.1 (12.6) |
| 0.4 C | 100 ( 0) | 27.5 (10.7) | 16.8 (6.7) | 12 ( 5.7) | 11.5 (5.7) | 52.1 (17.3) | 70.3 (14.0) |
| 0.4 S | 100 ( 0) | 19.3 ( 5.7) | 10.0 (2.0) | 5 ( 1.3) | 4.8 (1.3) | 39.4 (20.7) | 53.3 (17.0) |
| 1.0 N | 101 ( 1) | 23.4 ( 4.6) | 13.7 (2.1) | 2 ( 0.9) | 2.2 (0.9) | 10.4 ( 3.6) | 17.9 ( 6.0) |
| 1.0 C | 101 ( 1) | 18.1 ( 6.0) | 8.2 (2.1) | 4 ( 1.5) | 4.0 (1.5) | 17.2 ( 6.0) | 38.4 (13.7) |
| 1.0 S | 100 ( 0) | 22.8 ( 7.2) | 15.3 (5.5) | 9 ( 3.6) | 9.3 (3.6) | 46.1 (11.0) | 67.0 (11.8) |
| *Pseudotsuga* | | | | | | | |
| ctl N | 593 (217) | 7.3 ( 1.9) | 7.1 (2.1) | 18 (14.2) | 2.0 (1.2) | 29.4 (12.6) | 30.9 (12.2) |
| ctl C | 435 (129) | 9.5 ( 3.6) | 9.4 (3.7) | 15 (11.9) | 2.8 (1.7) | 25.5 (14.1) | 25.5 (14.1) |
| ctl S | 424 (125) | 10.9 ( 5.0) | 9.6 (4.4) | 4 ( 2.8) | 0.6 (0.4) | 8.5 ( 4.1) | 9.6 ( 4.6) |
| 0.2 C | 462 (140) | 9.5 ( 2.5) | 8.5 (2.4) | 16 ( 6.4) | 4.1 (1.2) | 49.1 (18.0) | 52.1 (16.1) |
| 0.4 N | 350 ( 83) | 11.6 ( 4.1) | 11.4 (4.0) | 21 (11.1) | 5.4 (1.6) | 55.8 (11.7) | 56.8 (12.0) |
| 0.4 C | 363 (115) | 17.6 ( 6.8) | 17.6 (6.8) | 38 (14.4) | 10.6 (1.9) | 72.8 (12.9) | 72.8 (12.9) |
| 0.4 S | 385 (129) | 11.7 ( 4.4) | 11.6 (4.5) | 26 (17.8) | 6.0 (2.5) | 47.3 (22.9) | 47.3 (22.9) |
| 1.0 N | 370 ( 73) | 10.9 ( 1.5) | 9.1 (1.1) | 16 ( 4.2) | 4.2 (0.8) | 41.7 (10.0) | 49.3 (10.9) |
| 1.0 C | 360 ( 59) | 8.1 ( 2.0) | 7.1 (1.9) | 17 ( 6.4) | 5.3 (2.2) | 58.9 (13.4) | 68.4 (14.4) |
| 1.0 S | 391 ( 62) | 10.0 ( 3.1) | 9.2 (3.3) | 27 (15.0) | 6.7 (3.7) | 58.1 (15.9) | 62.1 (13.9) |

**Table 2.8:** (continued).

| location | # seed | % of seed which: germinated | emerged | # survivors | % establishment as a fraction of: seed | germinants | emergents |
|---|---|---|---|---|---|---|---|
| *Tsuga* | | | | | | | |
| ctl N | 1965 (905) | 11.9 ( 4.6) | 11.8 (4.6) | 26 (24.5) | 0.8 (0.6) | 7.1 ( 5.8) | 7.1 ( 5.8) |
| ctl C | 1882 (854) | 10.4 ( 4.5) | 10.2 (4.5) | 4 ( 3.7) | 0.1 (0.1) | 1.7 ( 1.4) | 1.7 ( 1.4) |
| ctl S | 1789 (801) | 10.0 ( 4.5) | 9.8 (4.4) | 6 ( 5.5) | 0.1 (0.1) | 4.0 ( 4.0) | 4.0 ( 4.0) |
| 0.2 C | 1807 (754) | 18.8 ( 5.0) | 18.8 (5.0) | 95 (46.2) | 6.8 (3.5) | 38.0 (14.3) | 38.0 (14.3) |
| 0.4 N | 1079 (403) | 12.6 ( 2.0) | 12.3 (2.1) | 5 ( 2.8) | 0.7 (0.5) | 5.0 ( 2.8) | 5.1 ( 2.9) |
| 0.4 C | 1206 (558) | 20.5 ( 5.9) | 19.9 (6.0) | 60 ( 9.8) | 8.5 (2.6) | 39.9 (10.6) | 41.1 (10.2) |
| 0.4 S | 1093 (457) | 18.0 ( 4.4) | 17.9 (4.3) | 87 (34.2) | 9.6 (3.2) | 48.8 (10.6) | 48.9 (10.6) |
| 1.0 N | 1513 (618) | 13.1 ( 1.9) | 12.5 (1.9) | 2 ( 1.9) | 0.2 (0.1) | 1.1 ( 0.7) | 1.2 ( 0.7) |
| 1.0 C | 1311 (479) | 12.3 ( 1.5) | 11.8 (1.3) | 17 (14.4) | 0.8 (0.6) | 6.6 ( 4.7) | 7.2 ( 5.2) |
| 1.0 S | 1308 (486) | 18.6 ( 5.7) | 18.6 (5.7) | 98 (42.0) | 10.2 (4.2) | 49.0 ( 7.2) | 49.0 ( 7.2) |

**Table 2.9:** Different measures of seedling establishment for replicate 1 seed-plots in stand TCO for 1992 and 1993 (n=1).

| | | | % of seed which: | | | | | | % establishment as a fraction of: | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | # seed | | germinated | | emerged | | # survivors | | seed | | germinants | | emergents | |
| location | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 |
| *Abies* | | | | | | | | | | | | | | |
| ctl N | 100 | 100 | 16.0 | 4.0 | 10.0 | 2.0 | 8 | 1 | 8.0 | 1.0 | 50.0 | 25.0 | 80.0 | 50.0 |
| ctl C | 100 | 114 | 15.0 | 0.0 | 9.0 | 0.0 | 6 | 0 | 6.0 | 0.0 | 40.0 | -- | 66.7 | -- |
| ctl S | 100 | 112 | 19.0 | 14.3 | 1.0 | 14.3 | 0 | 14 | 0.0 | 12.5 | 0.0 | 87.5 | 0.0 | 87.5 |
| 0.2 C | 100 | 104 | 33.0 | 69.2 | 22.0 | 62.5 | 20 | 36 | 20.0 | 34.6 | 60.6 | 50.0 | 90.9 | 55.4 |
| 0.4 N | 100 | 100 | 41.0 | 0.0 | 16.0 | 0.0 | 6 | 0 | 6.0 | 0.0 | 14.6 | -- | 37.5 | -- |
| 0.4 C | 100 | 100 | 33.0 | 0.0 | 19.0 | 0.0 | 13 | 0 | 13.0 | 0.0 | 39.4 | -- | 68.4 | -- |
| 0.4 S | 100 | 100 | 25.0 | 1.0 | 15.0 | 1.0 | 10 | 1 | 10.0 | 1.0 | 40.0 | 100.0 | 66.7 | 100.0 |
| 1.0 N | 104 | 100 | 14.4 | 0.0 | 7.7 | 0.0 | 2 | 0 | 1.9 | 0.0 | 13.3 | -- | 25.0 | -- |
| 1.0 C | 102 | 100 | 27.5 | 0.0 | 9.8 | 0.0 | 5 | 0 | 4.9 | 0.0 | 17.9 | -- | 50.0 | -- |
| 1.0 S | 100 | 100 | 28.0 | 2.0 | 20.0 | 1.0 | 15 | 1 | 15.0 | 1.0 | 53.6 | 50.0 | 75.0 | 100.0 |
| *Pseudotsuga* | | | | | | | | | | | | | | |
| ctl N | 268 | 108 | 4.9 | 1.9 | 4.9 | 1.9 | 8 | 1 | 3.0 | 0.9 | 61.5 | 50.0 | 61.5 | 50.0 |
| ctl C | 216 | 108 | 5.6 | 0.9 | 5.6 | 0.9 | 8 | 0 | 3.7 | 0.0 | 66.7 | 0.0 | 66.7 | 0.0 |
| ctl S | 276 | 104 | 2.5 | 2.9 | 2.2 | 1.9 | 3 | 1 | 1.1 | 1.0 | 42.9 | 33.3 | 50.0 | 50.0 |
| 0.2 C | 262 | 108 | 8.0 | 0.9 | 8.0 | 0.9 | 19 | 0 | 7.2 | 0.0 | 90.5 | 0.0 | 90.5 | 0.0 |
| 0.4 N | 252 | 112 | 8.3 | 3.6 | 7.9 | 3.6 | 17 | 3 | 6.8 | 2.7 | 81.0 | 75.0 | 85.0 | 75.0 |
| 0.4 C | 252 | 108 | 13.5 | 1.9 | 13.5 | 1.9 | 31 | 2 | 12.3 | 1.9 | 91.2 | 100.0 | 91.2 | 100.0 |
| 0.4 S | 212 | 104 | 11.3 | 0.0 | 11.3 | 0.0 | 21 | 0 | 9.9 | 0.0 | 87.5 | -- | 87.5 | -- |
| 1.0 N | 304 | 160 | 12.8 | 2.5 | 9.2 | 2.5 | 16 | 4 | 5.3 | 2.5 | 41.0 | 100.0 | 57.1 | 100.0 |
| 1.0 C | 300 | 114 | 12.3 | 0.9 | 11.0 | 0.9 | 31 | 1 | 10.3 | 0.9 | 83.8 | 100.0 | 93.9 | 100.0 |
| 1.0 S | 308 | 120 | 5.8 | 3.3 | 5.8 | 1.7 | 16 | 1 | 5.2 | 0.8 | 88.9 | 25.0 | 88.9 | 50.0 |

**Table 2.9:** (continued).

| | # seed | | % of seed which: germinated | | emerged | | # survivors | | % establishment as a fraction of: seed | | germinants | | emergents | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| location | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 |
| *Tsuga* | | | | | | | | | | | | | | |
| ctl N | 4228 | 1380 | 9.6 | 10.8 | 9.6 | 10.4 | 254 | 33 | 6.0 | 2.4 | 62.7 | 22.2 | 62.7 | 22.9 |
| ctl C | 4012 | 1540 | 6.3 | 2.7 | 6.3 | 2.6 | 114 | 9 | 2.8 | 0.6 | 45.1 | 21.4 | 45.1 | 22.5 |
| ctl S | 3808 | 1468 | 3.7 | 4.6 | 3.7 | 4.6 | 57 | 14 | 1.5 | 1.0 | 41.0 | 20.9 | 41.0 | 20.9 |
| 0.2 C | 2970 | 1368 | 11.6 | 6.3 | 11.6 | 5.6 | 270 | 65 | 9.1 | 4.8 | 78.5 | 75.6 | 78.5 | 85.5 |
| 0.4 N | 2212 | 1372 | 7.7 | 6.4 | 6.9 | 6.1 | 1 | 16 | 0.1 | 1.2 | 0.6 | 18.2 | 0.7 | 19.1 |
| 0.4 C | 2848 | 1316 | 8.1 | 5.4 | 6.8 | 5.0 | 46 | 54 | 1.6 | 4.1 | 20.0 | 76.1 | 23.7 | 81.8 |
| 0.4 S | 2436 | 1364 | 14.0 | 6.7 | 14.0 | 6.5 | 256 | 44 | 10.5 | 3.2 | 74.9 | 48.4 | 74.9 | 49.4 |
| 1.0 N | 3020 | 1248 | 8.6 | 2.0 | 7.7 | 1.8 | 1 | 0 | 0.0 | 0.0 | 0.4 | 0.0 | 0.4 | 0.0 |
| 1.0 C | 2396 | 1090 | 12.1 | 6.2 | 11.0 | 5.9 | 67 | 35 | 2.8 | 3.2 | 23.2 | 51.5 | 25.4 | 54.7 |
| 1.0 S | 2460 | 1276 | 21.1 | 7.4 | 21.1 | 6.1 | 397 | 61 | 16.1 | 4.8 | 76.6 | 64.9 | 76.6 | 78.2 |

germination, or emergence. Establishment as a fraction of total seed rarely exceeded 5% for the 1993 seedling cohort, although *Abies* establishment reached 12% and 35% in two locations.

### Survival of marked seedlings

Estimates of seedling establishment based on counts of individuals can over-estimate true survival by not recording seedlings that die between counts and are replaced by new emergents. This potential for over-estimation of survival was evaluated by comparing survival based on marked seedlings with establishment calculated from simple counts on the same seed-plots. Comparisons of survival and establishment estimates on individual locations indicate that over-estimation using the count method ranged between 0 and 4% for *Abies*, 0 and 13% for *Pseudotsuga*, and 0 and 5% for *Tsuga* (Table 2.10). Over-estimation was greatest in the 1.0 Center location for *Pseudotsuga* and *Tsuga*. These trends suggest that the patterns of gap size and within-gap position effects on survival (Figure 2.4) would not change significantly for *Abies* and *Tsuga*, but that *Pseudotsuga* survival in 1.0 locations may have been significantly lower relative to other locations. A similar comparison for the 1993 seedling cohort (Table 2.11) indicated that over-estimation of survival using the count method was less than 1% for *Abies* and *Pseudotsuga*, and ranged from 0 to 4% for *Tsuga*. The differences in over-estimation between cohorts may have been due to low initial population size of *Abies* and *Pseudotsuga* and better accounting of dead seedlings in 1993.

### Causes of seedling mortality

Causes of seedling mortality varied among gap locations. General observations on the appearance of dead seedlings were recorded for the 1992 cohort, while counts were kept for the 1993 seedling cohort (Table 2.12). The most common

**Table 2.10:** Comparisons of establishment of emerged seedlings in 1992 cohort calculated from marked individuals and from counts in seed-plots. Data are from one replicate location in each gap.

| | | | % establishment calculated from: | | |
|---|---|---|---|---|---|
| Stand | location | | marked | counts | Difference |
| *Abies* | | | | | |
| PCM | ctl | C | 40.0 | 40.0 | 0.0 |
| PCM | 1.0 | C | 0.0 | 0.0 | 0.0 |
| TCO | ctl | C | 29.1 | 33.3 | 4.2 |
| TCO | 1.0 | N | 23.4 | 25.0 | 1.6 |
| TCO | 1.0 | C | 49.4 | 50.0 | 0.6 |
| TCO | 1.0 | S | 48.8 | 50.0 | 1.2 |
| *Pseudotsuga* | | | | | |
| PCM | ctl | C | 36.8 | 39.4 | 2.6 |
| PCM | 1.0 | C | 74.7 | 80.6 | 6.0 |
| TCO | ctl | C | 58.3 | 58.3 | 0.0 |
| TCO | 1.0 | N | 39.4 | 42.9 | 3.5 |
| TCO | 1.0 | C | 80.6 | 93.9 | 13.3 |
| TCO | 1.0 | S | 73.7 | 77.8 | 4.1 |
| *Tsuga* | | | | | |
| PCM | ctl | C | 0.8 | 0.9 | 0.1 |
| PCM | 1.0 | C | 1.3 | 1.3 | 0.0 |
| TCO | ctl | C | 5.6 | 5.9 | 0.4 |
| TCO | 1.0 | N | 0.0 | 0.0 | 0.0 |
| TCO | 1.0 | C | 20.0 | 24.7 | 4.6 |
| TCO | 1.0 | S | 39.4 | 40.9 | 1.5 |

form of mortality in all gaps, over both years, consisted of seedlings which disappeared without a trace during the one month interval between counts, possibly due to removal by insect predators (rodents also succeeded in entering exclosures occasionally, especially in 1993). Many *Abies* and *Tsuga* seedlings disappeared over winter (92-93) in gap size 0.2, possibly due to fragile seedlings being crushed under the snow-pack. Many of the dead seedlings in the controls and in exposed locations (1.0 North and Center, 0.4 North) were wilted and faded ("standing brown" in Table

**Table 2.11:** Comparisons of establishment of emerged seedlings in 1993 cohort calculated from marked individuals and from counts in seed-plots. Data are means of two replicates in stand TCO.

| location | | **% establishment calculated from:** marked | counts | Difference |
|---|---|---|---|---|
| *Abies* | | | | |
| ctl | N | 55.3 | 56.2 | 0.9 |
| ctl | C | 40.9 | 40.9 | 0.0 |
| ctl | S | 81.2 | 81.2 | 0.0 |
| 0.2 | C | 73.1 | 73.1 | 0.0 |
| 0.4 | N | 13.1 | 13.1 | 0.0 |
| 0.4 | C | 26.2 | 26.2 | 0.0 |
| 0.4 | S | 66.3 | 66.3 | 0.0 |
| 1.0 | N | 0.0 | 0.0 | 0.0 |
| 1.0 | C | 0.0 | 0.0 | 0.0 |
| 1.0 | S | 100.0 | 100.0 | 0.0 |
| *Pseudotsuga* | | | | |
| ctl | N | 33.3 | 33.3 | 0.0 |
| ctl | C | 9.1 | 9.1 | 0.0 |
| ctl | S | 69.4 | 69.4 | 0.0 |
| 0.2 | C | 50.0 | 50.0 | 0.0 |
| 0.4 | N | 58.1 | 58.1 | 0.0 |
| 0.4 | C | 61.3 | 61.3 | 0.0 |
| 0.4 | S | 14.3 | 14.3 | 0.0 |
| 1.0 | N | 50.0 | 50.0 | 0.0 |
| 1.0 | C | 50.0 | 50.0 | 0.0 |
| 1.0 | S | 25.0 | 25.0 | 0.0 |
| *Tsuga* | | | | |
| 0.4 | N | 26.9 | 27.4 | 0.5 |
| 0.4 | C | 78.3 | 81.8 | 3.5 |
| 1.0 | N | 9.1 | 9.1 | 0.0 |
| 1.0 | C | 47.0 | 47.8 | 0.8 |

2.12), potentially caused by drought and/or exposure to high temperatures. Clipping of seedlings (most likely by cutworms, family *Noctuidae* [Overhulser 1990]) was variable, but occasionally severe, in all shaded locations (controls, 0.2 Center, 0.4 South, and 1.0 South). The low levels of germination for *Abies* and *Pseudotsuga* in the 1993 cohort in stand TCO appear to be due in part to insect and rodent predation (empty seed and evidence of burrowing were found in several seed-plots).

**Table 2.12:** Condition of mortality for 1993 seedling cohort in seed-plots in stand TCO by species and gap size, in percent by species.

| | no trace | fungi/ molds | clipped stem/root | standing brown | trample | row sum |
|---|---|---|---|---|---|---|
| *Abies* | | | | | | |
| ctl | 9 | 3 | 4 | 5 | 1 | 23 |
| 0.2 | 3 | 4 | 7 | 2 | -- | 16 |
| 0.4 | 1 | 1 | 56 | 1 | 1 | 60 |
| 1.0 | 1 | -- | -- | -- | -- | 1 |
| sum | 14 | 8 | 68 | 9 | 1 | 100 |
| *Pseudotsuga* | | | | | | |
| ctl | 15 | 4 | 6 | 1 | -- | 26 |
| 0.2 | -- | -- | 1 | -- | -- | 1 |
| 0.4 | 5 | 2 | 61 | 1 | -- | 70 |
| 1.0 | 1 | -- | 2 | -- | -- | 4 |
| sum | 21 | 6 | 71 | 2 | 0 | 100 |
| *Tsuga* | | | | | | |
| ctl | 14 | 0.4 | 3 | 17 | -- | 35 |
| 0.2 | 4 | -- | 2 | -- | -- | 6 |
| 0.4 | 20 | 0.2 | 8 | 12 | -- | 41 |
| 1.0 | 8 | -- | 4 | 3 | 2 | 18 |
| sum | 46 | 1 | 18 | 32 | 2 | 100 |

## Seedling growth

Seedling size after two growing seasons (*i.e.* growth since germination) differed significantly among gap sizes, within-gap positions, species, and gap size by within-gap position interactions ("locations") in the controlled seed-plot study (Table 2.13). Although seedlings in old-growth stands were larger than those in mature stands (25% larger on average), particularly for *Abies* and *Tsuga* in the 0.4 and 1.0 gap sizes, the effect was not significant probably due to lower sample size (affecting

**Table 2.13:** Results of split-split plot ANOVA on seedling size (height*basal area). Factor abbreviations are: age= age class, gap= gap size, pos= position, spp= species. Significant effects (p < .05) are marked with asterisks (*).

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| age | 1 | 5.37803 | 1.59 | 0.3346 |
| Error: stand(age) | 2 | 3.38514 | | |
| gap | 3 | 44.55659 | 17.75 | 0.0022 * |
| age*gap | 3 | 3.75960 | 1.50 | 0.3078 |
| Error: stand*gap(age) | 6 | 2.51077 | | |
| pos | 2 | 23.49505 | 12.74 | 0.0001 * |
| age*pos | 2 | 0.89085 | 0.48 | 0.6214 |
| gap*pos | 4 | 13.68695 | 7.42 | 0.0002 * |
| age*gap*pos | 4 | 1.80755 | 0.98 | 0.4323 |
| spp | 2 | 84.44066 | 45.78 | 0.0001 * |
| age*spp | 2 | 1.56147 | 0.85 | 0.4383 |
| gap*spp | 6 | 3.46569 | 1.88 | 0.1151 |
| pos*spp | 4 | 2.97700 | 1.61 | 0.1948 |
| age*gap*spp | 6 | 0.54635 | 0.30 | 0.9342 |
| age*pos*spp | 4 | 1.35517 | 0.73 | 0.5751 |
| gap*pos*spp | 7 | 1.19728 | 0.65 | 0.7123 |
| age*gap*pos*spp | 5 | 0.14499 | 0.08 | 0.9951 |
| Error: stand*gap*pos *spp(age) | 32 | 1.84455 | | |
| Total | 95 | | | |

the weighting by number of seedlings measured) in the mature stands. Larger seedlings in the old-growth stands may have been due to greater soil moisture levels relative to the mature stands. Seedling size increased significantly with gap size (Table 2.14), and the largest seedlings in the 0.4 and 1.0 gap sizes were usually found in Center positions (Figure 2.7). Size patterns may be due to interacting resource gradients: light levels increased with gap size, while soil moisture levels didn't, but moisture was lower at gap edges than at gap centers. Stress associated with high temperatures at North positions in large gaps may have also limited growth there. The few *Tsuga* surviving in 1.0 North locations grew as well as those in the center, however. Seedling size increased in all locations from *Tsuga* to *Abies* to *Pseudotsuga*. Changes in seedling size with gap size also appeared to differ among

**Table 2.14:** Separation of means for significant interactions in ANOVA on seedling size (height*basal area) of 1992 cohort. Values are least-square means and standard errors of log-transformed sizes. Different letters indicate significant differences at the p = .05 level. Missing values were not estimable due to unbalanced data.

| Gap | Pos |  |  |
|---|---|---|---|
| ctl | N | 2.673 ± 0.271 | a |
| ctl | C | . |  |
| ctl | S | . |  |
| 0.2 | C | 3.121 ± 0.191 | ab |
| 0.4 | N | 3.346 ± 0.234 | bc |
| 0.4 | C | 3.916 ± 0.184 | d |
| 0.4 | S | 3.339 ± 0.194 | bc |
| 1.0 | N | 4.674 ± 0.326 | e |
| 1.0 | C | 5.072 ± 0.254 | e |
| 1.0 | S | 3.520 ± 0.179 | c |

species ($p$=.12 for gap size by species interaction). *Pseudotsuga* size was relatively small in all locations except for the 1.0 Center location, while *Tsuga* size appeared to increase dramatically in the larger gaps and *Abies* size increased more steadily with gap size. These differences in species' response are illustrated by relative growth rates between 1992 and 1993 for the 1992 cohort (Figure 2.8). While patterns of relative growth rates among locations were similar to patterns of seedling size, *Tsuga* had the highest values, followed by *Pseudotsuga* and *Abies* (values for *Tsuga* and *Pseudotsuga* were similar in 1.0 locations, however).

Observations on the timing of setting of terminal buds suggest some of the patterns in seedling growth are due to length of growing season. By early August of 1992, almost all seedlings in gap sizes 0 and 0.2 had set buds. The timing of bud-set in the larger gaps varied by stand, but *Abies* tended to set buds before the other species, and seedlings set buds latest in the 1.0 gap size (especially the 1.0 Center location). Since the distribution of *Abies amabilis* tends to be greatest at higher elevations than the other species (Franklin and Dyrness 1973), earlier bud-set may be a genetically-controlled response that constrained its growth in the gaps.

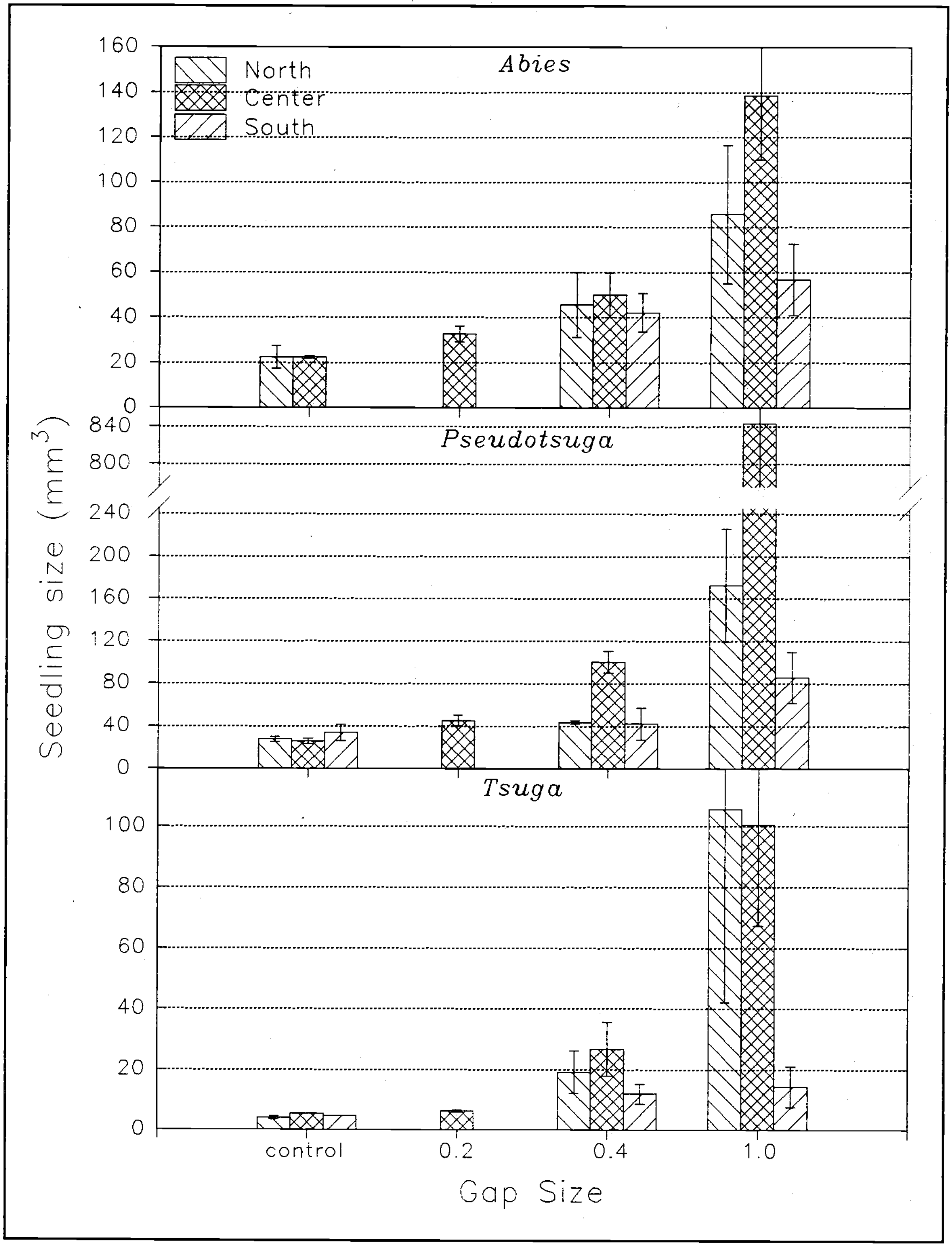

**Figure 2.7:** Seedling size (basal area*height) after two growing seasons for 1992 cohort in seed-sowing experiment by gap size, within-gap position, and species. Data are means and standard errors of replicate 1 locations from each stand (n≤4, depending on presence of seedlings).

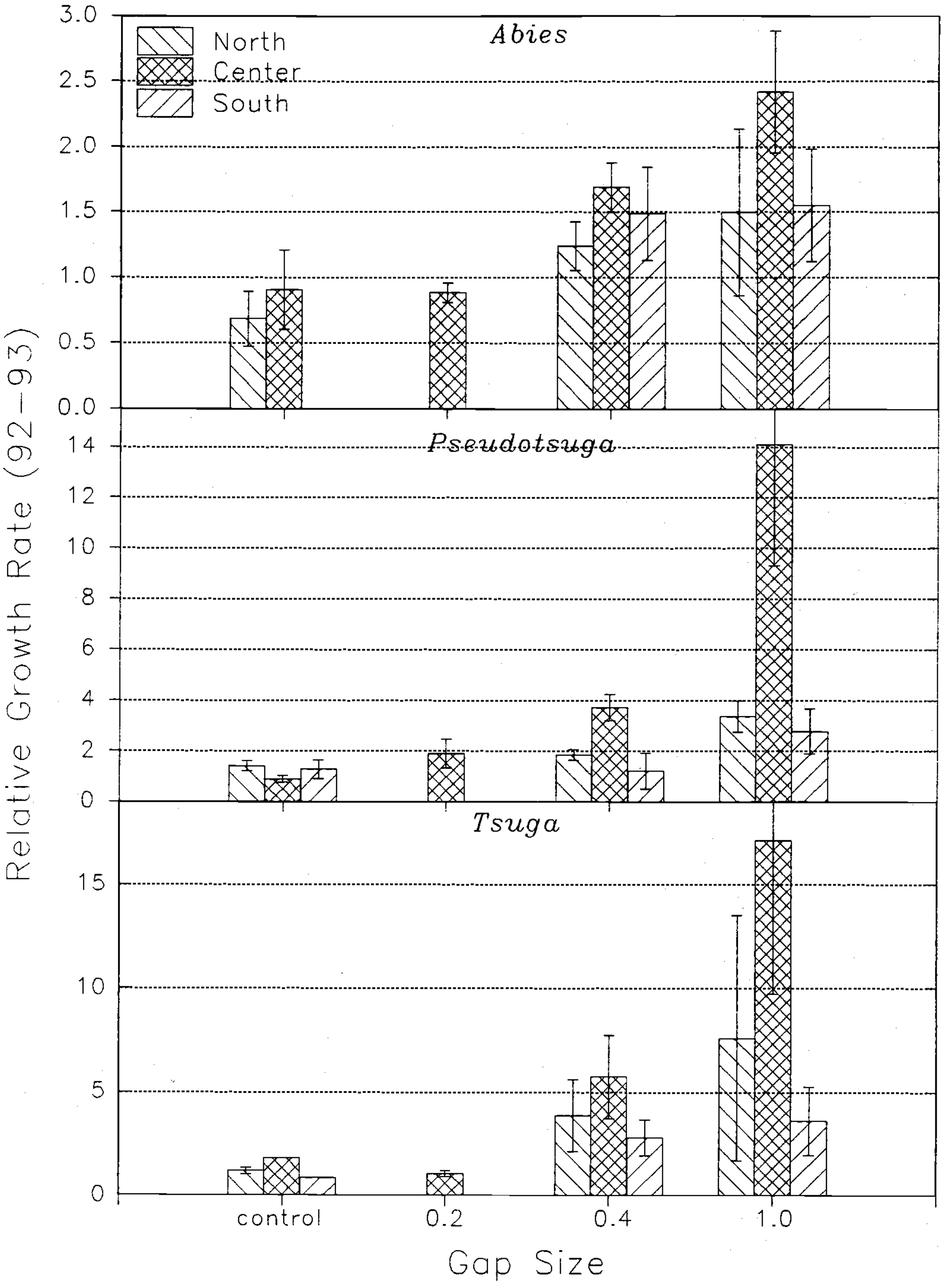

**Figure 2.8:** Relative growth rates of seedling size (basal area*height) from October 1992 to October 1993 ($[size_{93}-size_{92}]/size_{92}$) for the 1992 cohort in seed-sowing experiment by gap size, within-gap position, and species. Data are means and standard errors of replicate 1 locations from each stand ($n \leq 4$, depending on presence of seedlings).

## Survival of natural regeneration

The abundance of naturally-seeded tree species varied significantly among stands. The effect of age class was dramatic, with large numbers of *Pseudotsuga* emergents found in both age classes, large numbers of *Tsuga* emergents found in the old-growth stands and few in the mature stands, and only a few *Abies* emergents found in the old-growth stands (total number of marked seedlings per species was 1443, 2202, and 11, respectively). Since only 13 *Tsuga* were found in the 8 gaps examined in both mature stands (of which 3 were alive after 2 years), analysis and results for *Tsuga* will only be presented for the old-growth stands.

Survival of natural regeneration after two growing seasons differed significantly by gap size and within-gap position for *Pseudotsuga* and by within-gap position for *Tsuga*, while the gap size effect and gap size by within-gap position interaction were almost significant for *Tsuga* ($p < .08$) (Table 2.15). *Pseudotsuga* survival increased significantly with gap size, although survival in the 0.4 and 1.0 gap sizes was similar (Table 2.16). North and South position means were not estimable for the separation of position means analyses for *Pseudotsuga* or *Tsuga* due to missing cells in the design. Nevertheless, survival of *Pseudotsuga* tended to decrease from south to center to north positions within the larger gaps (Figure 2.9). Curiously, survival tended to be greater at the more exposed 1.0 North locations than at 0.4 North locations. This result may be somewhat misleading, because even though individual emergents were identified early in the growing season (late May/early June 1992), those found in more exposed locations (*e.g.* 1.0 North) may have already survived a wave of mortality that had not yet impacted less exposed locations (*e.g.* 1.0 Center and 0.4 North), making survival on exposed locations appear better than it really was. There was a tendency towards higher survival of *Pseudotsuga* in Center and South positions, and lower survival in North positions, in old-growth stands compared to mature stands, but variation was high. Survival of *Tsuga* was very low in controls, higher in 0.2 and 0.4 gap sizes, and then declined somewhat in the 1.0 gap size. A strong gradient of decreasing survival from South to North positions was evident for *Tsuga* in 0.4 and 1.0 gap sizes.

**Table 2.15:** Results of ANOVA on seedling survival of marked natural regeneration. The analysis for *Pseudotsuga* is based on data from all stands; the analysis for *Tsuga* is based on data from the old-growth stands. Factor abbreviations are: age= age class, gap= gap size, pos= position. Stand*gap(age) left out of model because Mean Square was less than that of stand*gap*pos(age). Significant effects ($p < .05$) are marked with asterisks (*).

*Pseudotsuga*

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| age | 1 | 1.02583 | 0.87 | 0.4498 |
| Error: stand(age) | 2 | 1.18132 | | |
| gap | 3 | 18.93039 | 37.37 | 0.0001 * |
| age*gap | 3 | 0.23003 | 0.45 | 0.7176 |
| Error: stand*gap(age) | | **n.a.** | | |
| pos | 2 | 3.16866 | 6.26 | 0.0087 * |
| gap*pos | 4 | 0.81981 | 1.62 | 0.2129 |
| age*pos | 2 | 0.73185 | 1.44 | 0.2618 |
| age*gap*pos | 4 | 0.11942 | 0.24 | 0.9145 |
| Error: stand*gap *pos(age) | 18 | 0.50651 | | |
| Total | 39 | | | |

*Tsuga*

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| gap | 3 | 9.01311 | 5.44 | 0.0677 |
| Error: gap(stand) | 4 | 1.65677 | 1.00 | 0.4740 |
| pos | 2 | 15.72577 | 9.52 | 0.0138 * |
| gap*pos | 4 | 6.03238 | 3.65 | 0.0772 |
| Error: gap*pos(stand) | 6 | 1.65196 | | |
| Total | 19 | | | |

## Density of natural regeneration

The density of naturally regenerated seedlings from the 1992 cohort found in the gaps in the summer of 1993 differed greatly by species, gap size, and position. As found in the study of survival of natural regeneration, *Pseudotsuga* seedlings were plentiful in all four stands, while *Tsuga* seedlings were rare in the mature age class.

**Table 2.16:** Separation of means for significant gap size effect in ANOVA on survival of naturally-regenerated *Pseudotsuga* seedlings. Values are least-square means and standard errors of arcsin of square-root transformed survival data. Means with different letters were significantly different at the p = .05 level. The mean for the 0.2 gap size was not estimable due to missing position cells in the design.

| | | |
|---|---|---|
| ctl | 0.124 ± 0.040 | a |
| 0.2 | . | |
| 0.4 | 0.578 ± 0.042 | b |
| 1.0 | 0.559 ± 0.042 | b |

Since only two *Tsuga* seedlings were found in the vegetation plots in the north-south strips of the 20 gaps examined in the mature stands, analysis and results for *Tsuga* will only be presented for the old-growth stands.

Density of *Pseudotsuga* seedlings differed significantly by gap size and by the within-gap position and age class interaction (Table 2.17). Density of *Pseudotsuga* was significantly higher in gaps than in controls, with no significant differences among gaps (Table 2.18). Density tended to increase from North to Center to South positions within gaps, but the variation around this trend was high (Figure 2.10). The cause of this variation appears to be due to differences between age-classes for the larger gaps: density increased dramatically from North to South positions in old-growth stands, while density was similar across positions in mature stands (Figure 2.11) (North and South position means were not estimable for the separation of age class by position means analysis due to missing cells in the design). This difference between age classes may be due to the relatively high understory density in mature stands (Table 2.1), which may have ameliorated exposure in high-light areas, but depressed survival in shaded areas, relative to old-growth stands. Exploration of understory cover effects on seedling survival is undertaken in Chapter 3. In terms of a mean seed rain over 1991-92 of 425 Pseudotsuga/m$^2$ across all stands, establishment rates for the 1992 cohort varied from 0.02 to 0.6%.

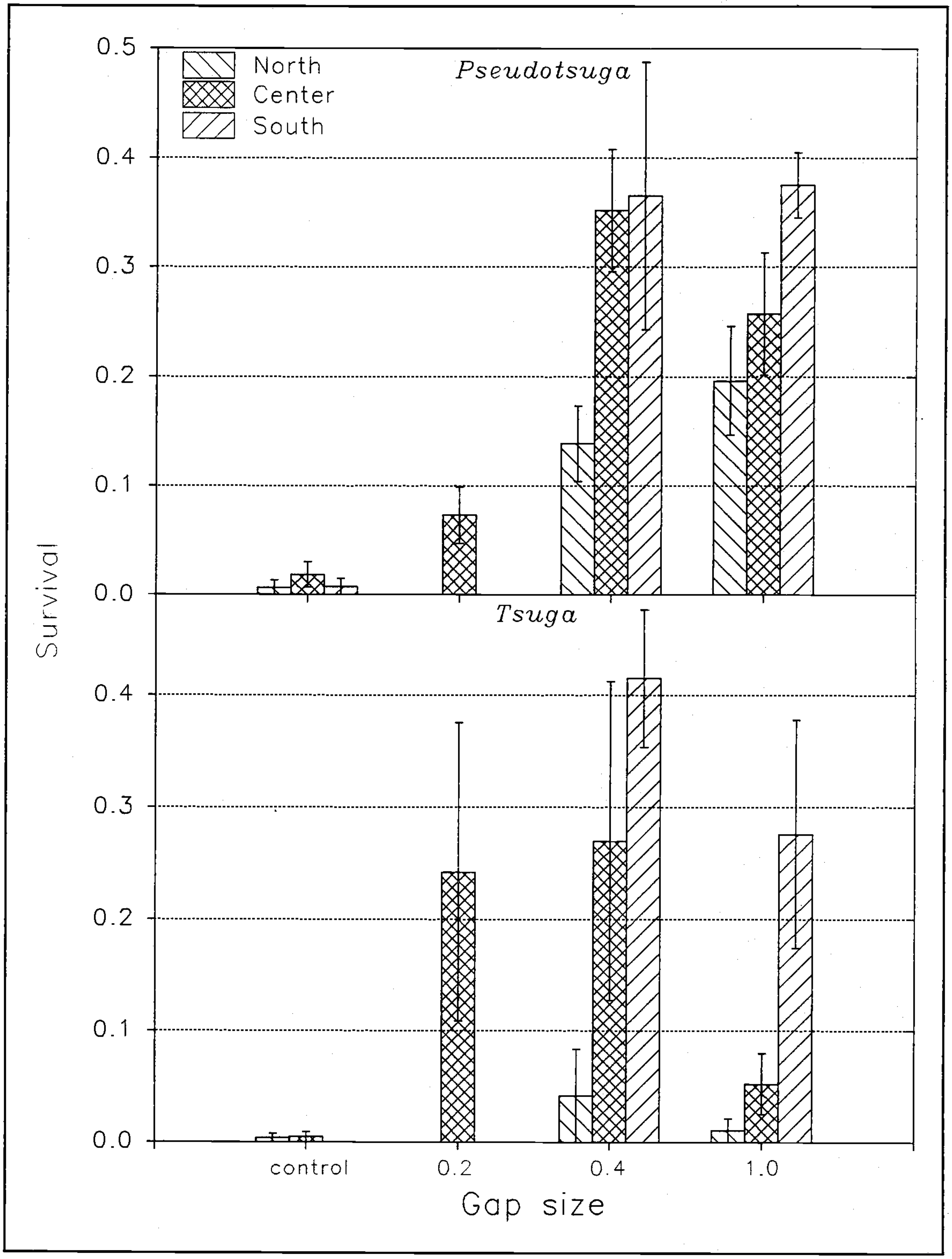

**Figure 2.9:** Survival (%) of natural regeneration after two growing seasons by gap size and within-gap position. Data are means and standard errors of replicate 1 locations in all stands for *Pseudotsuga* (n=4) and in old-growth stands for *Tsuga* (n=2).

**Table 2.17:** Results of ANOVA on density of naturally-regenerated seedlings. The analysis for *Pseudotsuga* is based on data from all stands; the analysis for *Tsuga* is based on data from the old-growth stands. Factor abbreviations are: age= age class, rep= gap replicate within stand, gap= gap size, pos= position. Significant effects (p < .05) are marked with asterisks (*).

*Pseudotsuga*

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| age | 1 | 0.00437 | 0.00 | 0.9875 |
| Error: stand(age) | 2 | 13.90295 | | |
| gap | 4 | 11.65176 | 4.82 | 0.0284 * |
| age*gap | 4 | 0.40626 | 0.17 | 0.9488 |
| Error: stand*gap(age) | 8 | 2.41946 | | |
| rep(age*stand*gap) | 20 | 2.00110 | | |
| pos | 2 | 1.01550 | 0.75 | 0.4797 |
| age*pos | 2 | 6.35470 | 4.67 | 0.0141 * |
| gap*pos | 6 | 1.19838 | 0.88 | 0.5166 |
| age*gap*pos | 6 | 2.66280 | 1.96 | 0.0908 |
| Error: rep(age*stand *gap*pos) | 48 | 1.36154 | | |
| Total | 103 | | | |

*Tsuga*

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| gap | 4 | 33.51651 | 0.96 | 0.5036 |
| Error: gap(stand) | 5 | 35.06828 | | |
| rep(stand*gap) | 10 | 10.01544 | | |
| pos | 2 | 90.04993 | 11.75 | 0.0042 * |
| gap*pos | 6 | 25.37521 | 3.31 | 0.0607 |
| Error: gap*pos(stand) | 8 | 7.66279 | | |
| rep(stand*gap*pos) | 16 | 4.50879 | | |
| Total | 51 | | | |

Density of *Tsuga* seedlings in the old-growth stands differed significantly by within-gap position, and the gap size by position effect was strong (p < .07) (Table 2.17) (North and South position means were not estimable for the separation of position means analysis due to missing cells in the design). Seedling density tended to increase from North to South positions for 0.4, 0.6, and 1.0 gap sizes (Figure 2.10). *Tsuga* density was low in North positions in all gap sizes and decreased with

**Table 2.18:** Separation of means for significant gap size effect in ANOVA on density of naturally-regenerated *Pseudotsuga* seedlings. Values are least-square means and standard errors of log-transformed density data. Means with different letters were significantly different at the p = .05 level. The mean for the 0.2 gap size was not estimable due to missing position cells in the design.

| | | |
|---|---|---|
| ctl | 0.104 ± 0.148 | a |
| 0.2 | . | |
| 0.4 | 0.815 ± 0.175 | b |
| 0.6 | 0.506 ± 0.159 | b |
| 1.0 | 0.622 ± 0.148 | b |

gap size in Center positions. Seedling density patterns in the 0.6 gap size, which was not used in the seed-sowing or survival of natural regeneration studies, appear to be intermediate between patterns in the 0.4 and 1.0 gap sizes. In terms of a mean seed rain over 1991-92 of 2881 Tsuga/m$^2$ in the old-growth stands, establishment rates for the 1992 cohort varied from 0.07 to 2.4%.

## Differences among studies

Seedling survival patterns for naturally regenerated seedlings differed from those found for the seed-sowing experiment in several ways. Establishment percentages of both *Pseudotsuga* and *Tsuga* were greater in the seed-plot study (Figure 2.4) than survival percentages in the study of naturally-seeded emergents (Figure 2.9). Trends among locations also differed between these studies. While survival of naturally-seeded *Pseudotsuga* was generally lower in 0.2 gaps than in larger gaps, establishment of *Pseudotsuga* in seed-plots was similar among gaps. The north-south gradient in survival of naturally-seeded *Pseudotsuga* in the larger gaps was also not evident in the seed-plot study. Trends in *Tsuga* survival across locations were similar between the two studies, although establishment was relatively higher in 1.0 Center locations in the seed-plot study. Greater establishment in seed-plots may

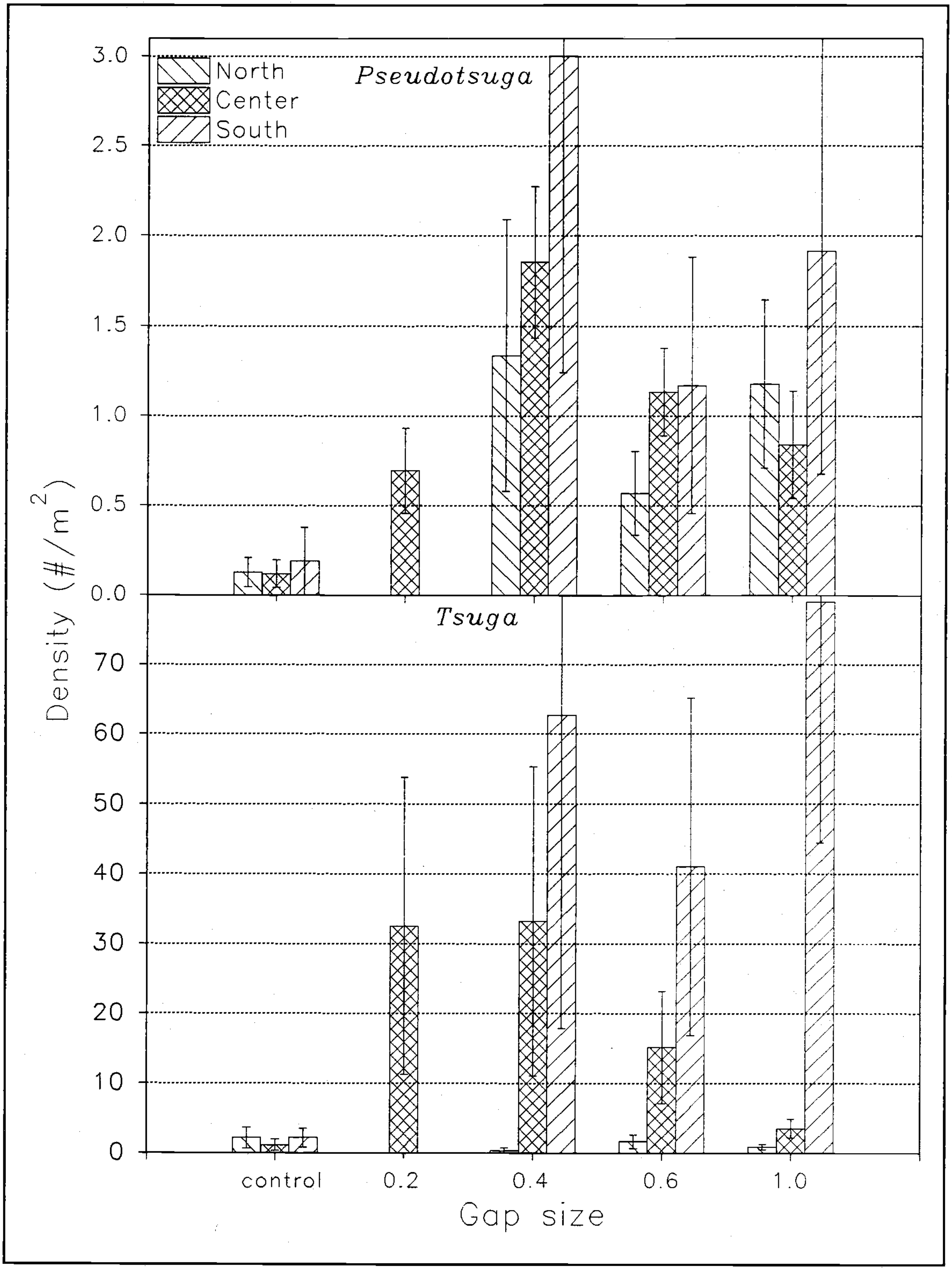

**Figure 2.10:** Density of 1992 natural regeneration cohort in the summer of 1993 by gap size and within-gap position. Data are means and standard errors of both replicates in all stands for *Pseudotsuga* (n=8) and in old-growth stands for *Tsuga* (n=4).

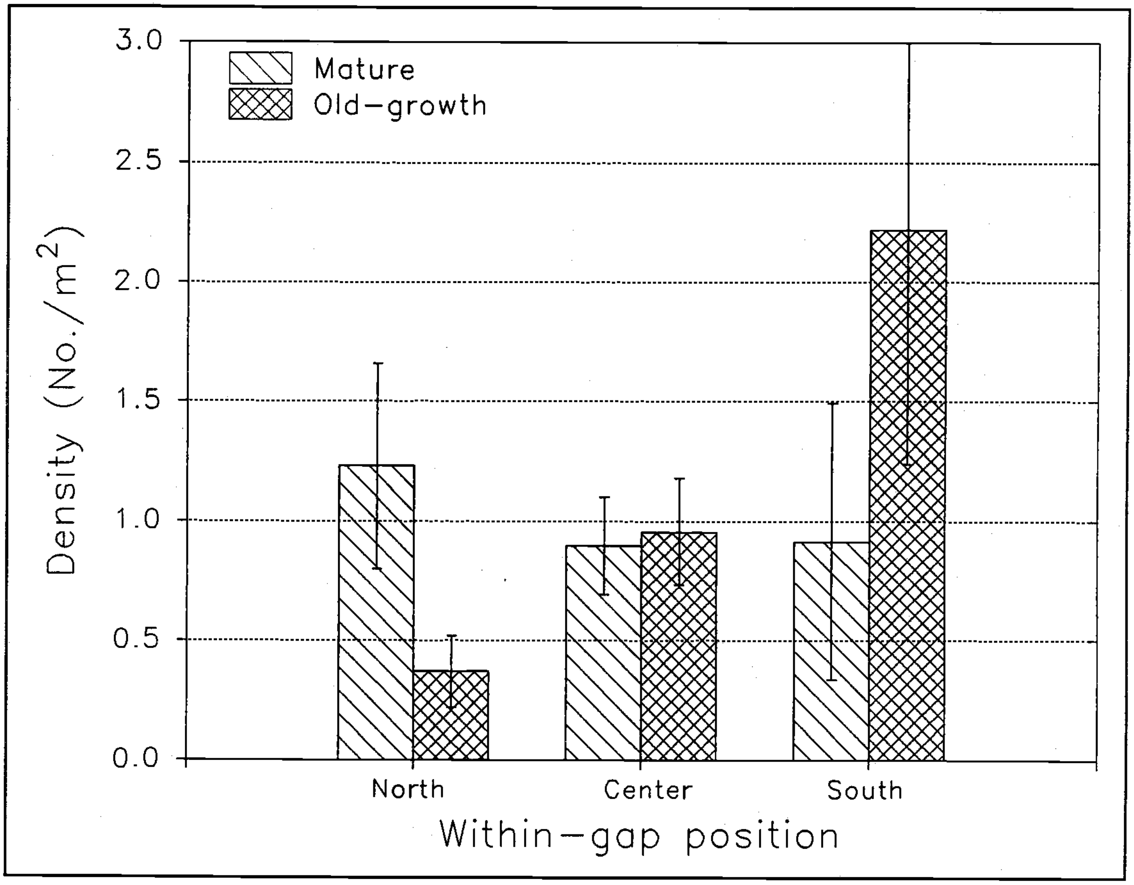

**Figure 2.11:** Density of *Pseudotsuga* 1992 natural regeneration cohort in the summer of 1993 by age class and within-gap position. Data are means and standard errors of positions in both replicates of two stands per age class (n=16 for North and South positions, n=20 for Center positions).

have been due to increased resource levels caused by removal of forest floor and surrounding vegetation, and/or reduced predation, inside seed-plot exclosures. The lack of within-gap survival gradients for *Pseudotsuga* in seed-plots within larger gaps may be due to the greater success of this species on mineral soil substrates relative to intact forest floor in exposed locations (Isaac 1943). Effects of substrate and vegetation on seedling survival are addressed in Chapter 3.

Patterns of survival and density of naturally-regenerated seedlings differed somewhat between the density (Figure 2.10) and survival studies (Figure 2.9). Although *Tsuga* seedling patterns across locations were similar in both studies, within-gap gradients were steeper in the density study than in the survival study, possibly due to not recording early mortality in the survival study (discussed above). The density study also suggested greater establishment of *Pseudotsuga* in gap size 0.2 relative to other gaps than did the survival study. The added value of conducting the controlled seed-plot study appears to lie in the greater precision of defining differences among locations and the ability to study species which had no natural seed crop in a given year (*e.g. Abies*, or *Tsuga* in the mature stands).

## Discussion

### Gap size and within-gap position effects

Although differences among forest canopy gaps are often cited as a mechanism for coexistence of different species within mature forests (*e.g.* Ricklefs 1977, Denslow 1980, Runkle 1982, Brandani *et al.* 1988), this is the first study that examined the process of seedling establishment for three common species over a range of gap sizes. Gradients in light levels are commonly emphasized in gap studies, but this study suggests that below-ground controls on seedling establishment may be more important than light levels within gaps. Establishment of all three species was significantly greater in gaps than in closed-canopy areas. Predictions of establishment success in different gap sizes based on shade-tolerance were not supported, however. Although *Abies amabilis* and *Tsuga heterophylla* are considered very shade-tolerant, and *Pseudotsuga menziesii* the least shade-tolerant of the three species (Minore 1979), establishment of *Abies* and *Pseudotsuga* in control areas was similar and greater than that of *Tsuga*. Greater survival of *Abies* over *Tsuga* has been attributed to burial of young *Tsuga* by litter during snow-melt (Thornburgh 1969), yet most of the *Tsuga* mortality in my study occurred during the first summer after germination. Ability to extract soil moisture during the summer droughts may have had more to do with survival in deep shade than shade-tolerance or resistance to burial; both *Abies* and *Pseudotsuga* have larger seed than *Tsuga* (seed weights are 22 and 9 times greater, respectively [Schopmeyer 1974]), enabling them to develop deeper rooting systems and conferring an advantage for early survival (Zobel and Antos 1991, Scott *et al.* 1976, Haig *et al.* 1941). Another indication of the importance of below-ground controls on early seedling establishment was the greater establishment of both *Tsuga* and *Pseudotsuga* in controls compared to gaps on disturbed seed-beds (Figure 2.4) than on intact forest floor (Figure 2.10).

Predictions of gap partitioning by different species of regenerating seedlings (Ricklefs 1977, Denslow 1980) were not greatly supported by this study. Some variation in species establishment within gaps did occur, but only in areas exposed to direct solar radiation. Establishment of *Abies* and *Tsuga* was similar in shaded environments in 0.2 gaps and southern portions of the larger gaps, but lower in high-light portions of larger gaps. Establishment of *Pseudotsuga* on seed-plots was the same across gap environments (Figure 2.4), although it did show some sensitivity to exposure on intact forest floor (Figure 2.9). Mortality of young seedlings in exposed environments is commonly associated with high surface temperatures, which can kill the cambium at the soil line (Silen 1960, Helgerson 1990), or lead to high transpiration rates (Livingston and Black 1988). The lower sensitivity to exposure of *Abies* compared to *Tsuga* was also found by Minore (1986), and may be due to better moisture supply from its deeper rooting habit, greater protection from high temperatures from its thicker stem, and/or less evaporative demand due greater distance between cotyledons and soil. *Pseudotsuga* is the least susceptible of the three species to mortality in exposed microsites (Minore 1986).

Annual variation in seedling establishment suggests that patterns of seedling establishment were not fixed in relation to gap size and within-gap position, but varied with annual weather. *Tsuga* seedling establishment in exposed locations was greater for the year with a cooler, wetter early summer, which has been noted in clearcuts by Ruth (1976) and Stathers (1983). While establishment in closed canopy areas was significantly lower for *Tsuga* in the cooler, wetter year, it tended to be higher for *Abies*; *Abies*' ability to germinate earlier in cool environments (Kotar

1972) may have allowed this species to benefit from the relatively abundant moisture available in the early summer prior to substantial depletion by the overstory canopy.

Growth of all species increased with gap size, particularly in gap center positions, a common pattern for trees in canopy gaps (Minckler *et al.* 1973, Runkle and Yetter 1987, Denslow *et al.* 1990, Uhl *et al.* 1988). Species' growth response appeared to differ by gap size, however, with *Pseudotsuga menziesii* growth relatively low in all locations except for the 1.0 Center location, *Tsuga heterophylla* growth increasing substantially with gap size, and *Abies amabilis* growth responding the least to gap size. Lord (1938) also found that while *Pseudotsuga* density didn't vary with gap size, saplings in openings smaller than 0.6 (my calculation) were "not vigorous". Although *Abies* seedlings are initially larger than *Tsuga* seedlings, *Tsuga* growth rates are greater (Kotar 1972, Harrington and Murray 1982, Herman 1967, Long 1976), and the difference increases with decreasing canopy cover (Zobel and Antos 1991). Hibbs (1982) found some shifting in ranks of eastern hardwood species' growth rates with gap size, but ranking of relative growth rates was *Tsuga* > *Pseudotsuga* > *Abies* regardless of gap location in my study (although *Pseudotsuga* growth rates were similar to those of *Tsuga* in 1.0 gap centers). A shift in ranks may have occurred in even larger gaps, however; growth of *Pseudotsuga* usually exceeds that of *Tsuga* following establishment in clear-cuts or large burns (Handley 1976, Wierman and Oliver 1979).

The gap partitioning hypothesis predicts that species regeneration strategies should be keyed to particular gap environments, due to strong selective pressures on seedlings during the dispersal and establishment phase (Ricklefs 1977, Denslow 1980). Specialization among seedlings for establishment in distinct gap environments did not occur in this study, given that *Pseudotsuga* was relatively abundant in all gaps, and all species had their greatest establishment rates in the same environments (shaded portions of gaps). Thus there appears to be substantial overlap in the regeneration niches (Grubb 1977) of these species. Some differentiation among species was found, associated with the ability of *Abies* and *Pseudotsuga* to establish in closed-canopy areas and the ability of *Pseudotsuga* to tolerate exposure in large gaps. Lack of greater differentiation among species may be due to a lack of time for species to sort themselves out clearly with competitive interactions or mortality from suppression or low vigor. Spies *et al.* (1990) found that seedling density in Cascade forest gaps was better related to gap age than to gap size, and Poulson and Platt (1989) found that patterns of species composition in hardwood forest gaps changed over time due to competition and phenological differences among species. Thus competitive interactions and differences in ecophysiology may be more important than differences in regeneration strategies for species partitioning of gap environments.

Initial establishment patterns and seedling growth rates suggest that differences in species composition among gap environments will increase over time. Differences in growth among species may be a useful measure of long-term survival, since many species are able to establish in areas that eventually prove unsuitable for survival (Silvertown 1987). The relatively low growth rates of *Pseudotsuga* in small gaps suggest that it may be susceptible to mortality from competition or suppression in all but the largest gaps. As trees grow larger, they often have more difficulty surviving in shade due to relatively greater maintenance respiration costs (Waring 1987) and decreased productivity of older foliage (Lassoie *et al.* 1985). Although *Tsuga*'s higher growth rates may provide a competitive advantage over *Abies* in shaded gap environments, growth of *Abies* tends to increase with age more than growth of *Tsuga* (Harrington and Murray 1982, Herman 1967), so it is unclear which species will dominate in these areas. The generally low growth rates of *Abies* and *Tsuga* in the 0.2 gaps suggest that these shade-tolerant seedlings may require subsequent gap events to grow into the canopy, a common pattern for shade-tolerants in small gaps (Canham 1985, 1989; Runkle and Yetter 1987). *Tsuga* may be able to persist and grow into the canopy more readily than *Abies* in intact forests (Stewart 1986b).

The experimental gaps used in this study differ from some types of natural gaps. The conditions in the experimental gaps were most similar to those caused by standing dead or wind-snapped trees, which account for 58-87% of the tree mortality in Cascade forests (Franklin *et al.* 1987, Franklin and DeBell 1988, Spies *et al.* 1990), with minimal disturbance to the forest floor and understory vegetation. The natural regeneration studies examined seedling establishment on similarly undisturbed microsites. Environments within natural gaps would tend to be modified somewhat by shading from snags and logs, effects that are considered in Chapter 3. Windthrow gaps (which account for 9-23% of the mortality in Cascade forests) can create large areas of disturbed soil; results from the mineral soil seed-plots in this study may reflect performance on these substrates, although pit-and-mound topography can modify substrate effects (Beatty 1984). A potentially important difference which cannot be reproduced in the experimental gaps is the rapidity of tree mortality. Resources freed up by trees which are killed over an extended period of time (by root rot or other diseases) might be consumed by response of established vegetation, leaving fewer microsites for new colonization. Some evidence suggests this is not the case, however: Holah (1991) found that seedling establishment was more abundant in root rot pockets than in surrounding forest.

## Stand structure effects

Seedling establishment and growth within canopy gaps varied among forest stands, and both above- and below-ground controls may have been important. Establishment on seed-plots in exposed locations of large gaps tended to be greater in old-growth stands than in mature stands, while establishment in shaded locations of large gaps tended to be lower in old-growth than in mature stands. Greater soil moisture levels in old-growth gaps compared to mature gaps may have aided seedling establishment in exposed environments, while greater light levels in the moist, shaded portions of mature gaps (primarily in stand PCM, which dominated this effect) compared to old-growth gaps may have aided seedling establishment in those locations. Despite similarly low-light conditions in 0.2 gaps, lower moisture levels may have shifted the balance back in favor of the wetter old-growth stands. These age-class patterns across gap locations were seen primarily in *Abies amabilis* and *Tsuga heterophylla* (Figure 2.5a), which tend to be more sensitive to drought stress than *Pseudotsuga menziesii* (Hinckley *et al.* 1982). Seedling size tended to be greater in old-growth stands than in mature stands, possibly due to greater soil moisture content in old-growth stands. Soil moisture differences between age classes may have been caused by greater organic matter content and moisture-holding capacity in the old-growth stands (Gray and Spies *in press*), less understory vegetation in the old-growth stands, or differences in soil texture (Table 2.1).

Establishment of *Pseudotsuga* on natural microsites differed from the patterns of establishment on mineral soil seed-plots in that density in exposed north positions was greater in mature stands than in old-growth stands, while density in shaded south positions was greater in old-growth stands than in mature stands. Since *Pseudotsuga* is more susceptible to heat-related mortality on forest floor than on mineral soil in exposed environments (Isaac 1943, Haig *et al.* 1941), greater levels of understory cover in mature stands compared to old-growth stands may have ameliorated surface temperatures in north positions, facilitating seedling survival. Greater levels of understory cover in mature stands may have also depleted light and moisture levels on many microsites in south positions, excluding seedling establishment. Understory vegetation can override or modify species establishment patterns in gaps in other forests (Nakashizuka 1989, Veblen 1982). Effects of understory vegetation and substrate are examined in detail in Chapter 3.

The tendency towards greater establishment in old-growth control plots than in mature control plots did not match predictions based on generalized patterns of stand structural development. I hypothesized that greater light levels in closed-canopy areas of mature, *Pseudotsuga*-dominated stands would lead to greater seedling establishment than in closed-canopy areas of old-growth stands which contained large proportions of *Tsuga* in the canopy. A study by Spies *et al.* (1990), where the ratio of seedling density inside and outside gaps was greater in old-growth than mature stands, seems to support this hypothesis. The lack of support in my results for this hypothesis may be due to the specific differences among stands in this study. The lowest light levels (Table 2.2), and the lowest seedling establishment rates (Table 2.5), were actually found in mature stand MCY, which had the shortest overstory trees (resulting in dense packing of crowns) and the highest cover of mid-story trees. The next highest seedling establishment rates were found in old-growth stand HJA, which had a high density of *Tsuga* in a relatively uniform mid-canopy layer (which established following a fire about 150 years ago [Teensma 1987]). Thus the lowest seedling establishment rates occurred in the stands which had dense canopy layers distributed relatively close to the forest floor. In contrast, stand PCM, which had the highest light levels, was dominated by widely spaced crowns of relatively tall *Pseudotsuga* and a moderate cover of mid-story trees, while stand TCO had trees in a broad distribution of size classes and a heterogenous, multi-layered canopy. Seedling establishment rates in closed-canopy areas in stand TCO were generally higher than those in stand PCM, possibly due to greater levels of soil moisture. In sum, there appeared to be a relationship between canopy structure and seedling establishment in closed-canopy areas that was modified by soil moisture content. (Canham *et al.* [1994] found that understory light levels are correlated more with crown depth and the distance from the forest floor to the base of the crown than with canopy composition. The lack of a stronger relationship between canopy structure and measured light levels in the closed-canopy areas in this study may be due to the inherent difficulty of capturing the temporal and spatial variability of light regimes under forest canopies [Chazdon 1988].) Thus age-class classifications based on dominant species and number of tree canopy layers may be too simplistic to account for variations in stand structure and stand histories that are important for tree seedling establishment.

### Gaps and forest development

Canopy gaps in Douglas-fir forests are important sites for establishment of shade-tolerant tree seedlings, thus providing a mechanism for forest development from stands dominated by *Pseudotsuga menziesii* to stands containing multiple size classes and canopy layers of different species. Establishment of *Abies amabilis* and *Tsuga heterophylla* in non-gap areas of mature forests does occur, although *Abies* tends to establish in areas with relatively open overstory and understory canopies (Stewart 1986a, Wilson 1991) and *Tsuga* establishment is generally limited to logs in a particular state of decay (Thornburgh 1969, Christy and Mack 1984, Harmon and Franklin 1989). Change in forest structure following establishment of shade-tolerants seedlings in these forests may be slow, however: seedling growth rates in controls and 0.2 gaps (the most common gap size in Cascade forests [Spies *et al.* 1990]) were quite low. Many gaps in the Pacific Northwest can last for more than 50 years without development of saplings (Spies and Franklin 1989, Lertzman 1992). Both *Abies* and *Tsuga* can survive with little growth for many decades in shaded environments as "advance regeneration" (Oliver and Larson 1990) which may resume growth into the canopy in response to subsequent disturbance. Multiple-tree gaps are not naturally as common as single-tree gaps, but may be important sites for forest development by allowing abundant establishment and relatively high growth rates of established seedlings.

The larger experimental gaps in this study were important sites for establishment and growth of shade-intolerant *Pseudotsuga*. Most regional observations indicate that the presence of saplings in natural stands is rare (Munger 1940, Franklin and Dyrness 1973), possibly due to the rarity of this size of gap (Spies *et al.* 1990). Germination in shade and establishment on intact forest floor were certainly not limiting factors in this study. *Pseudotsuga* can develop multi-aged stands on in mesic forests in response to moderate-intensity fire (Means 1982, Teensma 1987). In contrast to tree-fall gaps, moderate-intensity fire tends to impact entire stands at one point in time, create larger gaps, remove much of the litter layer, and kill most of the (above-ground portions of) understory vegetation.

Although canopy gaps may not strictly be required for the establishment of shade-tolerant trees in *Pseudotsuga*-dominated forest, the results from this study suggest that the transformation from mature forests to old-growth forests will be more rapid where gaps do occur. At least two important caveats must be added, however. The very low levels of seed rain and establishment of *Abies* and *Tsuga* natural regeneration in the mature stands in this study underscores the importance of seed sources in forest development. Seed-dispersal limitations on establishment of shade-tolerants has been suggested elsewhere in the region (Thornburgh 1969, Gray 1990). Forest development under such conditions may require rare initial establishment events and time for established trees to begin producing an on-site source of seed. The fact that establishment of natural regeneration was not observed in the mature stands also means that it is unclear how well shade-tolerants can establish in gaps with high levels of understory and mid-story vegetation (*Tsuga* regeneration in areas of high understory cover in old-growth gaps is addressed in Chapter 3).

Gap size and within-gap position are important considerations for any general strategy to accelerate development of old-growth Douglas-fir forests. Single-tree gaps are suitable locations for seedling establishment, but development of mature shade-tolerant trees may not occur without subsequent disturbance. While seedling growth is greater in larger gaps, substantial portions of large (*e.g.* 1.0 size) gaps may be unsuitable for establishment of late-successional species. This restriction on establishment in large gaps may be reduced by shortening the north-south width of gaps to reduce the amount of area subject to high exposure. On the other hand, sapling development in 1.0 and even 0.4 gap sizes may result in even-aged, single canopy-layered patches rather than the multi-layered canopy structure usually associated with old-growth forests. Thus there may be a trade-off between the speed of structural change and the heterogeneity of canopy structure resulting from gap formation in mature forests.

# CHAPTER 3: MICROSITE CONTROLS ON TREE SEEDLING ESTABLISHMENT IN CONIFER FOREST CANOPY GAPS

## Introduction

Tree-fall gaps are small-scale disturbances that are important to the species dynamics of many forest types (Pickett and White 1985). A complex number of factors, ranging from the size and intensity of the disturbance itself to microclimate and the presence of competitors, influences the succession of species on a disturbed site over time (Pickett *et al.* 1987). While gap size and shape are usually emphasized as determinants of species composition in gaps (Runkle 1982, Denslow 1987, Poulson and Platt 1989), the importance of environmental heterogeneity within gaps has also been recognized (Brandani *et al.* 1988, Veblen 1989). Compositional change in plant communities is mediated by the establishment and growth of individual plants, which are sensitive to environmental heterogeneity at the microsite scale of a few $cm^2$. The number of microsites which are "habitable" and the speed with which they are colonized determines the population size of any given species in a community (Harper 1977). While controls on the establishment process can determine patterns of species composition, the causes of those patterns may not be discernible through observation of established plants (Watt 1947, Grubb 1977, Harper 1977). The multiplicity of factors affecting microsite environments and species establishment can be profitably arranged in a hierarchy of higher-level constraints on lower level processes (Allen and Hoekstra 1992). Using light intensity in forest gaps as an example, climate at the landscape scale determines light intensity above forest stands, the structure and composition of stands determines light penetration through the canopy, gap size and shape determines light intensity within gaps, and the density of understory vegetation and woody debris determines light levels on the forest floor. Most work in forest gaps tends to stress the role of individual factors in controlling species composition, without elucidating the importance of interactions among them.

The purpose of this study was to determine the role of within-gap heterogeneity, within the context of gap size and forest structure, on tree species establishment in mature conifer forests of the Pacific Northwest. Most of the disturbance research in the region has focused on succession following relatively large disturbances like fire or clear-cutting (Isaac and Meagher 1936, Agee and Huff 1981, Dyrness 1973, Halpern and Franklin 1990). Yet gap disturbances appear to have a similar site return interval as fire in these forests, and may be important for the development of young stands dominated by *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) in a single canopy layer into multi-layer old-growth forests containing increasing amounts of shade-tolerant *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) (Spies and Franklin 1989). The successional role of gaps in mature Douglas-fir forests has important implications for ecosystem management in the Pacific Northwest. The loss and fragmentation of late-successional forests has been a contentious issue in the region for decades. Recent proposals for management of federal lands emphasize moving young forests toward greater structural and compositional diversity (FEMAT 1993). While passively allowing stands to age may accomplish this goal, selective harvest has been proposed as a way to achieve structural complexity more rapidly and allow some commodity extraction as well (McComb *et al.* 1993, Spies *et al.* 1991). For either strategy, it is important to know how canopy gaps influence development of old-growth forests, how long it would take for old-growth structure to develop naturally, and whether patch selection harvesting can mimic this process.

The gap partitioning hypothesis proposes that tree seedlings should display distinct distributions over the resource gradients between intact forest and canopy gaps (Ricklefs 1977, Denslow 1980). This concept is predicated on niche specialization among species and is an extension of the competitive exclusion principle (Gause 1934). The multitude of differences in species requirements for regeneration (their "regeneration niche"), however, may allow establishment of many species in similar environments and their subsequent survival in the face of competition (Grubb 1977). The importance of subtle microsite conditions for the establishment of seedlings (Harper *et al.* 1965, Harper 1977) provides a mechanism for the establishment of many species on similar portions of the gradient from intact forests to canopy gaps, as well as for the control of species composition by the lack of suitable microsite conditions. In some forests, the density of understory plants and presence of specific substrates (*e.g.* logs or mounds) are more important to tree species success than gap size (Veblen 1985, Ehrenfeld 1980, Nakashizuka 1989).

Microsite heterogeneity within gaps in Douglas-fir forests are potentially important to tree seedling establishment and growth. Although the relatively shade-intolerant *Pseudotsuga menziesii* is generally regarded as a strong competitor, it can be excluded by dense understory vegetation (Isaac 1943). In high-light environments, however, establishment of *Pseudotsuga* can be facilitated by shading from vegetation, woody debris, or standing trees (Isaac 1943, Franklin 1963). Establishment of *Pseudotsuga* is also sensitive to substrate type, usually being most successful on mineral soil in exposed environments due to lower surface temperatures (Isaac 1943, Hermann 1963). The shade-tolerant *Tsuga heterophylla* appears to be so sensitive to competition from understory plants that establishment is usually limited to the surface of decayed *Pseudotsuga* logs (Harmon and Franklin 1989, Christy and Mack 1984, Scott *et al.* 1976). While the shade-tolerant *Abies amabilis* commonly establishes on the forest floor in intact forest, but also appears to be sensitive to overstory and understory canopy density (Wilson 1991, Zobel and Antos 1991).

Although shade-tolerant *Tsuga heterophylla* and *Abies amabilis* seedlings are more abundant in canopy gaps than under closed canopies (Harmon 1987, Alaback and Tappeiner 1991, Thornburgh 1969, Long 1976, Stewart 1986a, Spies *et al.* 1990), many gaps are devoid of tree saplings more than 50 years after gap formation (Spies *et al.* 1990, Lertzman 1992). In comparison, canopy closure may take as little as 2 yrs in moist tropical forests (Lorimer 1989) or 5 yrs in temperate deciduous forests (Runkle 1990). It is unclear whether filling of gaps in the Pacific Northwest is limited by low light levels from narrow gaps surrounded by tall, deep tree crowns (Canham *et al.* 1990), or by lack of suitable microsites for tree establishment due to minimal disturbance to the forest floor and understory vegetation in most gaps (Spies *et al.* 1990).

Forest developmental stage is potentially important to tree seedling establishment in canopy gaps because the abundance of resources and of different types of microsites change with forest age. As Douglas-fir forests develop into the old-growth stage, the abundance of shade-tolerant species in the overstory tends to increase and overall light levels tend to fall (Spies and Franklin 1989). As forest stands mature, understory vegetation tends to increase in density as they enter the understory reinitiation stage (Oliver and Larson 1990), and then becomes more patchily distributed as they enter the old-growth stage (Stewart 1986a). The nature and quality of seedling substrates also changes with time since disturbance, with forest floor depth increasing with time (Spies and Franklin 1991), and abundance of large wood declining and then increasing as stands approach the old-growth stage (Spies *et al.* 1988).

The objective of this paper is to examine the effect of microsite heterogeneity on tree seedling establishment in Douglas-fir forest canopy gaps. The study described in Chapter 2 indicated that gap size and within-gap position were important to seedling establishment, but found differences among studies that may have been due to substrates or vegetation. Specific objectives of this study include 1) determine whether establishment and growth of different tree species is affected by substrates within different gap sizes, 2) determine whether shade near the ground (in the shrub layer) affects species response within gaps, and 3) compare species' response patterns on controlled experimental plots to the survival and density of naturally-regenerated seedlings in different microsites within gaps. Seedling establishment is a continuous process from seed dispersal through germination, emergence, and subsequent survival. Any one of these life-history stages represents a potential bottleneck to establishment. The focus of this study is on survival of emerged seedlings, but data on germination and seed rain are also examined to assess the relative importance of these stages in the process of early seedling establishment. Based on current knowledge of species dynamics in the Pacific Northwest, I hypothesize that: 1) establishment of all species will be greater on mineral soil than on forest floor, particularly in large gaps, 2) establishment of *Tsuga* will be much greater, and establishment of *Abies* and *Pseudotsuga* will be similar, on decayed wood compared to mineral soil, and 3) shade from understory vegetation and coarse woody debris will inhibit establishment of all species in closed-canopy areas and shaded portions of gaps, but facilitate establishment in exposed areas within large gaps.

## Methods

The seedling establishment study of microsite and gap size effects relied on six separate experiments within experimental canopy gaps. The study was conducted in four forest stands, two of which were old-growth (HJA and TCO), and two mature (MCY and PCM). Four sizes of circular gaps were created with two replicates of each size and two control plots. The gap diameter to tree height ratios for the four gap sizes were 0.2, 0.4, 0.6, and 1.0, and the control plots were equal in area to the 1.0 gap size. Descriptions of stand characteristics, gap creation, and microclimates within gaps are provided in Chapters 1 and 2 and will not be repeated here. The first three seedling establishment experiments were manipulative approaches using known quantities of sown seed or seedlings and attempting to control as much random variation as possible. The fourth, fifth, and sixth experiments characterized establishment from natural seed dispersal.

### Substrate effects

The manipulative study was conducted on three standardized substrates in three gap sizes and in controls, using two replicates of each per stand (Figure 3.1). Three 60 x 60 cm seed-plots were created for each mineral soil, forest floor, and decayed wood substrate in the center of each gap and control. For the mineral soil treatment, the forest floor and much of the A1 soil horizon was removed and the upper 10 cm of soil churned, and coarse fragments and roots over 1 cm in diameter were removed. This soil disturbance was believed to have little effect on the availability of mycorrhizal inocula (Randy Molina, *personal communication*). Mycorrhizal mats

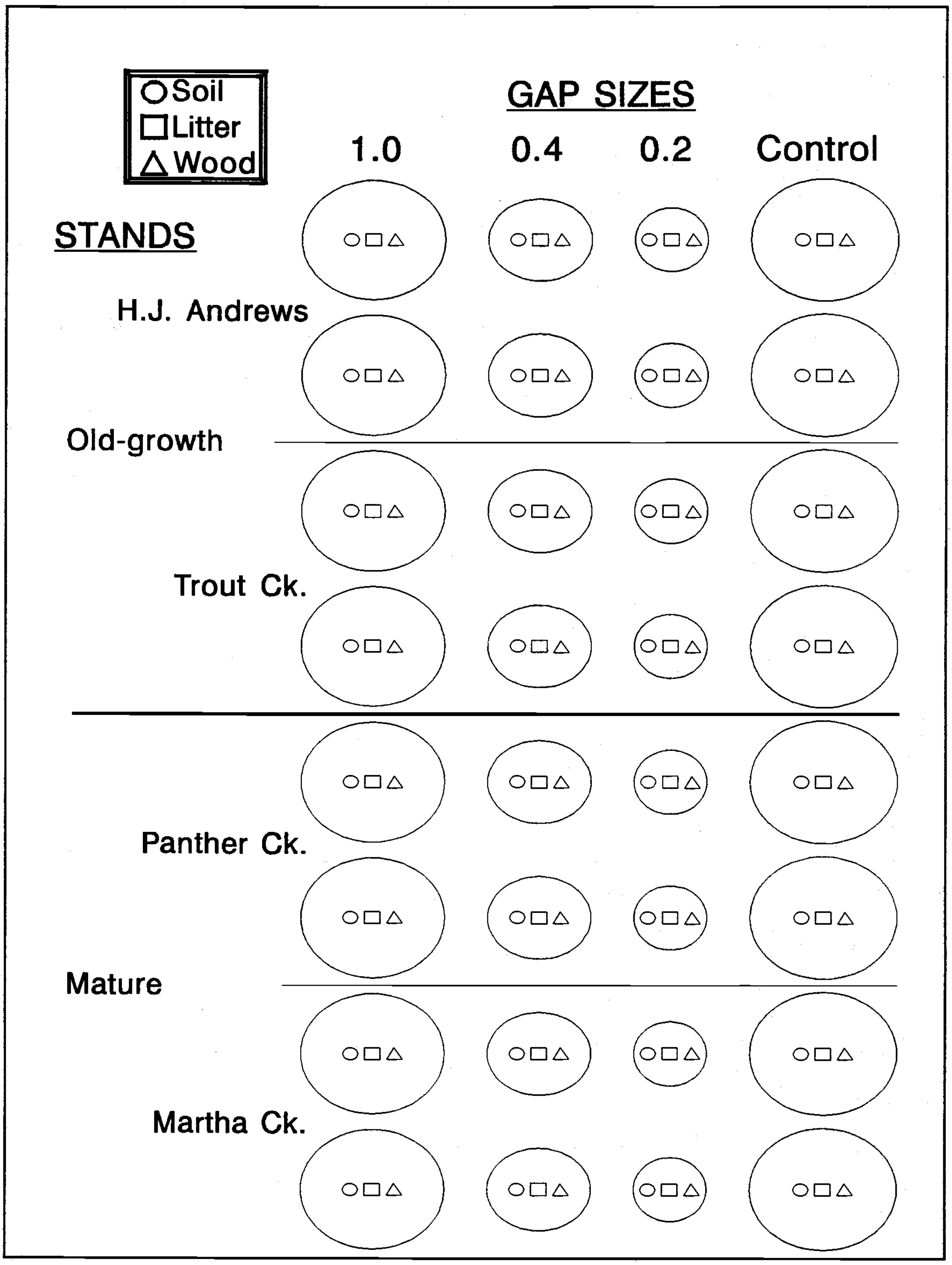

**Figure 3.1:** Schematic of experimental design for substrate study, showing age classes, stands, replicates, gap sizes, and substrates in gap centers. Each substrate symbol represents three seed-plots.

(Griffiths *et al.* 1991) were avoided if possible or removed. A uniform layer of B1 horizon soil was tilled at a road-side in the TCO stand and spread in a surface layer 2.5 cm deep across the mineral soil seed-plots at all of the stands to further reduce effects of soil variation on the experiment. For the forest floor treatment, seed-plots were located on flat areas with an intact litter layer over mineral soil. Decayed wood plots were created by chopping up large pieces of class IV logs (Maser *et al.* 1979) and placing them in square boxes with 15 cm high boards on the sides and window screen on the bottom. Smaller pieces of wood were packed around the larger pieces and a fine wood powder spread over the top for a uniformly soft surface to retain seed. Due to a lack of class IV logs in the mature stands, wood boxes were filled in stand TCO and transported to stands MCY and PCM.

Exclosures were placed over each seed-plot to deter seed and seedling predation by rodents and birds, which can deplete seedling populations by more than 60% (Gashwiler 1967). Exclosures were made of galvanized metal hardware cloth (12 mm mesh) and consisted of a 15 cm tall cylinder sunk 7-10 cm into the soil, covered with a removable cone about 40 cm tall at the peak. The cylinder was 56 cm in diameter, enclosing an area of 0.25 $m^2$. Exclosures reduced PAR quantum levels at an exposed site in a gap by 17.5%, but had no detectable effect on surface temperatures. Potentially competing understory vegetation in and around the seed-plots (growing above a 45° line projecting from the base of the exclosures) was clipped or uprooted at regular intervals throughout the course of the study. Seed-plots were either located away from the potential shade of mid-story trees, or trees were tied back to minimize shading. Seed-plots were created during the summer and fall of 1991 and seed was sown in the late fall of 1991 (one year after gap creation). Seed-plot surfaces were roughened slightly with a hand rake to discourage seed movement by raindrops (Lawrence and Rediske 1962).

One hundred *Abies amabilis*, 100 *Pseudotsuga menziesii*, and 500 *Tsuga heterophylla* seeds were divided evenly between the three seed-plots of each substrate treatment. All seeds were sown during the first three weeks of November 1991. The seeds used at the HJA stand were from a local seed zone, and those used at the other three stands were from a Wind River seed zone (all seedlots were from the Wind

River Nursery). Germination tests conducted by the Wind River nursery estimated seedlot viability for *Abies* at 95 and 93%, *Pseudotsuga* at 94 and 70%, and *Tsuga* at 76 and 76% for the Wind River and H.J. Andrews seed zones, respectively. Natural seed rain also added large numbers of seed in the fall of 1991, primarily *Pseudotsuga* in the mature stands (MCY and PCM), and both *Pseudotsuga* and *Tsuga* in the old-growth stands (HJA and TCO). Seed rain was monitored with seed traps placed in the centers of replicate 1 of each gap size and control in each stand. Since seed sowing and placement of exclosure tops occurred after natural seed dispersal had started, seeds which had already been shed at the time of sowing were more exposed to predation than seeds which were shed later.

Seedlings were counted in the seed-plots once each month from late April to October of 1992 and in June and October of 1993. Due to time constraints associated with establishing and maintaining other experiments, two of the counts (April and August 1992) were only made in replicate 1 of each gap size and control in each stand. Seedlings were considered "germinants" if there was any above-ground evidence of a radicle emerging from the seeds. Seedlings were considered "emergent" and counted if they were erect and rooted and had mostly shed their seed coats (dead seedlings were also counted). If the total number of live and dead seedlings on a plot exceeded the previous month's count of live seedlings, the number of dead seedlings in excess (*i.e.* which had never been counted as live) was recorded as "new mortality" (*e.g.* if there were 20 live seedlings @ $t_1$, and 18 live and 6 dead seedlings at $t_2$, then 4 seedlings were recorded as "new mortality"). Similarly, if the total number of germinants and emergents on a plot in one month exceeded the subsequent month's count, the number of seedlings in excess was recorded as "un-emerged germination" (*e.g.* if there were 10 germinants and 2 emergents @ $t_1$, and 0 germinants and 5 emergents at $t_2$, then 7 seedlings were recorded as "un-emerged germination"). Seedlings were considered dead when they were missing, cut at the stem, or entirely lacking green color. The types of damage and mortality seen were noted. The fate of individual seedlings was monitored on seed-plots in one control and one 1.0 size gap in stands PCM and TCO by marking all seedlings as they emerged (by inserting toothpicks into the soil on the north side of each seedling;

*Tsuga* were not monitored in decayed wood seed-plots in the control in stand TCO due to high density). At the end of the 1992 and 1993 growing seasons, basal diameter and height were measured on up to 5 randomly selected seedlings of each species from each replicate 1 seed-plot. Seedling growth began to be restricted by exclosure tops in 1993, so the tops were removed from all seed-plots in July 1993. Measurements from seedlings which had clipped or browsed tops was noted. Mean depth of litter layer to mineral soil was calculated from measurements at two points next to each forest floor seed-plot made in 1992.

Annual variation in seedling establishment was investigated by repeating the study the following year in the TCO stand. Unoccupied portions of plots were roughened with a hand rake and sown in the fall of 1992 with the same numbers of seed used the previous year. Density of *Tsuga* seedlings was so high in 25 of the 72 TCO seed-plots that patches of seedlings were removed (and individuals counted) to create space for the newly-sown seed. Seedlings were counted monthly from early June to mid-October 1993. The fate of individual seedlings was monitored with toothpicks in all plots for *Abies* and *Pseudotsuga*, while *Tsuga* was monitored only in seed-plots in 0.4 and 1.0 size gaps (*Tsuga* density was too high on other plots to reliably associate toothpicks with individuals). Causes of seedling mortality were identified and counted at each visit. Seedlings were measured in October 1993 using the procedure used for the 1992 cohort (seedling populations will be referred to by year of emergence, *i.e.* those which emerged in 1992 will be referred to as the "1992 cohort").

Surface temperatures were monitored on the three substrates in the center of a 1.0 size gap in stand PCM, using thermocouple wire (TT-E-24S chromel-constantan, Omega Engineering Inc., Stamford, Connecticut, USA) with single-strand sensor ends and data-loggers (CR-10, Campbell Scientific Inc., Logan, Utah, USA) which stored 10 minute averages and maxima of 1 minute samples. One thermocouple each was placed on two soil, litter, and wood seed plots, and pinned with wire "staples" so that sensor ends were within 3 mm of the surface. Forest floor depths (surface to mineral soil) were measured at two points next to each forest floor seed-plot and averaged.

## Understory shade effects

This manipulative study was designed to examine the effect of understory shade on seedling survival and growth. The effect of 0%, 40% and 90% shade over intact forest floor was investigated in the centers of controls and gap sizes 0.4 and 1.0 in the mature stands (MCY and PCM) (Figure 3.2). The forest floor plots from the substrate study were used for the unshaded treatment. Exclosure bottoms for the shaded plots were similar to those in the substrate study, but were square in shape,

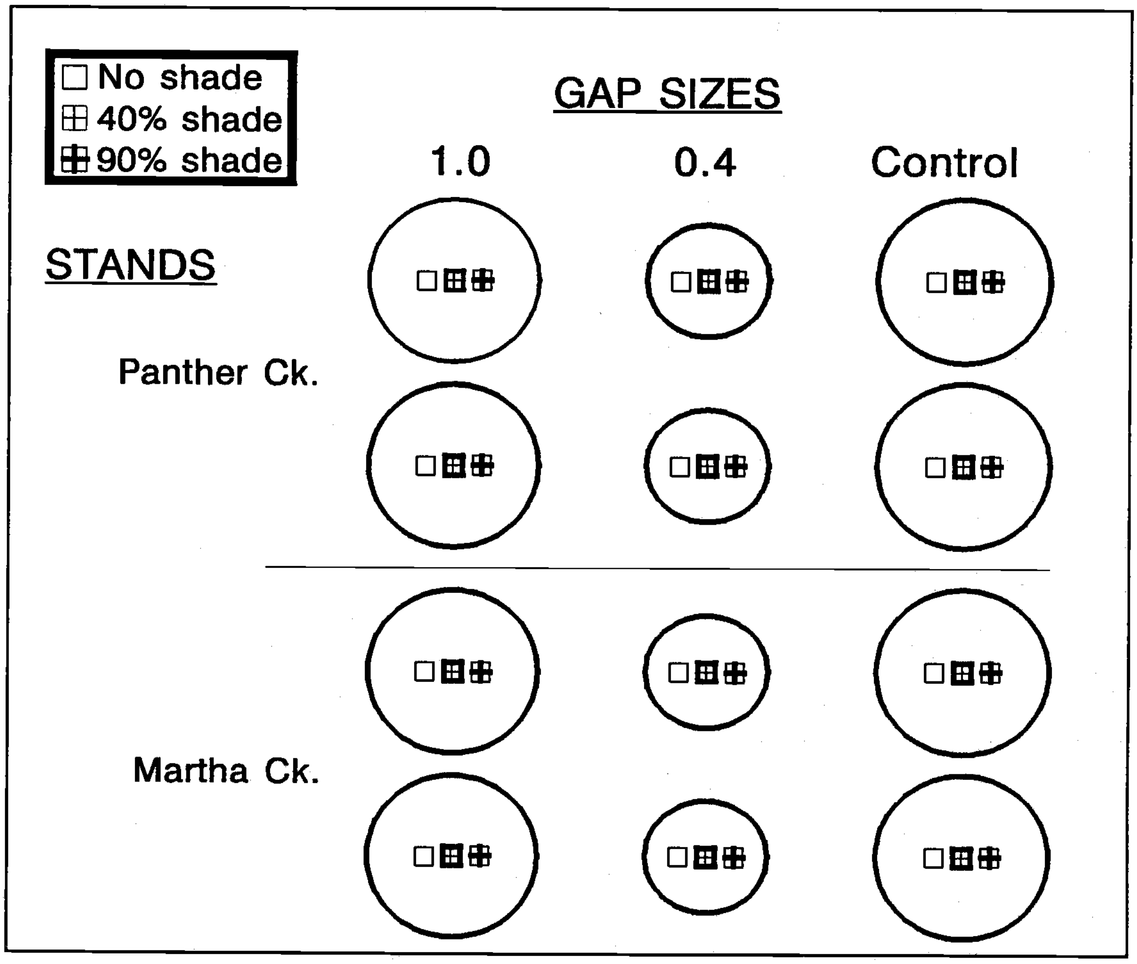

**Figure 3.2:** Schematic of experimental design for understory shade study, showing stands, replicates, gap sizes, and shade treatments in gap centers. Each shade treatment symbol represents three seed-plots.

while exclosure tops were flat pieces of hardware cloth (shade cloth could not be placed at a low enough height over the cone-shaped tops). Measurements indicated that light attenuation was the same under flat- and cone-top exclosures. Shade cloth was stapled to 1m by 1m square wooden frames, set 30 cm above the forest floor (the average height of tall herb and low shrub canopies) on stakes sunk into the ground. To approximate the partial shade of understory vegetation, the 40% and 90% shade levels were attained by cutting different densities of 5 cm diameter holes out of the 96% opaque black shade cloth.

Potentially shading vegetation was removed around the shade plots in the same way as done for the substrate experiment. The same Wind River seed lots used in the substrate study were sown at the same densities and in the same manner, and seedlings counted and measured at the same intervals. Shade-cloth frames were removed over winter (November to April) to avoid destruction from snow loads. Surface temperatures were measured on shade plots in the same gap and manner as done for the substrate study. In addition to the one thermocouple each placed on two litter plots, two thermocouples each were placed on two 40% and 90% shade plots.

### Log effects

This study was designed to characterize the effect of proximity to large logs on seedling survival by planting germinants on north and south sides of large log pieces in different environments associated with position inside a large gap. In stand TCO, log pieces approximately 50 cm in diameter and 1.5 m long were placed in north, center, and south positions within the two 1.0 gap sizes. The long axes of the logs were oriented east-west, and *Pseudotsuga* and *Tsuga* germinants were each planted in 5 north-south transects (5 cm apart) on the north and south sides of each log. Using the vertical projection from the log edge as a reference point, seedlings were planted at 3 cm intervals along each transect, beginning 6 cm under to 30 cm beyond the edge of the log. A mathematical model of direct radiation on north sides of logs in canopy gaps determined that a log length of 1.5 m was sufficient to prevent seedlings which were shaded during the middle of the day from receiving direct radiation (other than sunflecks) in the early morning or late afternoon.

Seedlings were grown from the same Wind River seedlots that were used in the substrate and shade experiments by stratifying seed for one month at 4°C and sowing seed in a peat-vermiculite mixture in styroblock containers at a greenhouse in Corvallis, OR. Seedlings were taken to the field and planted within two weeks of emergence in early June 1993 (seedlings were roughly the same age as naturally germinating seedlings in the gaps). All understory vegetation in the seedling plots and any from around the logs that might have cast shade was removed. At each seedling position, a steel spike was pushed into the ground and removed. Seedlings were carefully extracted from the planting mix and roots immediately inserted into the spike holes. The holes were then closed around the seedlings by inserting the spike about 1 cm away and pushing towards the seedling. Planted plots were immediately watered with equal amounts of water from a watering can to avoid planting shock. Plots were surrounded by square, flat-topped exclosures similar to those used for the shade plots in the understory shade experiment. Plots were revisited periodically throughout the summer and early fall of 1993 to assess seedling survival.

Measurements of PAR, surface temperature, and soil moisture were made next to the seedling transects for three logs in one of the gaps using calibrated quantum sensors (LI-190SZ, LI-COR Inc., Lincoln, Nebraska, USA), thermocouples as described above, and time domain reflectometry (TDR) soil moisture probes (method and calibration described in Gray and Spies *in press*) placed at 6 cm intervals on the north and south sides of each log. Quantum sensor surfaces were 2 cm above the forest floor, thermocouple sensors were placed within 3 mm of the surface, and soil moisture probes sampled to a depth of 15 cm from the top of the litter layer. Two microclimate stations were used, one each at the north and center logs in July, and one used again on the south log in August. Exclosure tops were removed while microclimate sensors were running. Over the entire period, additional light and temperature sensors were operating in the center of the gap. Data-loggers sampled the quantum sensors and thermocouples every 10 seconds and stored 10 minute averages, while soil moisture was sampled monthly with TDR.

### Survival of natural regeneration

The survival of seedlings originating from natural seed rain was monitored across a range of natural microsites within different gap sizes. In addition to exploring the effects of substrate and cover of understory vegetation, this study looked at the effect of different within-gap positions on survival. In late May or early June of 1992, within 2 weeks of emergence of many of the seedlings in the gaps, replicate 1 of each gap size (except 0.6) and control in each stand was searched and individuals or clumps of first-year *Pseudotsuga* and *Tsuga* were marked with small pin flags. A concerted effort was made to locate up to 15 seedlings in each treatment combination of gap size (control, 0.2, 0.4, and 1.0), position (north, center, south-- center only in 0.2's), understory cover level (0, 50, and 90 percent within 28 cm diameter circular plot rings), and substrate (forest floor and class III and IV decayed wood). Nevertheless, sample sizes varied considerably among treatment combinations, and *Tsuga* seedlings were rare in the mature stands (MCY and PCM). To avoid edge and any east-west effects, most marked seedlings were within 4-6 m of the north-south transect bisecting the gaps. Gap positions were delineated by dividing this north-south belt into three zones of similar area (*e.g.* for a 50 m diameter gap, south positions were 0-17 m, center positions were 17-34 m, and north positions were 34-50 m from the southern gap edge). Marked seedlings were revisited in September 1992, and July and October 1993 to assess survival.

### Density of natural regeneration

This study was designed to assess the density of tree seedlings originating from natural seed rain within the experimental gaps and control areas. Permanent vegetation sample plots (marked with PVC pipe stuck in the ground) were established prior to gap creation at a 2 m spacing on the north-south and east-west axes, and at a 4 m spacing throughout the remainder, of all gaps and controls. Understory cover by species and density of tree seedlings were estimated annually (beginning the summer prior to gap creation) in most of the 56 cm diameter (0.25 $m^2$) circular vegetation plots. Seedlings were classified as less than 1 yr old or older and their basal diameters were measured in 0.1 mm increments. Substrate cover within each plot was estimated in the summer of 1991, with substrates classified as forest floor, large wood by 3 combined log decay classes (I and II, III and IV, and V [Maser *et al.* 1979]), "skirts" of organic debris (commonly accumulated around tree boles), mineral soil, and rock. Vegetation and seedlings were sampled in all gaps on plots on the cardinal and diagonal transects in the summer of 1993. In addition to the gaps and control plots used in experiments 1 and 4, the 0.6 gap size was also sampled for this study.

### Microsite survey

This study was designed to compare the microsites of naturally established seedlings with the available microsites present in gaps. The basic approach was to locate 1992 cohort seedlings systematically and characterize their rooting substrate and the amount of understory vegetation over them and compare these with randomly placed points at which the same information was gathered. Sampling was conducted in one 1.0 size gap in mature stand PCM and one 1.0 and two 0.2 size gaps in old-growth stand TCO in August 1993. Within each gap, seedlings within 2 m of permanent vegetation plots (described in the natural regeneration density above) were located. Points around five vegetation plots (within 8 m to east or west of the north-south transect) were sampled at each 4 m interval along the north-south transects within each gap. Three *Pseudotsuga* and three *Tsuga* seedlings from the 1992 cohort closest to each permanent vegetation plot center were measured (basal diameter and height) and their microsites were characterized. Some within-gap locations had fewer than 3 seedlings within 2 m of the plots, so 1993 cohort seedlings were sampled if available.

Seedling microsites were characterized by rooting substrate (forest floor, mineral soil, class I, III or V log, or organic "skirt"), percent cover of "herb" or "shrub" (classified based on presence of perennial woody stems) in a 28 cm diameter (0.063 $m^2$) plot centered above the seedling, and level of southern shade (estimated as none, low (20-70% cover), and high (>70% cover)). Southern shade was estimated in an expanding cone from the base of the seedling corresponding to the summer sun-track to the south of the seedling (from 22 to 30° from zenith and 120 to 240° from north). The type of southern shade was classified as "live" (from plants) or "dead" (from branches, logs, or stumps).

## Statistical Analysis

The null hypotheses of the substrate, understory shade, and natural regeneration experiments were tested with split-split plot analyses of variance (ANOVA, using GLM procedure in SAS 6.10 [SAS Institute Inc. 1987]). Except for the analysis of establishment in the substrate effects experiment, which was tested with a Type III sums of squares model, experiments were unbalanced, either due to missing observations in one or more treatments (*e.g.* lack of emergents to analyze establishment, or lack of survivors to analyze growth) or due to missing treatments in the design (*e.g.* only one within-gap position in gap size 0.2 for the natural regeneration studies). Type IV sums of squares models were used for the analyses of unbalanced designs. The Type IV method on unbalanced designs, however, arbitrarily selects a subset of the full range of testable linear contrasts, requiring careful examination of the contrasts generated by the program and possibly further analyses using selected cell means (Milliken and Johnson 1984, Shaw and Mitchell-Olds 1993). Examination of the linear contrasts generated by SAS for the different analyses indicated they were appropriate. Since SAS constructs contrasts based on the sorting order of variables, the order was changed for multiple runs; probabilities that changed little with sort order were considered robust. Initial ANOVA tests for the substrate and understory shade experiments included two terms for sub-plot error: a term for the variation of gaps within stands, and a term for the variation of gap-size replicates within stands. If the Mean Squares for both terms were similar, additional ANOVAs were calculated with both terms combined in the sub-plot error (as the variation of gap-size replicates within stands); if the Mean Squares for the variation of gaps within stands was larger, then it was used as the sub-plot error. If Mean Squares for whole-plot error terms were smaller than Mean Squares for sub-plot error terms (which would require a negative variance --an impossibility-- under the ANOVA model [Milliken and Johnson 1992]), the whole-plot term was left out of the model and whole plot effects were tested with the larger sub-plot error terms. Results of the analyses were considered significant if the probability of a Type I error was less than 0.05. Determination of significant differences among treatment means was conducted for terms which were significant in the ANOVAs (analogous to Fisher's protected Least Significant Difference) using least-squared means and 95% confidence intervals calculated with the MIXED procedure in SAS 6.10 [SAS Institute Inc. 1987]). Means of interactions of interest which were not significant in the ANOVAs were graphed, and the degree of overlap of the standard errors of the means was used as an indication of potential differences which could be biologically significant.

### Substrate effects

The null hypothesis that tree seedling establishment was not affected by stand age, gap size, substrate, tree species, or interactions between them was evaluated with a four factor split-split ANOVA. The response variable for the analysis of establishment was the fraction of the maximum number of emerged seedlings counted on a treatment (plus all "new mortality" counts) that were still alive at the end of the experiment (termed "establishment"). This measure could potentially under-estimate seedling survival by missing seedlings that died and were replaced by new emergents; this "turnover" effect was evaluated by comparing survival of individually marked seedlings with establishment calculated from counts on the same seed-plots and is shown in the results. It is still possible that seedlings germinated and died without a trace between counts or before the first count; the frequency of this occurrence is unknown.

Establishment of the 1992 cohort may have been over-estimated on replicate 2 seed-plots if the greatest number of seedlings on a plot occurred at the time of the first sample, when replicate 2 seed-plots were not counted. This was evaluated by examining changes between the first and second counts on replicate 1 plots: a decline in seedling numbers occurred on 6 out of 36 species by gap size by substrate treatment combinations (Table 3.1). Some of this decline may have been captured on replicate 2 seed-plots with the dead seedling counts, which were included in the seed-plot maxima. Ignoring the first count on the replicate 1 plots would simplify interpretation of results, but would further over-estimate establishment by not including early mortality. Instead, the maximum number of emerged seedlings (live and dead) counted on a seed-plot was used to estimate establishment; implications of potential over-estimation of establishment is discussed with the results.

Since *Tsuga* seedlings were removed from 25 of the 72 TCO seed-plots to make room for the second-year sowing of seed, final seedling counts for the 1992 cohort were adjusted under the assumption that the original number of seedlings would have followed the same survival trajectory as those left after thinning did (*i.e.* final count/post-thin count = adjusted/pre-thin count). Final counts on the thinned plots were adjusted with the formula: adjusted count = (pre-thin count * final count)/post-thin count.

The experimental unit ("treatment") for this study was substrate within a particular gap. All seedling counts were summed across the three seed-plots (as

**Table 3.1:** Percent change in seedling numbers by gap size, position, and species for replicate 1 seed-plots for which counts declined from April to May 1992.

| Species | Gap size | Substrate | Percent decline |
|---|---|---|---|
| *Abies* | 1.0 | Litter | 24 |
| *Tsuga* | 0.4 | Litter | 26 |
| *Tsuga* | 0.4 | Soil | 6 |
| *Tsuga* | 1.0 | Litter | 83 |
| *Tsuga* | 1.0 | Soil | 31 |
| *Tsuga* | 1.0 | Wood | 37 |

experimental sub-plots) comprising a substrate treatment within a gap, and establishment calculated on those sums. As is common with binomial data, establishment percentages exhibited non-uniform variance and non-normality, and were transformed with an arcsin-square root equation specifically designed for data with several values close to zero (Zar 1984, eq. 14.5):

$$p' = 0.5 * \{\arcsin([N_f / (\max + 1)]^{½}) + \arcsin([(N_f + 1) / (\max + 1)]^{½})\}$$

where: $p'$ = transformed value
$N_f$ = number of seedlings alive at final count
max = maximum number of seedlings found on a treatment

Since establishment estimates were more precise for treatments with greater maximum numbers (*e.g.* establishment of 50 out of 100 seedlings is more precise than 5 out of 10), the ANOVA was weighted by the square root of the denominator ("max") values (square root of "max" reduced the weighting bias towards *Tsuga* in the old-growth stands, which had high emergence values due to natural seed rain). Due to missing values (*i.e.* treatments where max=0) 285 observations of the 288 possible treatment combinations were used in the analysis.

The comparison of measures of establishment used data from replicate 1 gaps in each stand, since seed rain and germination in April 1992 was only measured in these gaps. (Seed rain was monitored in a few seed replicate 2 gaps in the old-growth stands, and seed rain varied by as much as 200% between replicates.) Establishment as a fraction of seed was calculated by converting seed rain measurements to an area basis and dividing into the density of established seedlings on each treatment. Establishment as a fraction of germination was calculated by adding the maximum number of emerged seedlings and un-emerged germination and dividing into the number of established seedlings on each treatment. Trends in emergence and mortality over time were investigated for replicate 1 gaps only, due to missing sample periods in replicate 2 gaps.

The analysis of annual effects on seedling establishment in stand TCO was similar to the analysis described above, except that establishment for the first cohort was calculated using the last count of 1992 (before thinning of *Tsuga* from plots). Establishment for the second cohort was calculated using the last count of 1993. Stand age was not a factor for the ANOVA of annual effects (only one stand), and the cohort year factor was split within the gap and position factors. The same transformation and weighting was done for this ANOVA as is described above for the analysis of second-year establishment. Due to missing values, only 136 observations of the 144 possible treatment combinations were used in this analysis.

The analysis of seedling size for the 1992 cohort was similar to the analysis of establishment for the same cohort. The response variable for the ANOVA was the mean size of the seedlings measured in a treatment (*i.e.* three seed-plots), where size was calculated as seedling height multiplied by basal area. This volume-related measure of size was chosen as a better measure of seedling growth in a given environment than height, because many plants increase height growth relative to biomass in low light conditions (etiolation--observed in *Pseudotsuga*), and height on small seedlings can be sensitive to the depth in the soil at which seeds germinate (observed for all species). Measured seedlings with damaged tops (from animal browsing) were included in the analysis (their presence had no effect on ANOVA results). The data were log-transformed ($\log(y+1)$) before analysis. The ANOVA was weighted by the number of seedlings measured. Due to missing values (*i.e.* treatments without surviving seedlings) only 123 observations of the 144 possible treatment combinations were used in the analysis.

## Understory shade effects

The null hypothesis that tree seedling establishment was not affected by gap size, level of artificial shade, tree species, or interactions between them was evaluated with a three factor split plot ANOVA (Type III, balanced design). The response variable was the fraction of maximum counts of the 1992 cohort present after two growing seasons, and was transformed the same way as was done for the substrate analysis. The analysis was weighted by the maximum number of counts on a treatment. Due to missing values 106 observations of the 108 possible treatment combinations were used in the analysis. Seedling size was calculated and transformed the same way as was done for the substrate analysis. Due to missing cells (*i.e.* treatments without surviving seedlings), a Type IV ANOVA was used, and only 39 observations of the 54 possible treatment combinations were used in the analysis.

### Log effects

Due to high mortality from clipped seedlings (most likely by cutworms--family *Noctuidae* [Overhulser 1990]) in one of the gaps, log effects were assessed for the log in each position in one gap only. Statistical analyses of survival could therefore not be performed due to lack of replication of position. The number of surviving seedlings of each species is presented by side of log (*e.g.* north or south side) and distance from log edge. Light and temperature data were averaged over several hot and sunny days; based on measurements from the gap center station, "hot" days were identified as those where daily maximum surface temperatures exceeded 60°C. Daily quantum flux calculated from the 10 minute averages of PAR and daily temperature maxima were averaged over a period of 16 hot days between July 8-August 10, 1993 for the north and center logs, and over a period of 7 hot days between August 10-24 for the south log. Volumetric soil moisture data sampled on July 9, 1993 (by which time most seedling mortality had occurred) is also presented.

### Survival of natural regeneration

Survival of naturally germinated seedlings was analyzed with separate split-plot ANOVA's (Type IV sums of squares) for cover and substrate. Despite thorough searches, few seedlings were found on decayed wood across the range of age classes, within-gap positions and cover levels (see Appendix). Construction of reasonable contrasts for the full unbalanced design therefore proved infeasible, so separate analyses were done for cover over litter by gap size and position, and for substrate across gap size. The response variable was the percentage of the initial number of emerged seedlings counted for a treatment combination (*i.e.* substrate by cover level within a position) that were still alive at the end of the second growing season. The data were transformed for the ANOVA by the same arcsin-square root transformation as used for the substrate and understory shade experiments. Due to the very low number of *Tsuga* seedlings in the mature stands, separate analyses were done for *Pseudotsuga* (all four stands) and *Tsuga* (two old-growth stands). Each analysis was weighted by the denominator used to calculate survival (*i.e.* initial number of emergents). Due to missing treatments for *Pseudotsuga*, 113 out of 120, and 30 out of 32 potential treatment combinations were available for the cover and substrate tests, respectively. Due to missing treatments for *Tsuga*, 53 out of 60, and 16 out of 16 potential treatment combinations were available for the cover and substrate tests, respectively.

### Density of natural regeneration

Two approaches were used to analyze the natural regeneration density data: ANOVA on categorical variables, with substrate and vegetation data combined into classes, and correlation on numerical variables, using actual cover values of substrate and vegetation. For the ANOVA analysis, vegetation microplots were allocated to three within-gap positions by dividing the north-south transects of each gap into three equal lengths and only including plots within 4 m of the transects. Sample sizes were thus greater for center positions due to east-west transect plots. The cover values of understory species were summed for each vegetation plot (excluding cover of moss) and allocated to three cover classes: "low"= 0-20%, "medium"= 21-50%, and "high"= >51% cover. These cover classes were selected as a compromise between matching the cover classes in the other experiments and balancing sample sizes among classes in the different stands (to simplify the ANOVA analysis). The mean cover for all plots within a cover class was 6, 36, and 77% and the sample size by cover class was 354, 307, and 262 for low, medium, and high classes. Individual vegetation plots were allocated to three substrate classes (class III log, class V log, skirt) based on whether cover was greater than 49%; the remainder of the sampled plots were classified as litter. Litter substrate plots were well distributed across stands, gap sizes, within-gap positions, and cover classes, but the other substrates (particularly class III log) were poorly represented across all treatments.

The response variable for the ANOVA was the combined seedling density on all the vegetation plots in a treatment (*i.e.* number of seedlings was summed by stand, gap size, within-gap position, and cover class, and by stand, gap size, and substrate, and divided by the total area of the number of plots in each category). Due to the highly unbalanced nature of the substrate classes in association with the other factors (see Appendix), separate analyses (only slightly unbalanced) were done for cover by gap size and position, and for substrate by gap size only. The seedling density value was log-transformed ($\log(y+1)$) and weighted by the number of vegetation plots in each treatment. Due to the very low number of *Tsuga* seedlings in the mature stands, separate analyses were done for *Pseudotsuga* (all four stands) and *Tsuga* (two old-growth stands). Since there were few low cover plots in mature stands, and few high cover plots in old-growth stands, age class was not included as a factor in the analysis for *Pseudotsuga*. Several plots in stand HJA were excluded from the substrate analysis due to missing substrate data. These data were included in graphs of seedling density and understory cover.

The correlation analysis entailed the calculation of multiple correlations (CORR procedure in SAS) between seedling density and cover values for vegetation and substrate, and for gap size, position, and their interactions. Dependence among proximate vegetation plots was avoided by averaging all values across gap size and within-gap position. The categorical variable of "control" was changed to gap size 0.05 and within-gap positions of north, center, and south were given values of 3, 2, and 1, respectively, to correspond to the light gradient within gaps.

### Microsite survey

The analysis of seedling microsite data consisted of comparisons between microsites containing seedlings and those of randomly sampled points. Analyses were broken down by gap, within-gap position, and species. Comparisons involving categorical microsite variables were computed in contingency tables with the chi-square statistic, those involving numerical variables were computed with the *t*-test statistic (FREQ and TTEST procedures in SAS, respectively). Analyses were only done for 1992 cohort seedlings. Within-gap positions in the 1.0 size gaps were designated by dividing the north-south transect into thirds; since more plots were sampled near the north and south edges of the TCO 1.0 gap, the "center" position was constrained to the region between 4 m north and south of gap center to match the designation in the PCM 1.0 gap. The "no" and "low" south shade categories were combined for the analysis of south shade in gap PCM 1.0 due to low frequencies of "no" south shade. The mineral soil and class I log categories were excluded from the analysis of substrates due to low frequency. Identification of significant variables for factors which were significantly in the Chi-square analyses (*e.g.* under which level of south shade were seedling frequencies different from random) was accomplished by computing *t*-test confidence intervals for means and standard errors of frequencies.

## Results

### Substrate effects

### Establishment of 1992 cohort

Establishment of the 1992 cohort at the end of two growing seasons differed significantly among species and substrates. Interactions of substrate with age class and gap size, and of species with gap size and substrate, were also significant (Table

3.2). Establishment on decayed wood was significantly greater than establishment on mineral soil and forest floor (henceforth referred to as "wood", "soil", and "litter", respectively) in controls and 0.2 gaps, while there was a tendency towards lower establishment on litter than on the other substrates in 1.0 gaps (Table 3.3) (the difference between wood and litter in 1.0 gaps was significant at the $p < .07$ level). While establishment of *Abies amabilis* and *Tsuga heterophylla* was greater in 0.2 and 0.4 gaps than in controls and 1.0 gaps, establishment of *Pseudotsuga menziesii* only differed between gaps and controls. In addition, *Tsuga* establishment was significantly lower than that of the other species in 1.0 gaps. The significance of the

**Table 3.2:** Results of split-split plot ANOVA on seedling establishment (% of maximum count) for substrate study. Factor abbreviations are: age= age class, gap= gap size, rep= gap replicate within stand, subs= substrate, spp= species.

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| age | 1 | 1.72637 | 0.35 | 0.6138 |
| Error: stand(age) | 2 | 4.92294 | | |
| gap | 3 | 15.10825 | 3.41 | 0.0940 |
| age*gap | 3 | 0.97179 | 0.22 | 0.8797 |
| Error: stand*gap(age) | 6 | 4.43412 | | |
| rep(age*stand*gap) | 16 | 1.51504 | | |
| subs | 2 | 11.46485 | 52.40 | 0.0001 * |
| age*subs | 2 | 0.74351 | 3.40 | 0.0355 * |
| gap*subs | 6 | 1.94019 | 8.87 | 0.0001 * |
| age*gap*subs | 6 | 0.28562 | 1.31 | 0.2566 |
| spp | 2 | 10.42783 | 47.66 | 0.0001 * |
| age*spp | 2 | 0.25278 | 1.16 | 0.3172 |
| gap*spp | 6 | 1.85885 | 8.50 | 0.0001 * |
| subs*spp | 4 | 3.12208 | 14.27 | 0.0001 * |
| age*gap*spp | 6 | 0.32572 | 1.49 | 0.1840 |
| age*subs*spp | 4 | 0.34779 | 1.59 | 0.1788 |
| gap*subs*spp | 12 | 0.14665 | 0.67 | 0.7786 |
| age*gap*subs*spp | 12 | 0.06666 | 0.30 | 0.9880 |
| Error: rep(age*stand *gap*sub*spp) | 189 | 0.21881 | | |
| Total | 284 | | | |

**Table 3.3:** Separation of means for significant interactions in ANOVA on substrate effects on seedling establishment (% of maximum count). Values are least-square means and standard errors of transformed (arcsin of square-root) establishment data. Means within an interaction with different letters differed significantly ($p < .05$).

| | | | | |
|---|---|---|---|---|
| Gap size *substrate | ctl | soil | 0.321 ± 0.101 | a |
| | ctl | litter | 0.396 ± 0.103 | ab |
| | ctl | wood | 0.804 ± 0.098 | de |
| | 0.2 | soil | 0.798 ± 0.101 | cde |
| | 0.2 | litter | 0.774 ± 0.103 | cde |
| | 0.2 | wood | 1.072 ± 0.098 | f |
| | 0.4 | soil | 0.952 ± 0.101 | ef |
| | 0.4 | litter | 0.850 ± 0.102 | de |
| | 0.4 | wood | 0.960 ± 0.099 | ef |
| | 1.0 | soil | 0.711 ± 0.102 | cd |
| | 1.0 | litter | 0.594 ± 0.105 | bc |
| | 1.0 | wood | 0.788 ± 0.099 | cde |
| Gap size *species | ctl | Abies | 0.648 ± 0.105 | bc |
| | 0.2 | Abies | 0.971 ± 0.104 | e |
| | 0.4 | Abies | 0.970 ± 0.103 | e |
| | 1.0 | Abies | 0.753 ± 0.106 | cd |
| | ctl | Pseudotsuga | 0.506 ± 0.100 | ab |
| | 0.2 | Pseudotsuga | 0.855 ± 0.102 | de |
| | 0.4 | Pseudotsuga | 0.953 ± 0.101 | de |
| | 1.0 | Pseudotsuga | 0.931 ± 0.103 | de |
| | ctl | Tsuga | 0.367 ± 0.098 | a |
| | 0.2 | Tsuga | 0.817 ± 0.097 | cde |
| | 0.4 | Tsuga | 0.839 ± 0.097 | cde |
| | 1.0 | Tsuga | 0.411 ± 0.099 | a |
| Substrate *species | soil | Abies | 0.754 ± 0.066 | b |
| | litter | Abies | 0.737 ± 0.067 | b |
| | wood | Abies | 1.015 ± 0.060 | c |
| | soil | Pseudotsuga | 0.851 ± 0.060 | b |
| | litter | Pseudotsuga | 0.746 ± 0.064 | b |
| | wood | Pseudotsuga | 0.836 ± 0.057 | b |
| | soil | Tsuga | 0.482 ± 0.055 | a |
| | litter | Tsuga | 0.477 ± 0.059 | a |
| | wood | Tsuga | 0.867 ± 0.053 | b |
| Age class *substrate | mature | soil | 0.692 ± 0.075 | ab |
| | old-growth | soil | 0.699 ± 0.075 | ab |
| | mature | litter | 0.690 ± 0.077 | ab |
| | old-growth | litter | 0.618 ± 0.076 | a |
| | mature | wood | 0.971 ± 0.074 | c |
| | old-growth | wood | 0.841 ± 0.073 | bc |

substrate by species interaction was due in part to similar establishment of *Pseudotsuga* across substrates and greater establishment of *Abies* and *Tsuga* on wood than on soil and litter (Table 3.3, Figure 3.3). Field observation suggested that many of the surviving *Tsuga* seedlings on litter plots were clustered in the areas with the thinnest forest floors. Consideration of the effect of missed initial counts in replicate 2 seed-plots (Table 3.1) suggests that actual establishment of *Abies* and *Tsuga* on litter was substantially lower in large gaps than on soil and wood (*i.e.* a greater difference than shown in Figure 3.3), and that establishment of *Tsuga* in gap size 1.0 was even lower relative to the other gaps. The significant interaction between forest age class and substrate (Table 3.2) appeared to be due to greater establishment on wood in mature stands than in old-growth stands (Table 3.3-- difference was significant at $p <$ .06 level). Examination of the data indicated that most of the age class differences on wood were due to differential establishment of *Pseudotsuga* across all gap sizes, and of *Tsuga* and *Abies* in 0.4 gaps. Examination of gap light levels and seed-plot moisture contents revealed no compelling resource mechanisms for an age class effect on wood and a lack of an effect on the other substrates. Differences between age classes were smallest on soil (Table 3.3).

### Annual effects on establishment

First-year seedling establishment in stand TCO differed significantly by species between 1992 and 1993 (Table 3.4). The difference was primarily due to greater establishment of *Pseudotsuga* in 1992 than in 1993 (Table 3.5). The strength of the year by gap size by species interaction ($p= .075$) indicated that some differences occurred among gaps as well. There was a tendency towards lower establishment of *Pseudotsuga* and *Tsuga* in controls, and greater establishment of *Tsuga* on soil and wood in 0.4 and 1.0 gaps, in 1993 than in 1992 (Figure 3.4). Lower temperatures and greater moisture in 1993 than in 1992 may have depressed establishment in controls and facilitated establishment of *Tsuga* in the larger gaps. Establishment means for *Abies* and *Pseudotsuga* in 1993 were quite variable on many

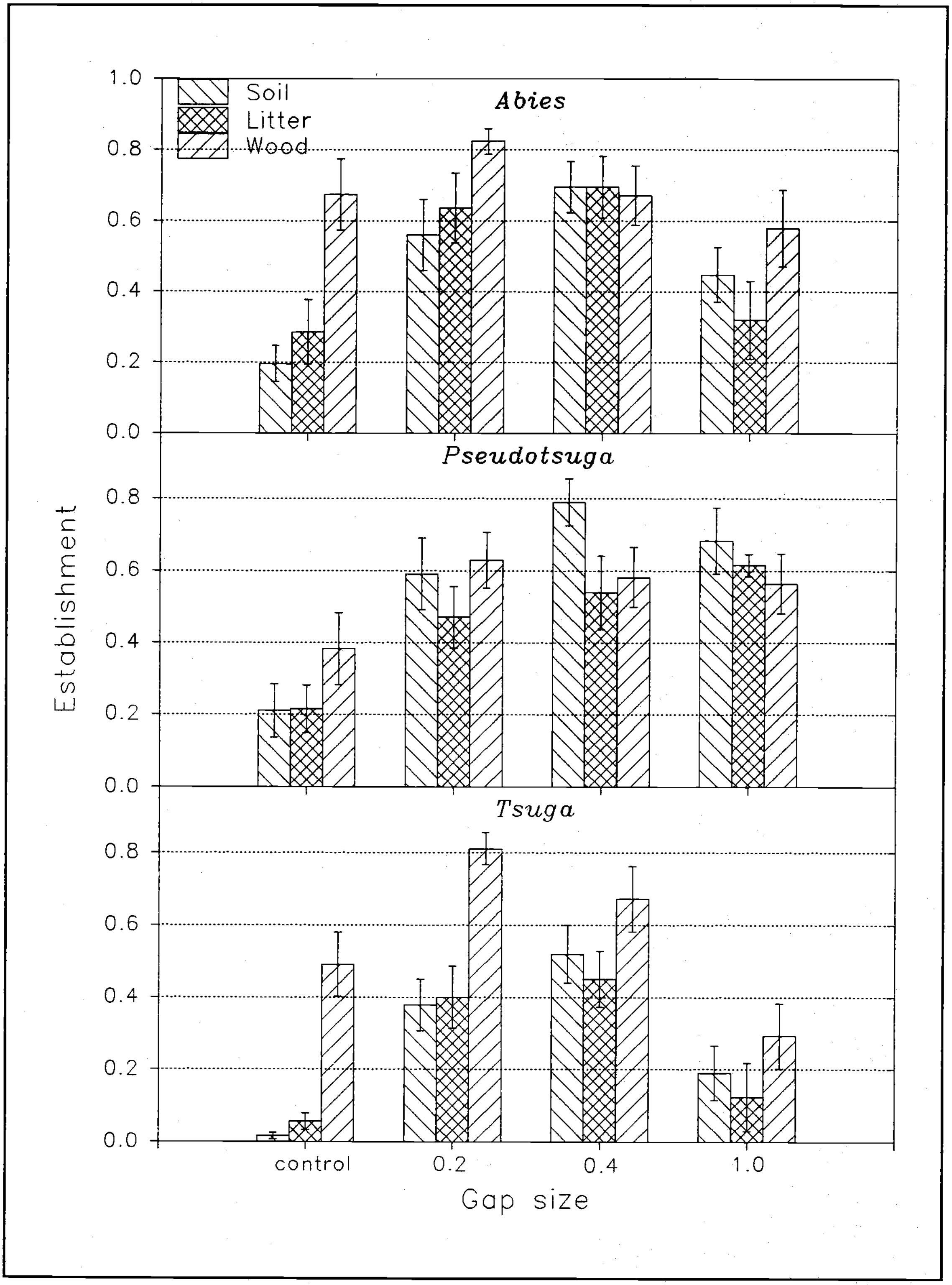

**Figure 3.3:** Seedling establishment (% of maximum emerged) in substrate study by species, gap size, and substrate. Data are means and standard errors of all replicates (n=8).

**Table 3.4:** Results of split-split plot ANOVA on first-year seedling establishment (% of maximum count) for 1992 and 1993 on substrate seed-plots in stand TCO. Factor abbreviations are: gap= gap size, rep= replicate, subs= substrate, yr= year, and spp= species. Significant effects (p < .05) are marked with asterisks (*).

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| gap | 3 | 5.25584 | 4.29 | 0.0967 |
| Error: rep(gap) | 4 | 1.22551 | | |
| subs | 2 | 3.91763 | 6.28 | 0.0229 * |
| gap*subs | 6 | 1.37680 | 2.21 | 0.1484 |
| Error: rep(gap*subs) | 8 | 0.62361 | | |
| yr | 1 | 0.65605 | 2.32 | 0.1336 |
| gap*yr | 3 | 0.62458 | 2.21 | 0.0976 |
| subs*yr | 2 | 0.06477 | 0.23 | 0.7960 |
| gap*subs*yr | 6 | 0.21986 | 0.78 | 0.5911 |
| spp | 2 | 2.13883 | 7.56 | 0.0013 * |
| gap*spp | 6 | 0.41503 | 1.47 | 0.2068 |
| subs*spp | 4 | 0.54535 | 1.93 | 0.1189 |
| yr*spp | 2 | 1.16285 | 4.11 | 0.0218 * |
| gap*subs*spp | 12 | 0.06527 | 0.23 | 0.9959 |
| gap*yr*spp | 6 | 0.57988 | 2.05 | 0.0745 |
| subs*yr*spp | 4 | 0.32935 | 1.16 | 0.3366 |
| gap*subs*yr*spp | 10 | 0.13776 | 0.49 | 0.8911 |
| Error: rep(gap*subs *yr*spp) | 5 | 0.28277 | | |
| Total | 135 | | | |

**Table 3.5:** Separation of means for year by gap size by species interaction in ANOVA on first-year seedling establishment (% of maximum count) for 1992 and 1993 on substrate seed-plots in stand TCO. Values are least-square means and standard errors of transformed (arcsin of square-root) establishment data. Means which differed significantly (p < .05) between 1992 and 1993 are marked with asterisks (*). Missing values were not estimable due to missing data.

| | 1992 | 1993 |
|---|---|---|
| *Abies* | 0.959 ± 0.059 | . . |
| *Pseudotsuga* | 1.035 ± 0.061 | 0.808 ± 0.092 * |
| *Tsuga* | 0.761 ± 0.042 | 0.843 ± 0.054 |

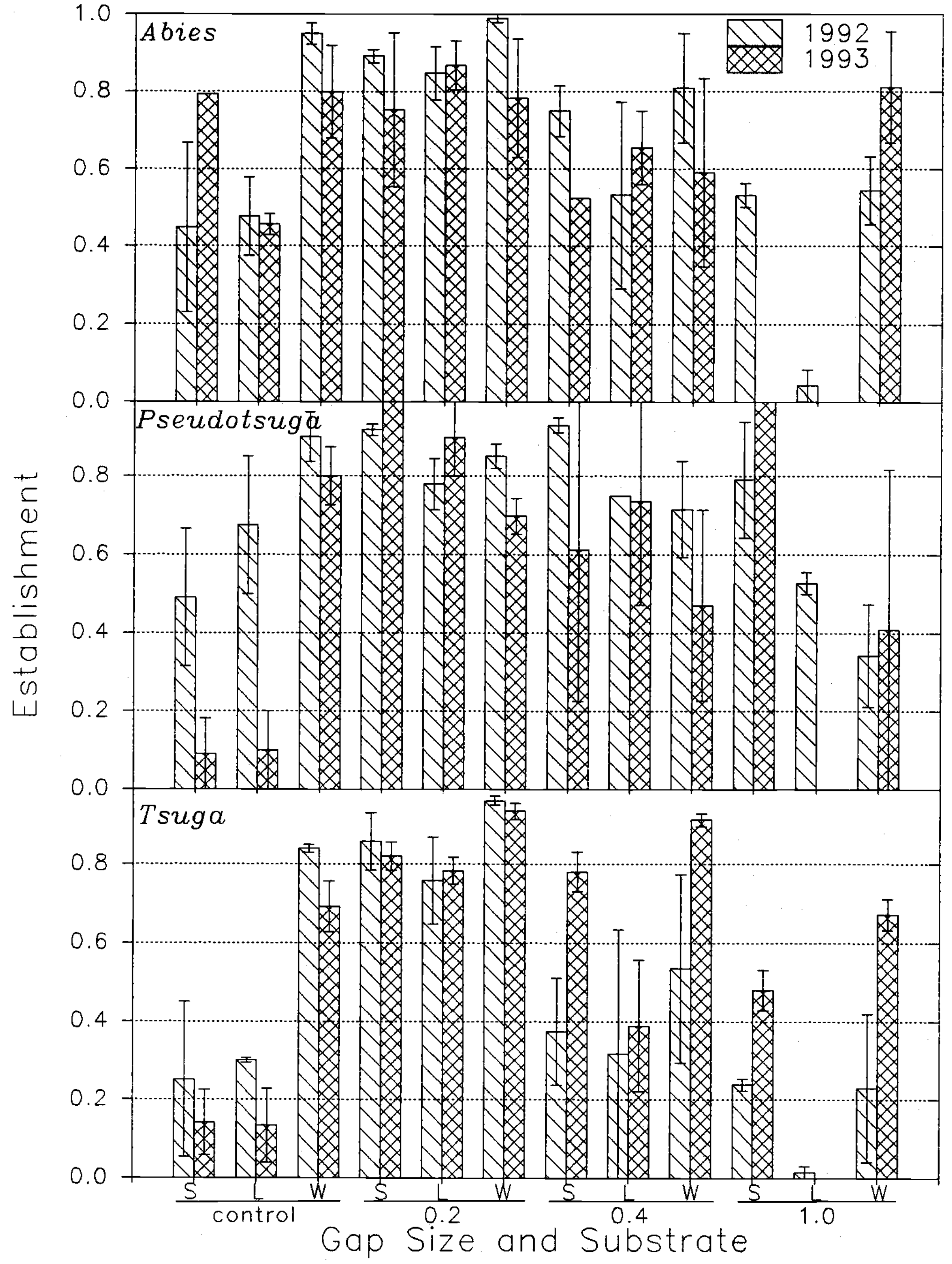

**Figure 3.4:** Comparison of seedling establishment (% of maximum emerged) in substrate study between 1992 and 1993 cohorts after one growing season in stand TCO by species, gap size, and substrate. Data are means and standard errors of both replicates ($n \leq 2$, depending on presence of emergents).

treatments due to low emergence of seedlings. Field observations suggested that predation of *Abies* and *Pseudotsuga* seed was high before the 1993 cohort emerged, despite identical exclosures for the 1992 and 1993 cohorts.

### Establishment as a fraction of seed or germination

Some trends in seedling population size among treatments were evident with the initial germination of seedlings. Germination of the 1992 seedling cohort (as a fraction of total seed--sown plus seed rain) tended to be greater on wood than on soil and litter for all species, and greater on soil than litter for *Pseudotsuga* and *Tsuga* (Table 3.6). Germination rates tended to be greatest in gap size 0.4 for all species, and were greatest for *Abies*, lower for *Tsuga*, and lowest for *Pseudotsuga* (seed lot viability tests [see Methods] indicated *Abies* and *Pseudotsuga* germination rates were similarly greater than those of *Tsuga*). A relatively high proportion of *Abies* germinants on mineral soil did not survive to emergence (*i.e.* died with their cotyledons within the seed coats), while most of the germinants of the other species did emerge. These measures may be somewhat biased against *Pseudotsuga* due to predator preference of that species (Gashwiler 1967) and the placement of exclosure tops on seed-plots after natural seed dispersal had begun. In addition, the viability of naturally-dispersed seeds is unknown. Trends in establishment by gap size and substrate differed somewhat depending on whether establishment was expressed as a fraction of total seed, germination, or emergence. Establishment of *Abies* on soil appeared relatively greater, and of *Pseudotsuga* on wood relatively lower, as a fraction of emergents than as a fraction of seed. Establishment as a fraction of total seed rarely exceeded 10% (except for wood) for the 1992 seedling cohort.

Seedling germination was generally lower in stand TCO in 1993 than in 1992, except for *Abies* in 0.2 gaps (Table 3.7) (germination of *Abies* was actually greater in 1993 on seed-plots in replicate 2 of gap size 0.4, however [not shown]). The 1992 pattern of high mortality of *Abies* germinants was not seen in 1993. Differences in germination and subsequent survival between years could lead to different conclusions

**Table 3.6:** Measures of establishment for 1992 seed-plot cohort in replicate 1 gaps. Substrate abbreviations are: S= soil, L= litter, and W= wood. Standard errors are in parentheses (n=4).

| treatment | # seed | % of seed which: | | # survivors | % establishment as a fraction of: | | |
|---|---|---|---|---|---|---|---|
| | | germinated | emerged | | seed | germinants | emergents |
| *Abies* | | | | | | | |
| ctl S | 100 (0) | 13.5 (2.2) | 7.2 (1.7) | 1 (0.8) | 1.3 (0.8) | 12.1 (7.2) | 18.3 (10.7) |
| ctl L | 100 (0) | 10.5 (3.1) | 10.0 (3.3) | 2 (1.7) | 2.3 (1.7) | 21.7 (12.8) | 25.9 (16.1) |
| ctl W | 100 (0) | 36.0 (5.7) | 36.0 (5.7) | 22 (8.8) | 21.8 (8.8) | 56.1 (16.9) | 56.1 (16.9) |
| 0.2 S | 100 (0) | 19.8 (7.2) | 12.8 (5.7) | 7 (3.9) | 7.0 (3.9) | 26.1 (11.2) | 43.1 (17.8) |
| 0.2 L | 100 (0) | 17.5 (6.8) | 15.5 (7.0) | 9 (6.0) | 9.0 (6.0) | 44.1 (14.3) | 51.6 (15.1) |
| 0.2 W | 100 (0) | 39.0 (8.0) | 37.5 (7.4) | 30 (6.7) | 30.3 (6.7) | 78.5 (6.0) | 81.1 (6.5) |
| 0.4 S | 100 (0) | 27.5 (10.7) | 16.8 (6.7) | 12 (5.7) | 11.5 (5.7) | 52.1 (17.3) | 70.3 (14.0) |
| 0.4 L | 100 (0) | 30.8 (3.5) | 25.0 (2.4) | 15 (3.7) | 15.3 (3.7) | 51.7 (12.8) | 61.0 (14.1) |
| 0.4 W | 100 (0) | 39.0 (12.1) | 38.3 (11.8) | 20 (6.9) | 20.3 (6.9) | 55.4 (7.5) | 56.1 (7.4) |
| 1.0 S | 101 (1) | 18.1 (6.0) | 8.2 (2.1) | 4 (1.5) | 4.0 (1.5) | 17.2 (6.0) | 38.4 (13.7) |
| 1.0 L | 101 (1) | 15.7 (5.0) | 12.7 (3.9) | 3 (1.0) | 2.5 (1.0) | 17.9 (4.4) | 20.0 (4.0) |
| 1.0 W | 101 (1) | 40.8 (12.4) | 33.8 (10.7) | 21 (7.8) | 20.4 (7.8) | 38.9 (15.3) | 45.6 (16.7) |
| *Pseudotsuga* | | | | | | | |
| ctl S | 435 (129) | 9.5 (3.6) | 9.4 (3.7) | 15 (11.9) | 2.8 (1.7) | 25.5 (14.1) | 25.5 (14.1) |
| ctl L | 435 (129) | 9.2 (3.1) | 8.5 (2.8) | 9 (7.2) | 1.7 (1.1) | 20.0 (11.7) | 20.1 (11.8) |
| ctl W | 435 (129) | 21.0 (2.3) | 20.3 (2.6) | 33 (24.0) | 6.6 (3.6) | 28.3 (14.3) | 28.4 (14.2) |
| 0.2 S | 462 (140) | 9.5 (2.5) | 8.5 (2.4) | 16 (6.4) | 4.1 (1.2) | 49.1 (18.0) | 52.1 (16.1) |
| 0.2 L | 462 (140) | 5.3 (1.1) | 5.3 (1.1) | 12 (5.2) | 2.6 (0.7) | 47.6 (8.1) | 47.6 (8.1) |
| 0.2 W | 462 (140) | 16.0 (1.8) | 15.0 (1.3) | 40 (13.3) | 8.9 (1.5) | 59.1 (11.9) | 61.5 (11.2) |
| 0.4 S | 363 (115) | 17.6 (6.8) | 17.6 (6.8) | 38 (14.4) | 10.6 (1.9) | 72.8 (12.9) | 72.8 (12.9) |
| 0.4 L | 363 (115) | 10.3 (4.7) | 10.1 (4.8) | 20 (12.2) | 4.7 (1.7) | 53.1 (12.4) | 56.8 (13.6) |
| 0.4 W | 363 (115) | 21.6 (8.9) | 20.4 (7.9) | 28 (9.8) | 8.7 (2.5) | 45.2 (7.3) | 46.6 (6.6) |
| 1.0 S | 360 (59) | 8.1 (2.0) | 7.1 (1.9) | 17 (6.4) | 5.3 (2.2) | 58.9 (13.4) | 68.4 (14.4) |
| 1.0 L | 360 (59) | 4.2 (1.3) | 3.8 (1.2) | 9 (3.1) | 2.2 (0.7) | 52.5 (2.0) | 56.4 (2.4) |
| 1.0 W | 360 (59) | 18.4 (5.7) | 17.4 (5.4) | 38 (15.4) | 9.8 (3.4) | 51.7 (5.5) | 54.1 (4.4) |

**Table 3.6** (continued)

| treatment | # seed | % of seed which: | | # survivors | % establishment as a fraction of: | | |
|---|---|---|---|---|---|---|---|
| | | germinated | emerged | | seed | germinants | emergents |
| *Tsuga* | | | | | | | |
| ctl S | 1882 (854) | 10.4 ( 4.5) | 10.2 ( 4.5) | 4 ( 3.7) | 0.1 (0.1) | 1.7 ( 1.4) | 1.7 ( 1.4) |
| ctl L | 1882 (854) | 9.0 ( 4.2) | 8.9 ( 4.1) | 10 ( 7.6) | 0.6 (0.4) | 4.4 ( 2.6) | 4.4 ( 2.6) |
| ctl W | 1882 (854) | 43.8 ( 4.8) | 43.7 ( 4.8) | 519 (427.) | 20.3 (9.2) | 41.4 (15.8) | 41.5 (15.8) |
| 0.2 S | 1807 (754) | 18.8 ( 5.0) | 18.8 ( 5.0) | 95 (46.2) | 6.8 (3.5) | 38.0 (14.3) | 38.0 (14.3) |
| 0.2 L | 1807 (754) | 8.0 ( 2.8) | 7.9 ( 2.8) | 45 (35.3) | 2.5 (1.2) | 34.4 (16.6) | 34.6 (16.5) |
| 0.2 W | 1807 (754) | 51.4 (11.6) | 45.1 ( 7.5) | 536 (209.) | 35.6 (6.2) | 72.2 ( 8.1) | 79.6 ( 8.2) |
| 0.4 S | 1206 (558) | 20.5 ( 5.9) | 19.9 ( 6.0) | 60 ( 9.8) | 8.5 (2.6) | 39.9 (10.6) | 41.1 (10.2) |
| 0.4 L | 1206 (558) | 14.0 ( 5.5) | 13.9 ( 5.5) | 36 (13.9) | 6.4 (3.0) | 33.8 (11.9) | 34.1 (12.1) |
| 0.4 W | 1206 (558) | 31.7 ( 8.6) | 31.5 ( 8.4) | 166 (34.0) | 19.2 (5.9) | 63.6 (12.6) | 63.8 (12.6) |
| 1.0 S | 1311 (479) | 12.3 ( 1.5) | 11.8 ( 1.3) | 17 (14.4) | 0.8 (0.6) | 6.6 ( 4.7) | 7.2 ( 5.2) |
| 1.0 L | 1311 (479) | 4.8 ( 1.9) | 4.7 ( 1.9) | 0 ( 0.0) | 0.0 (0.0) | 0.0 ( 0.0) | 0.0 ( 0.0) |
| 1.0 W | 1311 (479) | 24.0 ( 2.2) | 23.3 ( 2.3) | 32 (13.3) | 3.7 (2.5) | 13.2 ( 8.4) | 13.3 ( 8.4) |

**Table 3.7:** Different measures of seedling establishment for replicate 1 seed-plots in stand TCO for 1992 and 1993 (n=1). Substrate abbreviations are: S= soil, L= litter, and W= wood.

| | # seed | | % of seed which: germinated | | % of seed which: emerged | | # survivors | | % establishment as a fraction of: seed | | % establishment as a fraction of: germinants | | % establishment as a fraction of: emergents | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| treatment | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 |
| *Abies* | | | | | | | | | | | | | | |
| ctl S | 100 | 114 | 15.0 | 0.0 | 9.0 | 0.0 | 6 | 0 | 6.0 | 0.0 | 40.0 | 0.0 | 66.7 | 0.0 |
| ctl L | 100 | 114 | 19.0 | 28.1 | 19.0 | 27.2 | 11 | 15 | 11.0 | 13.2 | 57.9 | 46.9 | 57.9 | 48.4 |
| ctl W | 100 | 114 | 52.0 | 22.8 | 52.0 | 21.9 | 48 | 17 | 48.0 | 14.9 | 92.3 | 65.4 | 92.3 | 68.0 |
| 0.2 S | 100 | 104 | 33.0 | 69.2 | 22.0 | 62.5 | 20 | 36 | 20.0 | 34.6 | 60.6 | 50.0 | 90.9 | 55.4 |
| 0.2 L | 100 | 104 | 37.0 | 41.4 | 36.0 | 40.4 | 28 | 33 | 28.0 | 31.7 | 75.7 | 76.7 | 77.8 | 78.6 |
| 0.2 W | 100 | 104 | 50.0 | 65.4 | 48.0 | 59.6 | 47 | 39 | 47.0 | 37.5 | 94.0 | 57.4 | 97.9 | 62.9 |
| 0.4 S | 100 | 100 | 33.0 | 0.0 | 19.0 | 0.0 | 13 | 0 | 13.0 | 0.0 | 39.4 | 0.0 | 68.4 | 0.0 |
| 0.4 L | 100 | 100 | 34.0 | 8.0 | 24.0 | 8.0 | 7 | 6 | 7.0 | 6.0 | 20.6 | 75.0 | 29.2 | 75.0 |
| 0.4 W | 100 | 100 | 48.0 | 7.0 | 48.0 | 6.0 | 32 | 5 | 32.0 | 5.0 | 66.7 | 71.4 | 66.7 | 83.3 |
| 1.0 S | 102 | 100 | 27.5 | 0.0 | 9.8 | 0.0 | 5 | 0 | 4.9 | 0.0 | 17.9 | 0.0 | 50.0 | 0.0 |
| 1.0 L | 102 | 100 | 17.7 | 0.0 | 11.8 | 0.0 | 1 | 0 | 1.0 | 0.0 | 5.6 | 0.0 | 8.3 | 0.0 |
| 1.0 W | 102 | 100 | 49.0 | 22.0 | 45.1 | 22.0 | 21 | 21 | 20.6 | 21.0 | 42.0 | 95.5 | 45.7 | 95.5 |
| *Pseudotsuga* | | | | | | | | | | | | | | |
| ctl S | 216 | 108 | 5.6 | 0.9 | 5.6 | 0.9 | 8 | 0 | 3.7 | 0.0 | 66.7 | 0.0 | 66.7 | 0.0 |
| ctl L | 216 | 108 | 6.5 | 5.6 | 6.5 | 3.7 | 7 | 0 | 3.2 | 0.0 | 50.0 | 0.0 | 50.0 | 0.0 |
| ctl W | 216 | 108 | 19.9 | 10.2 | 19.9 | 6.5 | 36 | 7 | 16.7 | 6.5 | 83.7 | 63.6 | 83.7 | 100.0 |
| 0.2 S | 262 | 108 | 8.0 | 0.9 | 8.0 | 0.9 | 19 | 0 | 7.2 | 0.0 | 90.5 | 0.0 | 90.5 | 0.0 |
| 0.2 L | 262 | 108 | 5.0 | 1.9 | 5.0 | 1.9 | 11 | 2 | 4.2 | 1.9 | 84.6 | 100.0 | 84.6 | 100.0 |
| 0.2 W | 262 | 108 | 13.4 | 24.1 | 13.0 | 22.2 | 30 | 15 | 11.5 | 13.9 | 85.7 | 57.7 | 88.2 | 62.5 |
| 0.4 S | 252 | 108 | 13.5 | 1.9 | 13.5 | 1.9 | 31 | 2 | 12.3 | 1.9 | 91.2 | 100.0 | 91.2 | 100.0 |
| 0.4 L | 252 | 108 | 4.0 | 0.9 | 3.2 | 0.9 | 6 | 1 | 2.4 | 0.9 | 60.0 | 100.0 | 75.0 | 100.0 |
| 0.4 W | 252 | 108 | 23.4 | 6.5 | 23.4 | 6.5 | 35 | 5 | 13.9 | 4.6 | 59.3 | 71.4 | 59.3 | 71.4 |
| 1.0 S | 300 | 114 | 12.3 | 0.9 | 11.0 | 0.9 | 31 | 1 | 10.3 | 0.9 | 83.8 | 100.0 | 93.9 | 100.0 |
| 1.0 L | 300 | 114 | 0.7 | 1.8 | 0.7 | 0.9 | 1 | 0 | 0.3 | 0.0 | 50.0 | 0.0 | 50.0 | 0.0 |
| 1.0 W | 300 | 114 | 14.7 | 19.3 | 12.7 | 19.3 | 18 | 18 | 6.0 | 15.8 | 40.9 | 81.8 | 47.4 | 81.8 |

**Table 3.7** (continued)

| | # seed | | % of seed which: | | | | # survivors | | % establishment as a fraction of: | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | germinated | | emerged | | | | seed | | germinants | | emergents | |
| treatment | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 | 92 | 93 |
| *Tsuga* | | | | | | | | | | | | | | |
| ctl S | 4012 | 1540 | 6.3 | 2.7 | 6.3 | 2.6 | 114 | 9 | 2.8 | 0.6 | 45.1 | 21.4 | 45.1 | 22.5 |
| ctl L | 4012 | 1540 | 8.2 | 11.5 | 8.2 | 11.4 | 97 | 7 | 2.4 | 0.5 | 29.5 | 4.0 | 29.5 | 4.0 |
| ctl W | 4012 | 1540 | 53.4 | 18.0 | 53.4 | 17.4 | 1823 | 203 | 45.4 | 13.2 | 85.0 | 73.3 | 85.0 | 75.8 |
| 0.2 S | 2970 | 1368 | 11.6 | 6.3 | 11.6 | 5.6 | 270 | 65 | 9.1 | 4.8 | 78.5 | 75.6 | 78.5 | 85.5 |
| 0.2 L | 2970 | 1368 | 6.7 | 5.6 | 6.7 | 5.6 | 172 | 57 | 5.8 | 4.2 | 86.9 | 74.0 | 86.9 | 75.0 |
| 0.2 W | 2970 | 1368 | 38.5 | 24.3 | 38.5 | 24.3 | 1085 | 317 | 36.5 | 23.2 | 94.9 | 95.5 | 94.9 | 95.5 |
| 0.4 S | 2848 | 1316 | 8.1 | 5.4 | 6.8 | 5.0 | 46 | 54 | 1.6 | 4.1 | 20.0 | 76.1 | 23.7 | 81.8 |
| 0.4 L | 2848 | 1316 | 1.9 | 0.7 | 1.8 | 0.7 | 0 | 2 | 0.0 | 0.2 | 0.0 | 22.2 | 0.0 | 22.2 |
| 0.4 W | 2848 | 1316 | 30.8 | 10.9 | 30.8 | 10.9 | 258 | 92 | 9.1 | 7.0 | 29.4 | 63.9 | 29.4 | 64.3 |
| 1.0 S | 2396 | 1090 | 12.1 | 6.2 | 11.0 | 5.9 | 67 | 35 | 2.8 | 3.2 | 23.2 | 51.5 | 25.4 | 54.7 |
| 1.0 L | 2396 | 1090 | 0.7 | 0.2 | 0.4 | 0.2 | 0 | 0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 1.0 W | 2396 | 1090 | 23.8 | 1.7 | 21.2 | 1.7 | 21 | 12 | 0.9 | 1.1 | 3.7 | 63.2 | 4.1 | 63.2 |

on establishment success, depending on the measure used. For example, establishment of *Abies* seed on soil in the 0.2 gap was greater in 1993, while establishment of emergents was greater in 1992. Similarly, establishment of *Tsuga* seed on wood in the 0.2 gap was greater in 1992, while establishment of emergents was similar between years. Although survival of *Tsuga* emergents was greater in 0.4 and 1.0 gaps in 1993 than in 1992, survival as a fraction of seed was similar, due to lower emergence in 1993.

### Survival of marked seedlings

Estimates of seedling establishment based on counts of individuals can over-estimate true survival by not recording seedlings that die between counts and are replaced by new emergents. This potential for over-estimation of survival was evaluated by comparing survival of marked seedlings with establishment calculated from simple counts on the same seed-plots. Comparisons of survival and establishment estimates on individual treatments for the 1992 cohort indicate that over-estimation using the count method ranged between 0 and 8% for *Abies*, 0 and 17% for *Pseudotsuga*, and 0 and 5% for *Tsuga* (Table 3.8). The trends in over-estimation suggest that the patterns of gap size and substrate effects on establishment (Figure 3.3) would not change significantly for *Abies* and *Tsuga*, but that *Pseudotsuga* establishment in the control wood and 1.0 soil and litter treatments may have been substantially lower relative to other treatments. A similar comparison for the 1993 seedling cohort in stand TCO (Table 3.9) indicated that over-estimation of survival using the count method was less than 2% for *Abies* and *Pseudotsuga*, and ranged from 0 to 4% for *Tsuga*. The differences in over-estimation between cohorts may have been due to low emergence of *Abies* and *Pseudotsuga* and better accounting of dead seedlings in 1993.

**Table 3.8:** Comparisons of establishment of emerged seedlings calculated from marked individuals and from counts for 1992 cohort in substrate study. Data are from one replicate location in each gap.

| | | | **% establishment calculated from:** | | |
|---|---|---|---|---|---|
| Stand | gap | substrate | marked | counts | Difference |
| *Abies* | | | | | |
| PCM | ctl | soil | 40.0 | 40.0 | 0.0 |
| PCM | ctl | litter | 50.0 | 50.0 | 0.0 |
| PCM | ctl | wood | 77.8 | 77.8 | 0.0 |
| PCM | 1.0 | soil | 0.0 | 0.0 | 0.0 |
| PCM | 1.0 | litter | 25.0 | 25.0 | 0.0 |
| PCM | 1.0 | wood | 0.0 | 0.0 | 0.0 |
| TCO | ctl | soil | 29.1 | 33.3 | 4.2 |
| TCO | ctl | litter | 29.2 | 36.8 | 7.7 |
| TCO | ctl | wood | 88.5 | 88.5 | 0.0 |
| TCO | 1.0 | soil | 49.4 | 50.0 | 0.6 |
| TCO | 1.0 | litter | 8.0 | 8.3 | 0.3 |
| TCO | 1.0 | wood | 44.8 | 45.7 | 0.8 |
| *Pseudotsuga* | | | | | |
| PCM | ctl | soil | 36.8 | 39.4 | 2.6 |
| PCM | ctl | litter | 38.6 | 44.8 | 6.1 |
| PCM | ctl | wood | 50.2 | 56.8 | 6.6 |
| PCM | 1.0 | soil | 74.7 | 80.6 | 6.0 |
| PCM | 1.0 | litter | 55.0 | 60.0 | 5.0 |
| PCM | 1.0 | wood | 56.4 | 58.8 | 2.4 |
| TCO | ctl | soil | 58.3 | 58.3 | 0.0 |
| TCO | ctl | litter | 33.3 | 35.7 | 2.4 |
| TCO | ctl | wood | 36.2 | 48.8 | 12.6 |
| TCO | 1.0 | soil | 80.6 | 93.9 | 13.3 |
| TCO | 1.0 | litter | 33.3 | 50.0 | 16.7 |
| TCO | 1.0 | wood | 37.7 | 42.1 | 4.4 |
| *Tsuga* | | | | | |
| PCM | ctl | soil | 0.8 | 0.9 | 0.1 |
| PCM | ctl | litter | 0.0 | 0.0 | 0.0 |
| PCM | ctl | wood | 50.0 | 53.9 | 3.9 |
| PCM | 1.0 | soil | 1.3 | 1.3 | 0.0 |
| PCM | 1.0 | litter | 0.0 | 0.0 | 0.0 |
| PCM | 1.0 | wood | 0.0 | 0.0 | 0.0 |
| TCO | ctl | soil | 5.6 | 5.9 | 0.4 |
| TCO | ctl | litter | 11.9 | 11.9 | 0.0 |
| TCO | 1.0 | soil | 20.0 | 24.7 | 4.6 |
| TCO | 1.0 | litter | 0.0 | 0.0 | 0.0 |
| TCO | 1.0 | wood | 9.8 | 11.3 | 1.5 |

**Table 3.9:** Comparisons of establishment of emerged seedlings calculated from marked individuals and from counts for 1993 cohort substrate study. Data are means of two replicates in stand TCO.

| | | **% establishment calculated from:** | | |
|---|---|---|---|---|
| Gap size | substrate | marked | counts | Difference |
| *Abies* | | | | |
| ctl | soil | 40.9 | 40.9 | 0.0 |
| ctl | litter | 45.6 | 45.6 | 0.0 |
| ctl | wood | 80.0 | 80.0 | 0.0 |
| 0.2 | soil | 73.1 | 73.1 | 0.0 |
| 0.2 | litter | 84.4 | 84.4 | 0.0 |
| 0.2 | wood | 77.7 | 77.7 | 0.0 |
| 0.4 | soil | 26.2 | 26.2 | 0.0 |
| 0.4 | litter | 65.5 | 65.5 | 0.0 |
| 0.4 | wood | 59.0 | 59.3 | 0.3 |
| 1.0 | soil | 0.0 | 0.0 | 0.0 |
| 1.0 | litter | 0.0 | 0.0 | 0.0 |
| 1.0 | wood | 72.7 | 72.7 | 0.0 |
| *Pseudotsuga* | | | | |
| ctl | soil | 9.1 | 9.1 | 0.0 |
| ctl | litter | 10.0 | 10.0 | 0.0 |
| ctl | wood | 83.3 | 83.3 | 0.0 |
| 0.2 | soil | 50.0 | 50.0 | 0.0 |
| 0.2 | litter | 90.0 | 90.0 | 0.0 |
| 0.2 | wood | 68.5 | 70.3 | 1.8 |
| 0.4 | soil | 61.3 | 61.3 | 0.0 |
| 0.4 | litter | 73.6 | 73.6 | 0.0 |
| 0.4 | wood | 46.4 | 46.4 | 0.0 |
| 1.0 | soil | 50.0 | 50.0 | 0.0 |
| 1.0 | litter | 0.0 | 0.0 | 0.0 |
| 1.0 | wood | 40.9 | 40.9 | 0.0 |
| *Tsuga* | | | | |
| 0.4 | soil | 78.3 | 81.8 | 3.5 |
| 0.4 | litter | 22.2 | 22.2 | 0.0 |
| 0.4 | wood | 63.0 | 64.3 | 1.3 |
| 1.0 | soil | 47.0 | 47.8 | 0.8 |
| 1.0 | litter | 0.0 | 0.0 | 0.0 |
| 1.0 | wood | 66.4 | 67.5 | 1.1 |

Causes of seedling mortality

Causes of seedling mortality varied among gaps and substrates. General observations on the appearance of dead seedlings were recorded for the 1992 cohort, while counts were kept for the 1993 seedling cohort (Table 3.10). The most common form of mortality in all gaps, over both years, consisted of seedlings which disappeared without a trace during the one month interval between counts, possibly due to removal by insect predators (rodents also succeeded in entering exclosures occasionally, especially in 1993). Many of the dead *Abies* and *Tsuga* seedlings on soil and litter in controls and on all substrates in gap size 1.0 were wilted and faded

**Table 3.10:** Condition of mortality for 1993 seedling cohort in stand TCO in substrate study by species and gap size, in percent by species.

| | no trace | fungi/ molds | clipped stem/root | standing brown | row sum |
|---|---|---|---|---|---|
| *Abies* | | | | | |
| ctl | 3 | 0 | 1 | 21 | 26 |
| 0.2 | 6 | 5 | 17 | 6 | 34 |
| 0.4 | 3 | 2 | 33 | 0.4 | 39 |
| 1.0 | -- | -- | -- | 1 | 1 |
| | 12 | 7 | 51 | 29 | 100 |
| *Pseudotsuga* | | | | | |
| ctl | 13 | 5 | 3 | 4 | 25 |
| 0.2 | 4 | 1 | 6 | 1 | 11 |
| 0.4 | 7 | 1 | 50 | 1 | 59 |
| 1.0 | 2 | 1 | 1 | 1 | 4 |
| | 24 | 8 | 59 | 5 | 100 |
| *Tsuga* | | | | | |
| ctl | 21 | 0.1 | 2 | 19 | 41 |
| 0.2 | 14 | -- | 2 | 1 | 17 |
| 0.4 | 23 | 0.4 | 5 | 5 | 33 |
| 1.0 | 5 | 0.2 | 2 | 1 | 9 |
| | 62 | 1 | 12 | 25 | 100 |

("standing brown"), potentially caused by drought and/or exposure to high temperatures. Maximum surface temperatures recorded in one 1.0 size gap in the summer of 1992 commonly exceeded 50°C, with highest temperatures on litter and lowest temperatures on wood (Table 3.11). Cooler temperatures and lower emergence may be why this form of mortality was less visible in gap size 1.0 for the 1993 cohort (Table 3.10). Clipping of seedlings (most likely by cutworms, family *Noctuidae* [Overhulser 1990]) was variable, but occasionally severe, in controls and 0.2 gaps for both cohorts, and in 0.4 gaps for the 1993 cohort. The low levels of germination for the 1993 cohort of *Abies* and *Pseudotsuga* on many treatments appear to be due in part to insect and rodent predation (empty seed and evidence of burrowing were found in several seed-plots).

### Seedling growth

Seedling size after two growing seasons (*i.e.* growth since germination) differed significantly by age class, gap size, substrate, species, and the gap size by substrate, gap size by species, and substrate by species interactions in the substrate study for the 1992 cohort (Table 3.12). Seedlings in old-growth stands were 50% larger on average than those in mature stands. Most differences between age-classes

**Table 3.11:** Surface temperatures (°C) measured in seed-plots in a 1.0 size gap in stand PCM over 5 hot days in mid-August 1992. Daily maximum temperatures for each sensor were averaged for the 5 days; means and maxima for each substrate or shade treatment are shown (two sensors used for soil, litter, and wood; four sensors used for 40% and 90% shade).

| | soil | litter | wood | 40% shade | 90% shade |
|---|---|---|---|---|---|
| Means | 55.5 | 61.8 | 49.7 | 52.5 | 46.5 |
| Maxima | 57.2 | 65.3 | 53.7 | 57.5 | 56.7 |

**Table 3.12:** Results of split-split plot ANOVA on seedling size (height*basal area) for 1992 cohort in substrate study. Factor abbreviations are: age= age class, gap= gap size, subs= substrate, spp= species. stand(age) error term was left out of model because Mean Square was less than that of stand*gap(age). Significant effects ($p < .05$) are marked with asterisks (*).

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| age | 1 | 19.48465 | 9.91 | 0.0136 * |
| Error: stand(age) | | **n.a.** | | |
| gap | 3 | 163.91357 | 83.36 | 0.0001 * |
| age*gap | 3 | 6.19198 | 3.15 | 0.0864 |
| Error: stand*gap(age) | 8 | 1.96641 | 1.79 | 0.1040 |
| subs | 2 | 14.53141 | 13.21 | 0.0001 * |
| age*subs | 2 | 0.38246 | 0.35 | 0.7081 |
| gap*subs | 6 | 6.20345 | 5.64 | 0.0002 * |
| age*gap*subs | 6 | 0.34597 | 0.31 | 0.9261 |
| spp | 2 | 139.10678 | 126.50 | 0.0001 * |
| age*spp | 2 | 0.47112 | 0.43 | 0.6541 |
| gap*spp | 6 | 5.52608 | 5.03 | 0.0005 * |
| subs*spp | 4 | 6.30767 | 5.74 | 0.0008 * |
| age*gap*spp | 6 | 0.70698 | 0.64 | 0.6953 |
| age*subs*spp | 4 | 0.39025 | 0.35 | 0.8393 |
| gap*subs*spp | 11 | 0.99639 | 0.91 | 0.5420 |
| age*gap*subs*spp | 10 | 0.12970 | 0.12 | 0.9995 |
| Error: stand*gap*subs *spp(age) | 46 | 1.09965 | | |
| Total | 122 | | | |

were in gap size 1.0, where *Abies* and *Pseudotsuga* on litter plots and *Tsuga* on soil plots and wood plots were twice as large in old-growth stands as in mature stands (Figure 3.5). Lack of seedlings on several treatments in different stands appear to have made treatment interactions with age class non-significant, however. Greater growth on soil and litter may have resulted from the higher soil moisture levels in the old-growth stands (Chapter 2, Table 2.2). The appearance of lower growth on wood in 1.0 gaps in mature stands may be due to low wood quality in the gap in mature stand MCY and the lack of surviving seedlings in the gap in mature stand PCM.

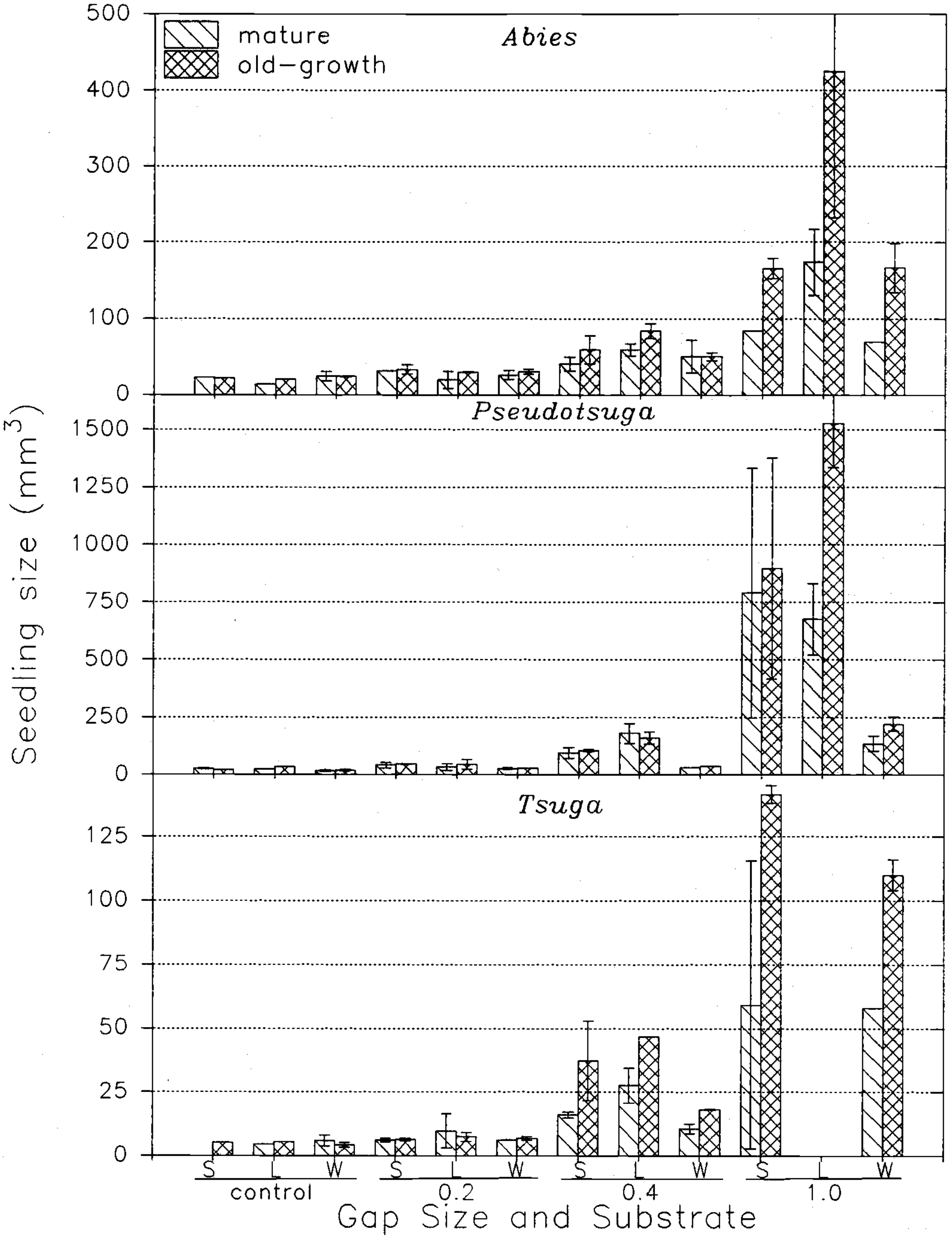

**Figure 3.5:** Seedling size (basal area*height) in substrate study by age class, species, gap size, and substrate. Data are means and standard errors of mean size on replicate 1 treatments in each stand ($n \leq 2$, depending on presence of seedlings).

Seedling size was similar in controls and 0.2 gaps,and increased with gap size, with the largest seedlings in 0.4 and 1.0 gaps found on litter and the smallest on wood (Table 3.13). This pattern among substrates in the larger gaps was not entirely consistent at the species level, however; seedling size was similar on wood and soil for *Abies* in 0.4 and 1.0 gaps and for *Tsuga* in 1.0 gaps (Figure 3.6). Seedling size increased in all treatments from *Tsuga* to *Abies* to *Pseudotsuga*. Patterns of relative growth rates (*i.e.* change in mean seedling size on a treatment between 1992 and 1993, divided by size in 1992) among substrates differed somewhat from patterns of seedling size in 1993. Relative growth rates of *Tsuga* and *Pseudotsuga* were much higher than those of *Abies* (Figure 3.7). There was a tendency towards lower relative growth rates on litter than on soil, although the reverse tended to occur for size (*e.g.* all species in gap size 0.4 and *Pseudotsuga* in gap size 1.0), suggesting greater growth on litter in the first year (and/or mortality of the smallest seedlings on soil treatments in the second year).

**Table 3.13:** Separation of means for gap size by substrate interaction in ANOVA on seedling size (height*basal area) in substrate study. Values are least-square means and standard errors of log-transformed size data. Means with different letters were significantly different (p < .05). Missing values were not estimable due to missing data.

| | | | | | |
|---|---|---|---|---|---|
| ctl | soil | . | | . | |
| ctl | litter | 2.688 | ± | 0.223 | ab |
| ctl | wood | 2.726 | ± | 0.107 | ab |
| 0.2 | soil | 3.102 | ± | 0.122 | b |
| 0.2 | litter | 3.075 | ± | 0.141 | b |
| 0.2 | wood | 2.915 | ± | 0.096 | ab |
| 0.4 | soil | 3.914 | ± | 0.116 | d |
| 0.4 | litter | 4.298 | ± | 0.120 | e |
| 0.4 | wood | 3.346 | ± | 0.105 | c |
| 1.0 | soil | 5.051 | ± | 0.183 | g |
| 1.0 | litter | . | | . | |
| 1.0 | wood | 4.723 | ± | 0.117 | f |

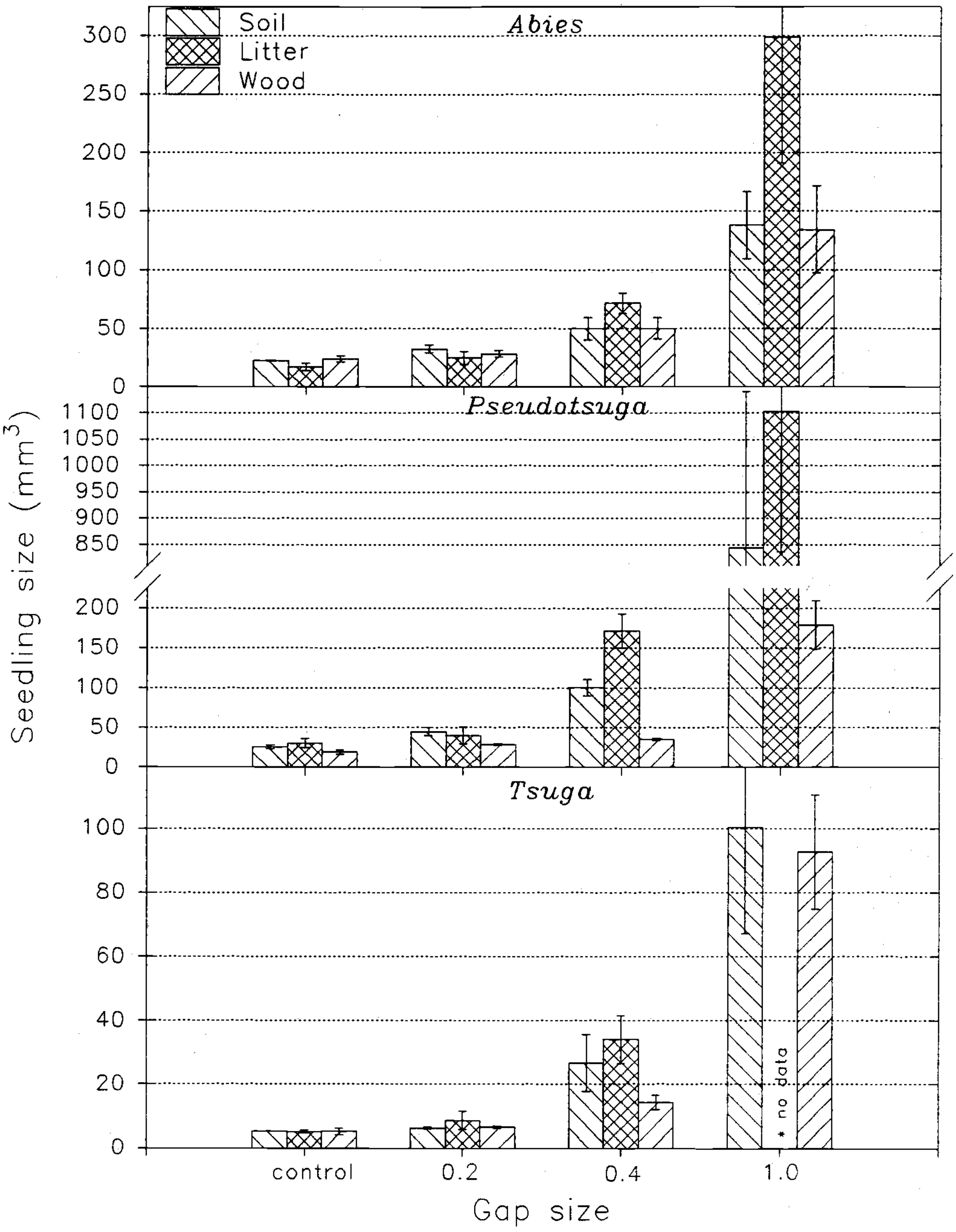

**Figure 3.6:** Seedling size (basal area*height) in substrate study by species, gap size, and substrate. Data are means and standard errors of mean size on replicate 1 treatments in each stand ($n \leq 4$, depending on presence of seedlings).

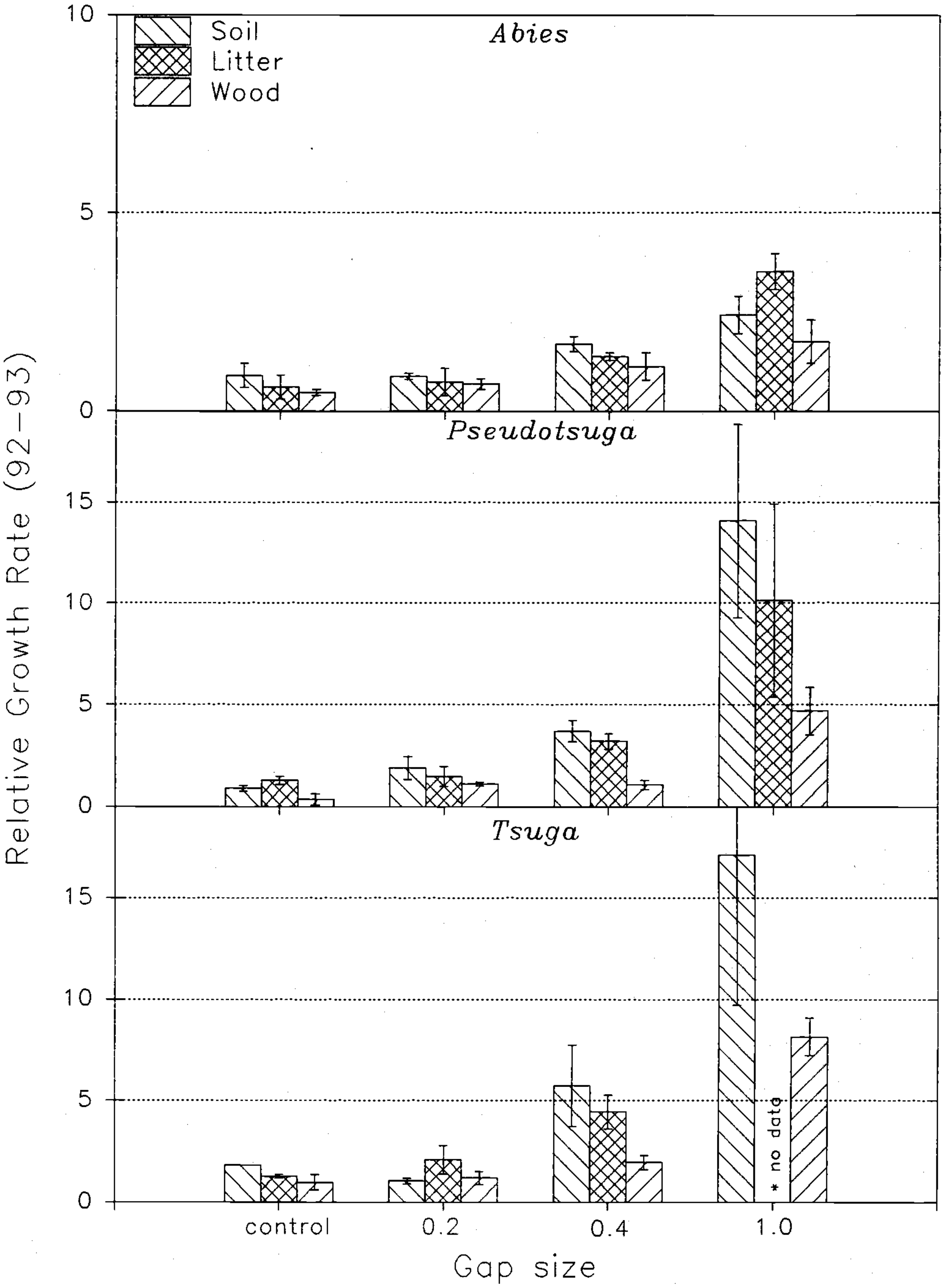

**Figure 3.7:** Relative growth rates of seedling size (basal area*height) from October 1992 to October 1993 ([size93-size92]/size92) in substrate study by species, gap size, and substrate. Data are means and standard errors of mean size on replicate 1 treatments in each stand (n≤4, depending on presence of seedlings).

## Understory shade effects

Establishment of the 1992 seedling cohort after two growing seasons differed significantly by shade level, species, and the gap size by shade level and gap size by species interactions in the controlled seed-plot study (Table 3.14). Establishment under 90% shade was lower than establishment under 40% or no shade in controls and 0.4 gaps (Table 3.15). Establishment of *Tsuga* in 0.4 gaps tended to be highest under 40% shade, and there was a tendency in 1.0 gaps towards greater establishment under 90% shade, particularly for *Abies* (Figure 3.8). Although I expected the 90% shade treatment to ameliorate the extreme surface temperatures on litter in gap size 1.0, temperatures commonly exceeded 50°C, despite the much shorter duration of "sunflecks" in the shade treatments (Table 3.11). The withered brown condition of mortality observed in all shade treatments in the large gaps supports the idea that extreme temperatures were a leading cause of mortality.

**Table 3.14:** Results of split-plot ANOVA on seedling establishment (% of maximum count) under different levels of artificial shade in understory shade study. Factor abbreviations are: gap= gap size, rep= gap replicate within stand, shade= shade level, spp= species. Significant effects (p < .05) are marked with asterisks (*).

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| gap | 2 | 52.54057 | 5.42 | 0.1009 |
| Error: gap(stand) | 3 | 9.69134 | | |
| rep(stand*gap) | 6 | 1.93139 | | |
| shade | 2 | 6.34952 | 6.73 | 0.0048 * |
| gap*shade | 4 | 5.97570 | 6.34 | 0.0013 * |
| spp | 2 | 17.26267 | 18.30 | 0.0001 * |
| gap*spp | 4 | 6.03222 | 6.40 | 0.0012 * |
| shade*spp | 4 | 0.28352 | 0.30 | 0.8747 |
| gap*shade*spp | 8 | 1.43045 | 1.52 | 0.2036 |
| Error: gap*shade *spp(stand) | 24 | 0.94325 | | |
| rep(stand*gap*subs*spp) | 46 | 0.69376 | | |
| Total | 105 | | | |

**Table 3.15:** Separation of means for gap size by understory shade interaction in ANOVA on seedling establishment (% of maximum count) in understory shade study. Values are least-square means and standard errors of log-transformed size data. Means with different letters were significantly different ($p < .05$). Species codes are: abam= *Abies amabilis*, psme= *Pseudotsuga menziesii*, tshe= *Tsuga heterophylla*.

| | | | |
|---|---|---|---|
| ctl | none | 0.437 ± 0.126 | bc |
| ctl | 40% | 0.354 ± 0.121 | b |
| ctl | 90% | 0.099 ± 0.119 | a |
| 0.4 | none | 0.907 ± 0.120 | ef |
| 0.4 | 40% | 0.970 ± 0.121 | f |
| 0.4 | 90% | 0.531 ± 0.119 | bcd |
| 1.0 | none | 0.654 ± 0.128 | cde |
| 1.0 | 40% | 0.764 ± 0.124 | def |
| 1.0 | 90% | 0.852 ± 0.123 | ef |

Patterns of establishment in shade treatments differed between measures as a fraction of total seed and measures as a fraction of maximum emergence. This comparison assumes that natural *Pseudotsuga* seed rain was the same in replicate 2 gaps as in the replicate 1 gaps in which it was sampled, which seems reasonable given the similarity in dominance and basal area of mature *Pseudotsuga* within each mature stand. The differences among survival measures are due to greater emergence of seedlings under shade treatments for most species in most gaps (Table 3.16). In contrast to establishment as a fraction of emergence, establishment as a fraction of total seed suggests that establishment of all species was aided by shade in gap size 1.0, due to greater germination rates under shade.

Seedling size after two growing seasons differed significantly by gap size, shade level, and species for the 1992 cohort (Table 3.17). Separation of significant means was not feasible for this analysis because least-square means were not estimable due to missing data in several treatments. Seedling size decreased from *Pseudotsuga* to *Abies* to *Tsuga* in all treatments and with level of shade in all gaps (no *Tsuga* survivors were present in the 1.0 no shade seed plots in replicate 1 gaps, however) (Figure 3.9). Thus while artificial shade may have facilitated establishment

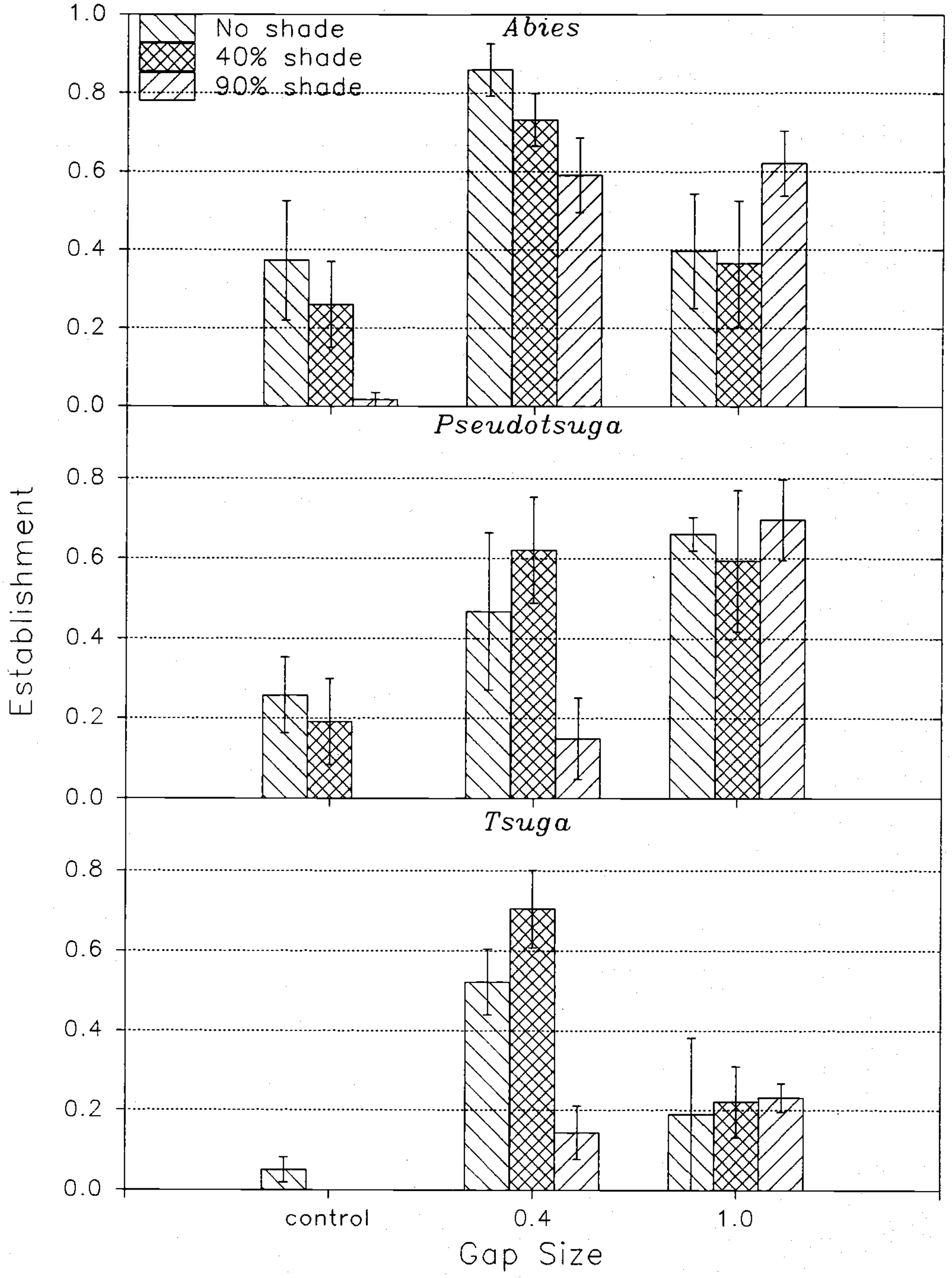

**Figure 3.8:** Seedling establishment (% of maximum emerged) in understory shade study by species, gap size, and shade level. Data are means and standard errors of all replicates (n=4).

**Table 3.16:** Measures of establishment for 1992 seed-plot cohort by level of understory shade. Standard errors are in parentheses (n=2 for seed variables, n=4 for rest).

| | | | **% of seed:** | | **% establishment of:** | |
|---|---|---|---|---|---|---|
| treatment | | # seed | emerged | # survivors | seed | emergents |
| *Abies* | | | | | | |
| ctl | none | 100 ( 0) | 8.0 (2.0) | 2.2 ( 0.9) | 2.3 (0.9) | 37.2 (15.3) |
| ctl | 40% | 100 ( 0) | 11.3 (2.7) | 2.7 ( 1.0) | 2.8 (1.0) | 26.0 (11.0) |
| ctl | 90% | 100 ( 0) | 18.0 (3.3) | 0.2 ( 0.2) | 0.3 (0.3) | 1.8 ( 1.8) |
| 0.4 | none | 100 ( 0) | 16.0 (5.1) | 13.0 ( 4.1) | 13.0 (4.1) | 86.0 ( 6.6) |
| 0.4 | 40% | 100 ( 0) | 15.3 (3.6) | 11.5 ( 3.4) | 11.5 (3.4) | 73.2 ( 6.7) |
| 0.4 | 90% | 100 ( 0) | 19.0 (2.1) | 10.8 ( 1.3) | 10.8 (1.3) | 59.1 ( 9.5) |
| 1.0 | none | 100 ( 0) | 11.3 (6.4) | 6.0 ( 4.7) | 6.0 (4.7) | 39.7 (14.7) |
| 1.0 | 40% | 100 ( 0) | 16.5 (7.7) | 9.5 ( 5.9) | 9.5 (5.9) | 36.5 (16.1) |
| 1.0 | 90% | 100 ( 0) | 14.8 (6.7) | 9.8 ( 5.0) | 9.8 (5.0) | 62.0 ( 8.3) |
| *Pseudotsuga* | | | | | | |
| ctl | none | 444 (136) | 8.2 (2.8) | 10.0 ( 6.9) | 1.6 (1.0) | 25.8 ( 9.5) |
| ctl | 40% | 444 (136) | 14.4 (0.9) | 18.5 (11.1) | 2.8 (1.6) | 19.1 (10.8) |
| ctl | 90% | 444 (136) | 11.6 (1.4) | 0.0 ( 0.0) | 0.0 (0.0) | 0.0 ( 0.0) |
| 0.4 | none | 424 (152) | 10.8 (4.5) | 21.5 (12.1) | 4.4 (1.9) | 46.7 (19.7) |
| 0.4 | 40% | 424 (152) | 8.8 (1.9) | 21.3 ( 9.3) | 4.8 (0.8) | 62.0 (13.3) |
| 0.4 | 90% | 424 (152) | 11.7 (6.3) | 5.0 ( 2.9) | 1.3 (0.7) | 15.0 (10.2) |
| 1.0 | none | 304 ( 19) | 4.1 (0.6) | 8.3 ( 1.3) | 2.7 (0.3) | 66.1 ( 4.2) |
| 1.0 | 40% | 304 ( 19) | 6.4 (2.2) | 12.5 ( 6.4) | 3.9 (1.9) | 59.4 (17.7) |
| 1.0 | 90% | 304 ( 19) | 7.3 (2.7) | 17.3 ( 7.0) | 5.4 (2.1) | 69.6 (10.1) |
| *Tsuga* | | | | | | |
| ctl | none | 500 ( 0) | 7.4 (4.5) | 2.2 ( 1.9) | 0.5 (0.4) | 5.1 ( 3.1) |
| ctl | 40% | 500 ( 0) | 9.8 (3.0) | 0.0 ( 0.0) | 0.0 (0.0) | 0.0 ( 0.0) |
| ctl | 90% | 500 ( 0) | 10.7 (4.9) | 0.0 ( 0.0) | 0.0 (0.0) | 0.0 ( 0.0) |
| 0.4 | none | 504 ( 2) | 14.5 (4.9) | 37.0 (12.1) | 7.3 (2.4) | 52.2 ( 8.2) |
| 0.4 | 40% | 504 ( 2) | 7.6 (1.7) | 26.3 ( 6.1) | 5.2 (1.2) | 70.4 ( 9.8) |
| 0.4 | 90% | 504 ( 2) | 11.3 (5.3) | 5.0 ( 1.5) | 1.0 (0.3) | 14.4 ( 6.7) |
| 1.0 | none | 504 ( 2) | 4.9 (1.8) | 4.0 ( 4.0) | 0.8 (0.8) | 19.1 (19.1) |
| 1.0 | 40% | 504 ( 2) | 4.5 (2.1) | 7.7 ( 5.2) | 1.5 (1.0) | 22.1 ( 8.9) |
| 1.0 | 90% | 504 ( 2) | 6.3 (1.0) | 7.7 ( 2.1) | 1.5 (0.4) | 23.2 ( 3.6) |

in large gaps, it tended to depress growth relative to unshaded plots. *Pseudotsuga* height was greater under 40% shade than without shade in gap size 1.0 (mean height of 164 vs. 147 mm), whereas basal diameter was greater without shade (mean of 2.3 vs. 1.8 mm), making the computed size measure greater on the unshaded treatments.

**Table 3.17:** Results of split-plot ANOVA on seedling size (height*basal area) after two growing seasons under different levels of artificial shade. Factor abbreviations are: gap= gap size, shade= shade level, spp= species. Gap(stand) error term was left out of model because Mean Square was less than that of gap*shade*spp(stand). Significant effects (p< .05) are marked with asterisks (*).

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| gap | 2 | 40.44348 | 41.74 | 0.0001 * |
| Error: gap(stand) | | **n.a.** | | |
| shade | 2 | 12.56508 | 12.97 | 0.0004 * |
| gap*shade | 4 | 0.83757 | 0.86 | 0.5062 |
| spp | 2 | 39.26860 | 40.53 | 0.0001 * |
| gap*spp | 4 | 0.71235 | 0.74 | 0.5813 |
| shade*spp | 4 | 1.43833 | 1.48 | 0.2534 |
| gap*shade*spp | 4 | 1.05366 | 1.09 | 0.3957 |
| Error: gap*shade *spp(stand) | 16 | 0.96882 | | |
| Total | 38 | | | |

## Log effects

Seedling survival was greatly affected by proximity to large logs in the 1.0 size gaps of stand TCO, and the effect varied by within-gap position (Figure 3.10). Only data from one of the two gaps were used to assess log effects because most of the seedlings in one of the gaps were clipped at the base within 3 weeks of planting (probably due to predation by cutworms inside exclosures). Survival of *Pseudotsuga* and *Tsuga* was greatest within 15 cm of the north sides of logs in the north and center of the gap (Figure 3.10). No *Tsuga* survived beyond this zone on the north sides, or anywhere on the south sides, of the north and center logs. Some *Pseudotsuga* did survive outside of the 15 cm north side zone, and survival in these areas was greater for the log at gap center than for the log at the north end of the gap. Almost all dead seedlings at north and center logs were either standing brown or withered and faded. Seedling survival was high regardless of proximity to the south log; almost all mortality was identified as clipping of stems by predators.

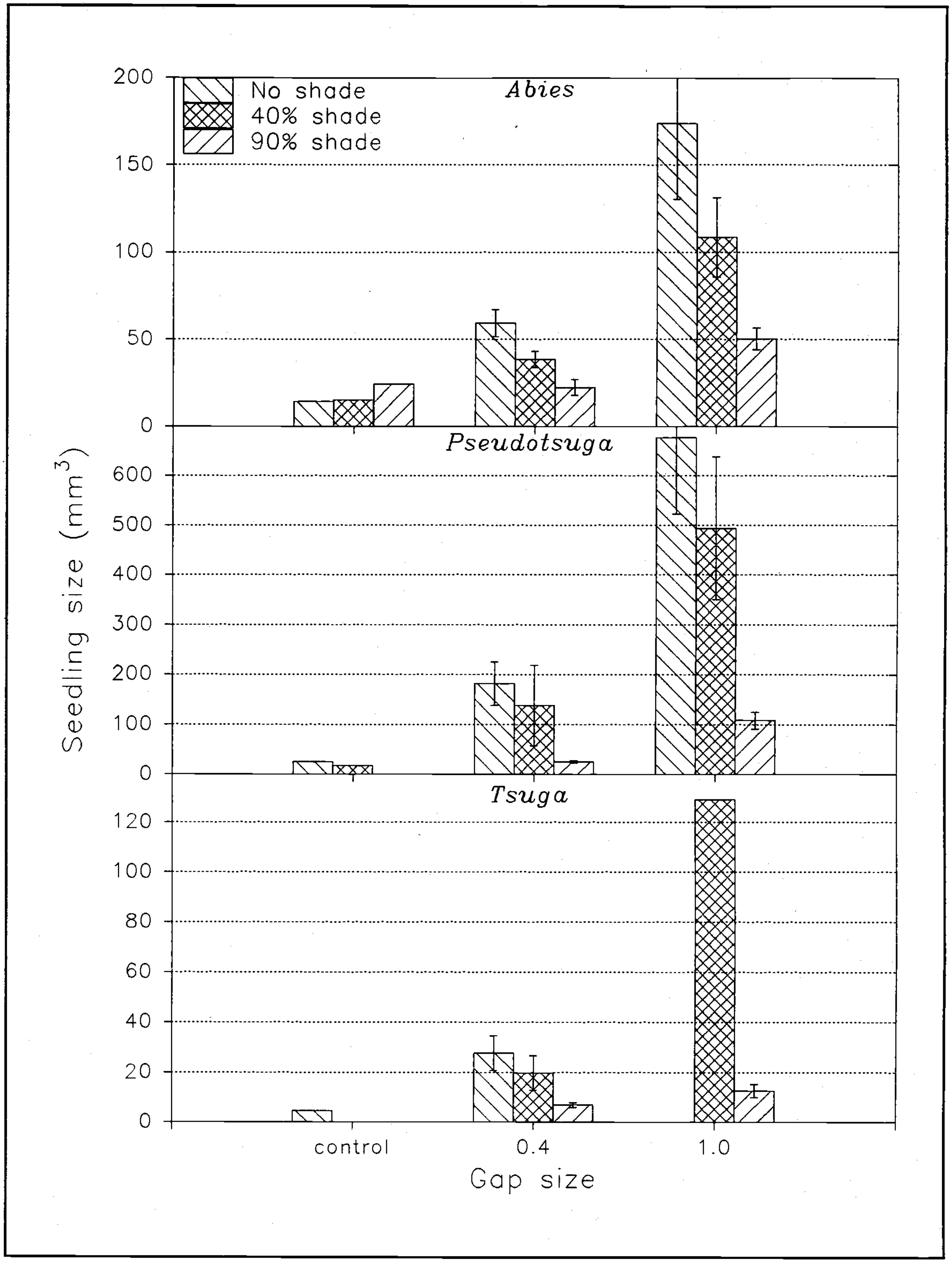

**Figure 3.9:** Seedling size (basal area*height) in understory shade study by species, gap size, and shade level. Data are means and standard errors of mean size on replicate 1 treatments in each stand (n≤2, depending on presence of seedlings).

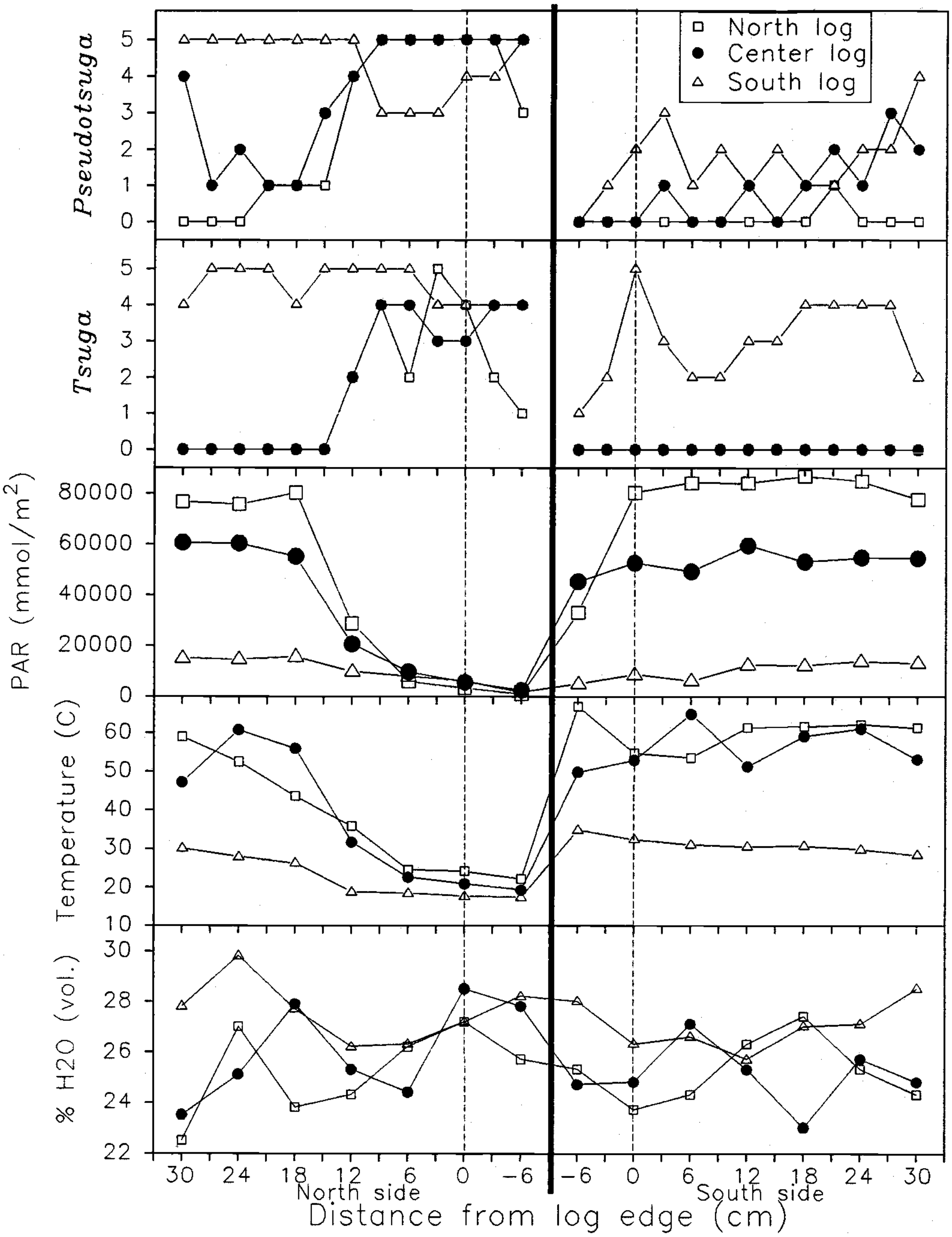

**Figure 3.10:** Seedling survival and microclimate along transects across logs in three position within a 1.0 size gap in stand TCO. Seedling data are in numbers of seedlings (total planted= 5). PAR is mean daily quantum flux of photosynthetically active radiation, and temperature is mean daily maxima on sunny days. Soil moisture data is from July 9, 1994.

Patterns of seedling survival next to logs corresponded well with measures of microclimate. Positions within 12 cm of the north sides of all logs received less light than other positions, and light levels at unshaded positions decreased from north to south log location within the gap (Figure 3.10). Temperature maxima paralleled light levels closely, with positions beyond 12 cm of the north sides and all positions on the south sides of the north and center logs experiencing surface temperatures in excess of 40°C. In contrast, temperature maxima did not exceed 30°C regardless of proximity to the south log. No obvious soil moisture patterns with distance from logs were visible, although moisture tended to be greater at the south log, and lower at the north log. Thus surface temperatures appear to be the best predictor of mortality in unshaded areas in large gaps, and logs appear to provide an effective refuge from exposure.

## Survival of natural regeneration

Survival of naturally regenerated *Pseudotsuga* after two growing seasons differed significantly by gap size, within-gap position, and substrate (Table 3.18). Survival of *Tsuga* differed significantly only by gap size, although the gap size by within-gap position by cover interaction was significant at $p < .06$ (Table 3.19). Lack of greater significance in the analyses may be due to the low numbers of (or lack of) seedlings found in some of the gap size by position by understory cover and substrate levels (see Appendix). Several trends were identified in the data which may be of biological significance, however.

Seedling survival tended to be greater on decayed wood than on litter for both *Pseudotsuga* and *Tsuga*, although not in controls, or for *Tsuga* in gap size 0.2 and in north and center positions of gap size 1.0 (Figure 3.11). These results differ substantially from those of the substrate experiment, where survival on decayed wood was greater in controls and gap size 0.2 than in the larger gaps. It is possible that established vegetation on the natural logs used in this study excluded new seedling establishment in controls but not in gaps, where resource levels were much higher.

**Table 3.18:** Results of ANOVA on survival of naturally regenerated *Pseudotsuga* seedlings. Separate analyses were done for understory cover (over litter only) and substrate. Factor abbreviations are: age= age class, gap= gap size, pos= within-gap position, covr= understory cover level, subs= substrate. Stand*gap*pos(age) error term was left out of the model because Mean Square was less than that of stand*gap*pos*cover(age). Significant effects (p <.05) are marked with asterisks (*).

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| age | 1 | 0.32628 | 0.26 | 0.6616 |
| Error: stand(age) | 2 | 1.26151 | | |
| gap | 3 | 5.84462 | 10.64 | 0.0081 * |
| age*gap | 3 | 0.03017 | 0.05 | 0.9815 |
| Error: stand*gap(age) | 6 | 0.54918 | | |
| pos | 2 | 1.01327 | 3.83 | 0.0289 * |
| gap*pos | 4 | 0.25370 | 0.96 | 0.4391 |
| age*pos | 2 | 0.67227 | 2.54 | 0.0898 |
| age*gap*pos | 4 | 0.23058 | 0.87 | 0.4883 |
| Error: stand*gap *pos(age) | | **n.a.** | | |
| cover | 2 | 0.03949 | 0.15 | 0.8618 |
| age*cover | 2 | 0.48368 | 1.83 | 0.1722 |
| gap*cover | 6 | 0.26638 | 1.01 | 0.4326 |
| pos*cover | 4 | 0.23321 | 0.88 | 0.4825 |
| age*gap*cover | 6 | 0.38123 | 1.44 | 0.2199 |
| age*pos*cover | 4 | 0.06234 | 0.24 | 0.9168 |
| gap*pos*cover | 8 | 0.13455 | 0.51 | 0.8437 |
| age*gap*pos*cover | 7 | 0.28282 | 1.07 | 0.3984 |
| Error: stand*gap*pos *cover(age) | 46 | 0.26459 | | |
| Total | 112 | | | |

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| gap | 3 | 12.15841 | 20.39 | 0.0001 * |
| Error: gap(stand) | 12 | 0.59624 | | |
| subs | 1 | 2.06752 | 6.33 | 0.0306 * |
| gap*subs | 3 | 0.55531 | 1.70 | 0.2298 |
| Error: gap*subs(stand) | 10 | 0.32677 | | |
| Total | 29 | | | |

**Table 3.19:** Results of ANOVA on survival of naturally regenerated *Tsuga* seedlings. Separate analyses were done for understory cover (over litter only) and substrate. Factor abbreviations are: gap= gap size, pos= within-gap position, covr= understory cover level, subs= substrate. Gap(stand) error term was left out of the model because Mean Square was less than that of gap*pos(stand). Significant effects (p < .05) are marked with asterisks (*).

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| gap | 3 | 1.62270 | 1.55 | 0.2687 |
| Error: gap(stand) | | **n.a.** | | |
| pos | 2 | 2.87158 | 2.74 | 0.1179 |
| gap*pos | 4 | 1.03196 | 0.98 | 0.4632 |
| Error: gap*pos(stand) | 9 | 1.04907 | | |
| cover | 2 | 0.07661 | 0.19 | 0.8265 |
| gap*cover | 6 | 0.15044 | 0.38 | 0.8801 |
| pos*cover | 4 | 0.25462 | 0.64 | 0.6413 |
| gap*pos*cover | 7 | 1.05435 | 2.66 | 0.0566 |
| Error: gap*pos *cover(stand) | 14 | 0.39656 | | |
| Total | 52 | | | |

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| gap | 3 | 2.47467 | 17.18 | 0.0095 * |
| Error: gap(stand) | 4 | 1.30814 | | |
| subs | 1 | 1.95608 | 1.88 | 0.2425 |
| gap*subs | 3 | 1.52314 | 1.46 | 0.3512 |
| Error: gap*subs(stand) | 4 | 1.04212 | | |
| Total | 15 | | | |

Several instances where the tops of *Pseudotsuga* seedlings were buried under litter after their first winter in gaps were noted; apparently seedling burial from litter accumulated over snow-packs (Thornburgh 1969) is not limited to *Tsuga* in closed canopy areas.

Survival of *Tsuga* and *Pseudotsuga* was low in controls, with no survivors under high understory cover (Figure 3.12). *Pseudotsuga* survival tended to be greater under high cover than low cover in exposed locations (*e.g.* 0.4 and 1.0 north, and 1.0 center), while the opposite tended to occur in open-shaded locations (*e.g.* 0.4 and 1.0

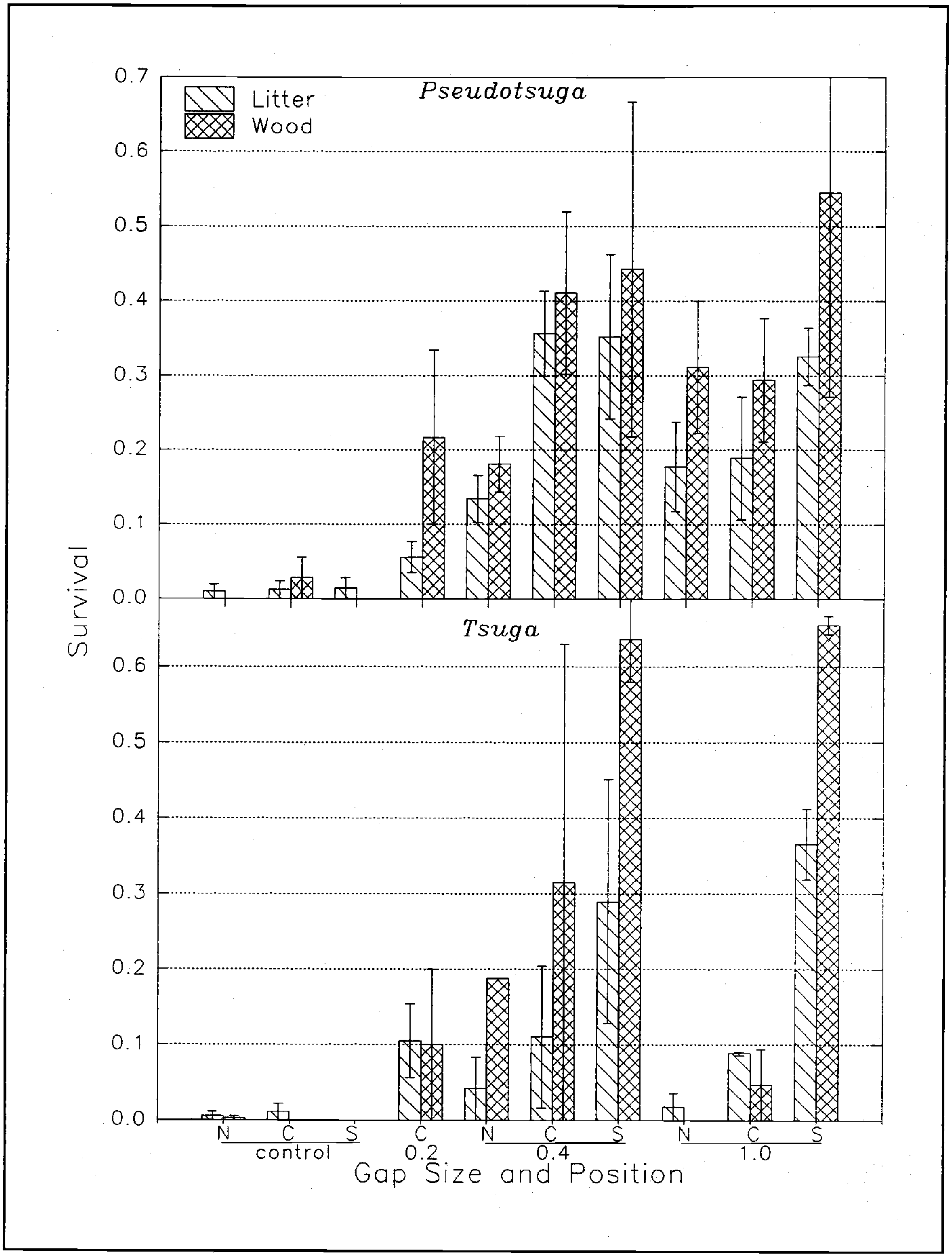

**Figure 3.11:** Survival of natural regeneration by substrate, species, gap size, and within-gap position (North, Center, South). Data are means and standard errors of survival in replicate 1 gaps in all stands for *Pseudotsuga* ($n \leq 4$) and in old-growth stands for *Tsuga* ($n \leq 2$, depending on presence of seedlings).

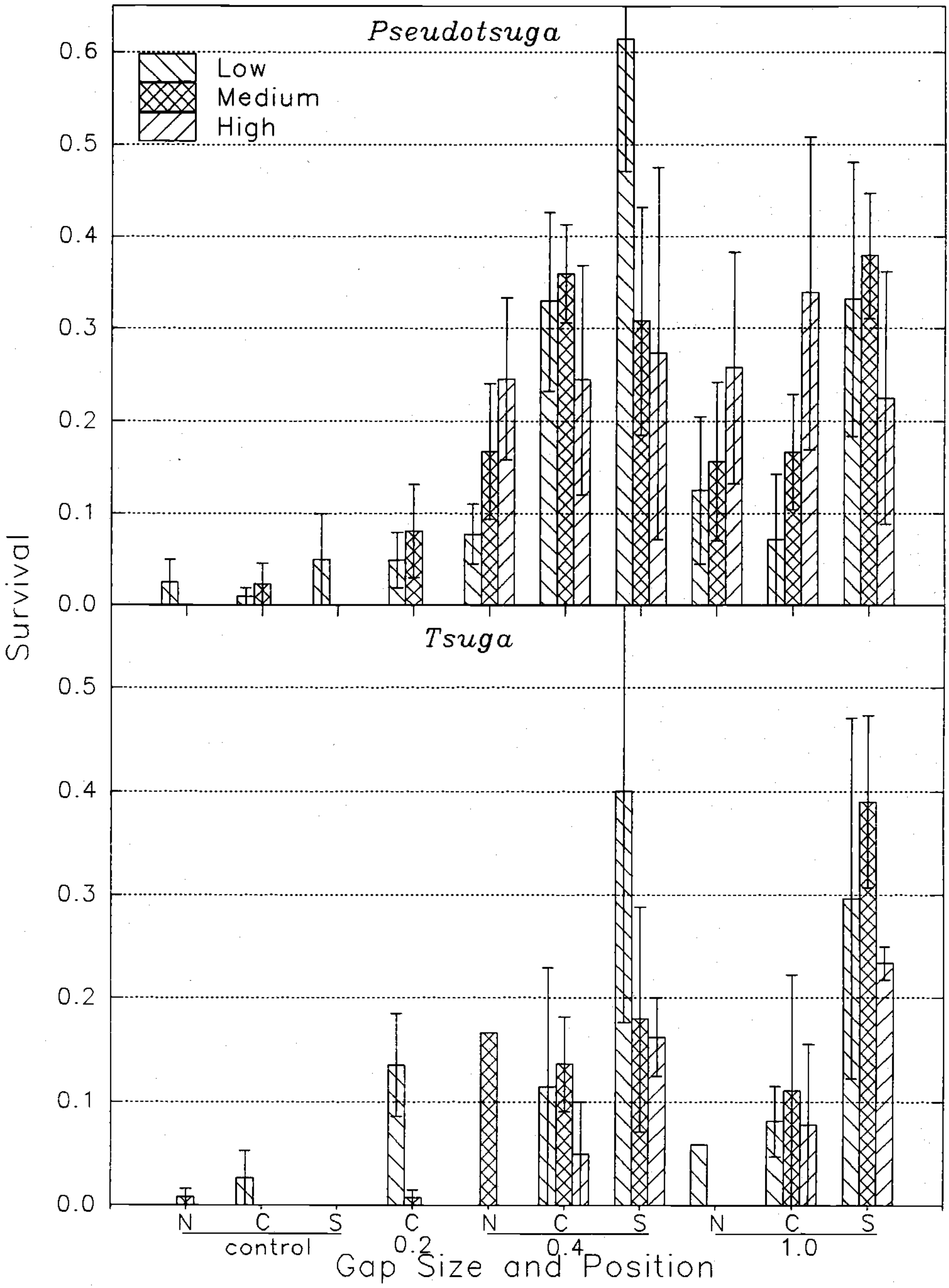

**Figure 3.12:** Survival of natural regeneration on forest floor by vegetation cover level, species, gap size, and within-gap position (North, Center, South). Data are means and standard errors of survival in replicate 1 gaps in all stands for *Pseudotsuga* ($n \leq 4$) and in old-growth stands for *Tsuga* ($n \leq 2$, depending on presence of seedlings).

south), suggesting amelioration of extreme temperatures by live shade in north positions, but competition, possibly for relatively low light levels, in south positions. Survival of *Tsuga* also tended to be lowest in high cover microsites in open-shaded locations, but did not appear to benefit from understory cover in exposed locations (0.4 and 1.0 north). There appeared to be an age by within-gap position interaction for *Pseudotsuga* ($p = .09$ in Table 3.18), where seedling survival in old-growth stands tended to be lower than survival in mature stands in north positions, but greater in south positions (Figure 3.13a). Examination of the data suggested this age class by position pattern was an aggregated result of greater survival under high cover, and lower survival under low cover, in mature stands compared to old-growth (Figure 3.13b). Since survival was similar across positions under high cover in mature stands, but declined greatly from south to north under low cover in old-growth stands, the aggregated result was greater survival in old-growth south positions and lower survival in old-growth north positions. While greater levels of soil moisture in the old-growth stands may account for greater survival in low cover microsites, biotic factors (*e.g.* predators, pathogens, or differences in the composition of vegetation) may have contributed to differences in survival in high cover microsites between age classes.

## Density of natural regeneration

Density of naturally regenerated *Pseudotsuga* after two growing seasons differed significantly by understory vegetation cover class and the gap size by substrate interaction (Table 3.20). Density of *Tsuga* differed significantly only by position, vegetation cover, and substrate (Table 3.21). Lack of greater significance in the analyses may be due to the lack of seedlings found in each of the gap size by position by understory cover levels (see Appendix). (At the $p < .15$ level, gap, position by cover, and substrate were also significant for *Pseudotsuga*, and gap by position and substrate were also significant for *Tsuga*.) Due to missing data, least-square means were not estimable for separation of means in significant factors.

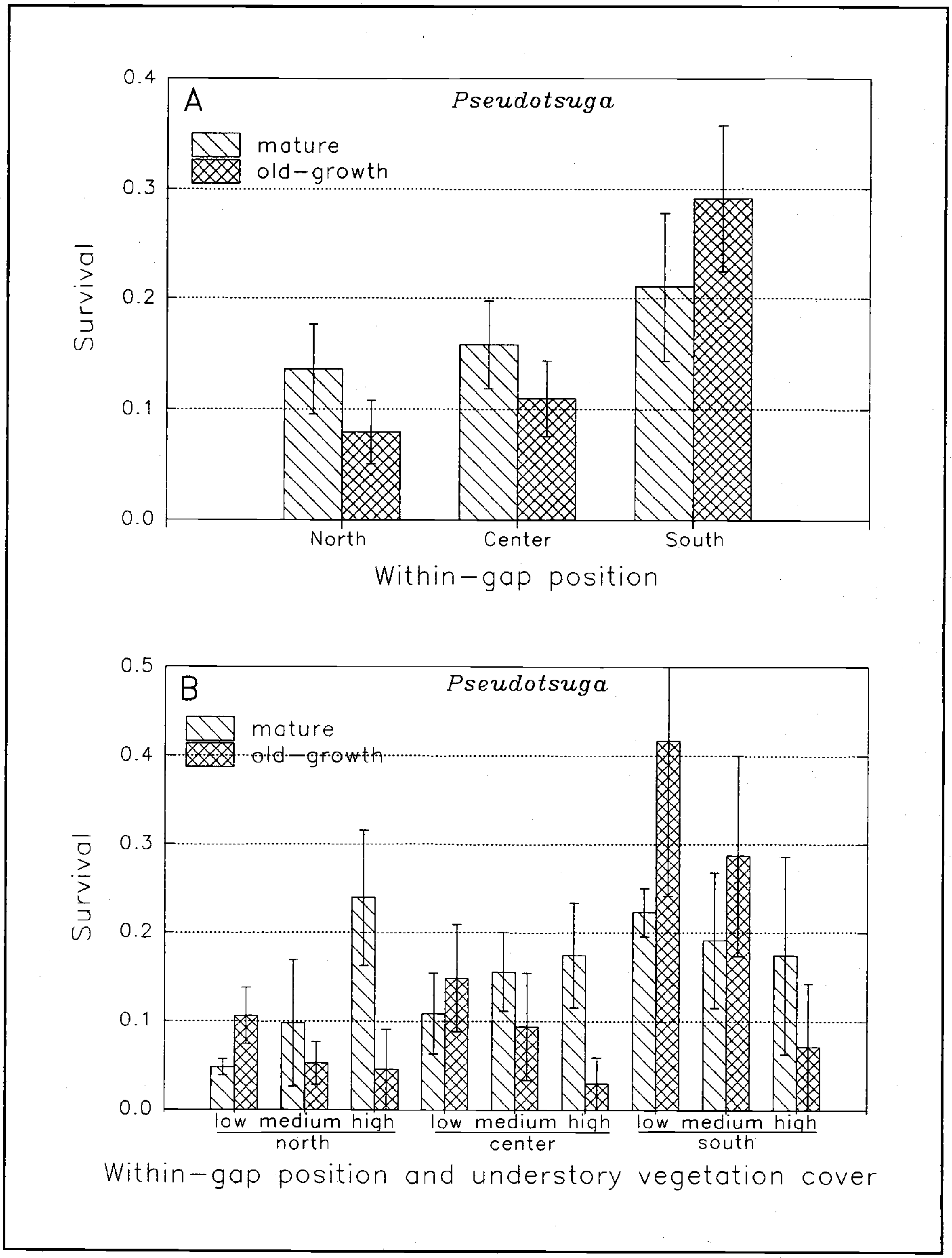

**Figure 3.13:** Age-class effects on survival of *Pseudotsuga* natural regeneration on forest floor by (a) within-gap position and (b) within-gap position by vegetation cover level. Data are means and standard errors of survival in all replicate 1 gaps of two stands per age class (n=2).

**Table 3.20:** Results of ANOVA on density of naturally regenerated *Pseudotsuga* seedlings. Separate analyses were done for understory cover (over litter only) and substrate. Factor abbreviations are: gap= gap size, pos= within-gap position, covr= understory cover level, subs= substrate. Significant effects (p < .05) are marked with asterisks (*).

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| gap | 4 | 3.54626 | 2.14 | 0.1262 |
| Error: gap(stand) | 15 | 1.65822 | | |
| pos | 2 | 0.27094 | 0.35 | 0.7090 |
| gap*pos | 6 | 0.62661 | 0.81 | 0.5745 |
| Error: gap*pos(stand) | 24 | 0.77646 | | |
| covr | 2 | 5.38679 | 7.07 | 0.0024 * |
| gap*covr | 8 | 0.62494 | 0.82 | 0.5898 |
| pos*covr | 4 | 1.39962 | 1.84 | 0.1409 |
| gap*pos*covr | 12 | 0.93350 | 1.22 | 0.3007 |
| Error: gap*pos *covr(stand) | 40 | 0.76223 | | |
| Total | 117 | | | |

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| gap | 4 | 9.46057 | 2.20 | 0.1178 |
| Error: gap(stand) | 15 | 4.29199 | | |
| subs | 3 | 1.74618 | 2.14 | 0.1123 |
| gap*subs | 12 | 2.11055 | 2.59 | 0.0140 * |
| Error: gap*subs(stand) | 35 | 0.81450 | | |
| Total | 69 | | | |

Several trends were identified in the data which may be of biological significance, however. Density of *Pseudotsuga* tended to be lower on high cover plots than on low and medium cover plots, while density of *Tsuga* tended to decrease with cover level (Figure 3.14). Both species were least dense on litter, while *Pseudotsuga* tended to be most abundant on skirts, and *Tsuga* tended to be most abundant on class III logs. There were few discernible trends with level of understory cover by positions within different gap sizes (Figure 3.15). Comparing the centers of the larger gaps, density of *Pseudotsuga* tended to be highest under low cover in 0.4 and 0.6 gaps, but relatively similar across cover types in gap size 1.0. (Results from North and South

**Table 3.21:** Results of ANOVA on density of naturally regenerated *Tsuga* seedlings. Separate analyses were done for understory cover (over litter only) and substrate. Factor abbreviations are: gap= gap size, pos= within-gap position, covr= understory cover level, subs= substrate. Gap*pos(stand) error term was left out of the model because Mean Square was less than that of gap*pos*covr(stand). Significant effects (p < .05) are marked with asterisks (*).

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| gap | 4 | 9.83527 | 0.60 | 0.6797 |
| Error: gap(stand) | 5 | 16.39923 | | |
| pos | 2 | 36.14142 | 11.05 | 0.0008 * |
| gap*pos | 6 | 6.64823 | 2.03 | 0.1168 |
| Error: gap*pos(stand) | | **n.a.** | | |
| covr | 2 | 2.30114 | 0.70 | 0.5085 |
| gap*covr | 8 | 2.65004 | 0.81 | 0.6030 |
| pos*covr | 4 | 1.42148 | 0.43 | 0.7817 |
| gap*pos*covr | 10 | 0.72238 | 0.22 | 0.9903 |
| Error: gap*pos *covr(stand) | 17 | 3.26934 | | |
| Total | 58 | | | |

| Source | DF | Mean Square | F Value | Pr > F |
|---|---|---|---|---|
| gap | 4 | 31.84233 | 0.60 | 0.6774 |
| Error: gap(stand) | 5 | 52.73823 | | |
| subs | 3 | 12.42646 | 2.81 | 0.1082 |
| gap*subs | 12 | 3.59014 | 0.81 | 0.6415 |
| Error: gap*subs(stand) | 8 | 4.42866 | | |
| Total | 32 | | | |

positions of gap sizes 0.4 and 0.6 are not reliable due to low sample sizes [*e.g.* the high density of both species on medium cover in 0.4 South, and of *Pseudotsuga* on medium cover in 0.4 North, are due to seedlings on one class V log plot in each position]). Comparing positions within gap size 1.0, *Pseudotsuga* density tended to be highest under high cover in North positions, and lowest under high cover in south positions. Density of *Tsuga*, on the other hand, tended to be highest under low cover, with no apparent benefit from cover in exposed locations (*e.g.* 1.0 North).

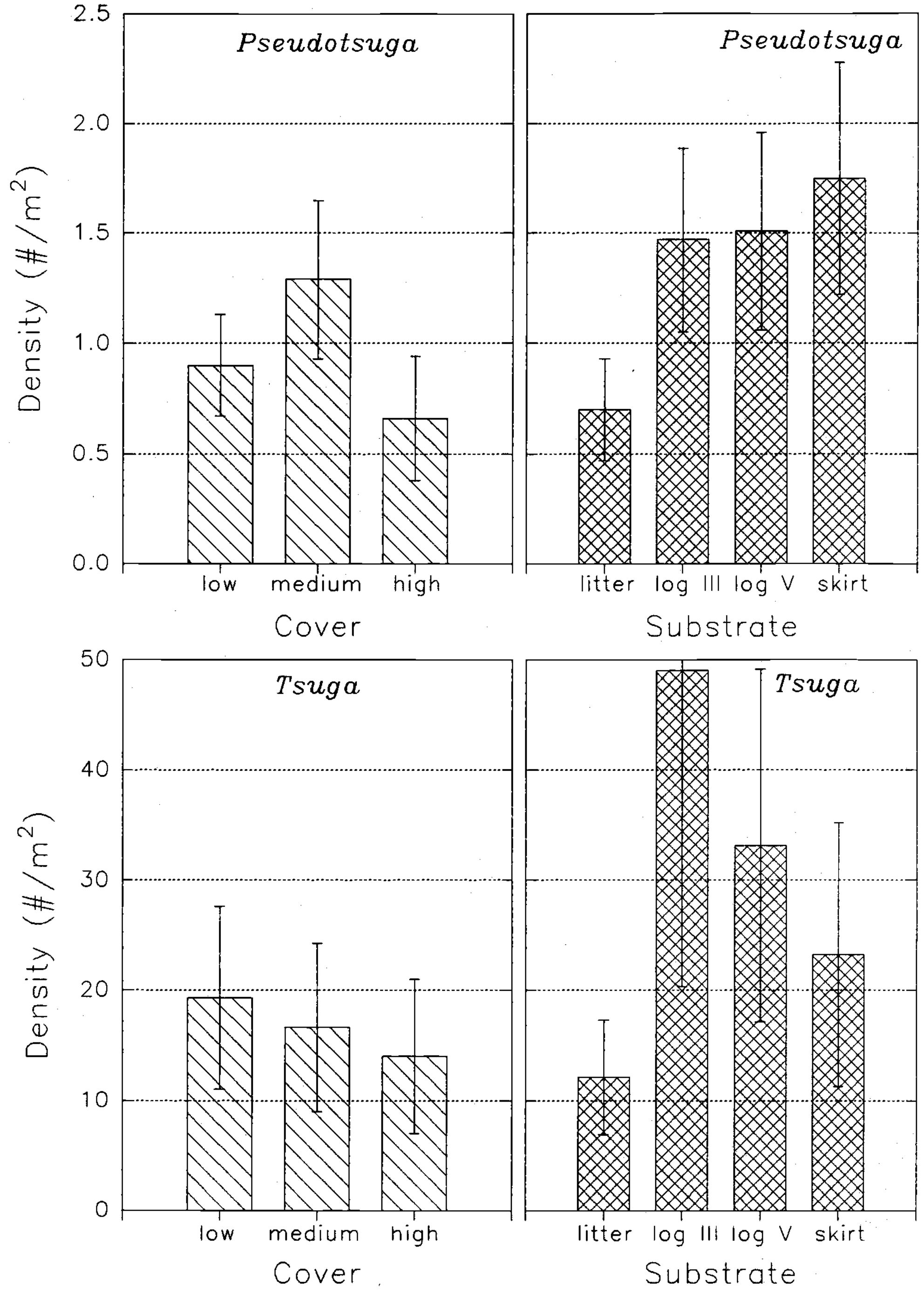

**Figure 3.14:** Density of natural regeneration by species for cover level and substrate. Data are means and standard errors (weighted by number of sample plots) from all stands for *Pseudotsuga* and from old-growth stands for *Tsuga*.

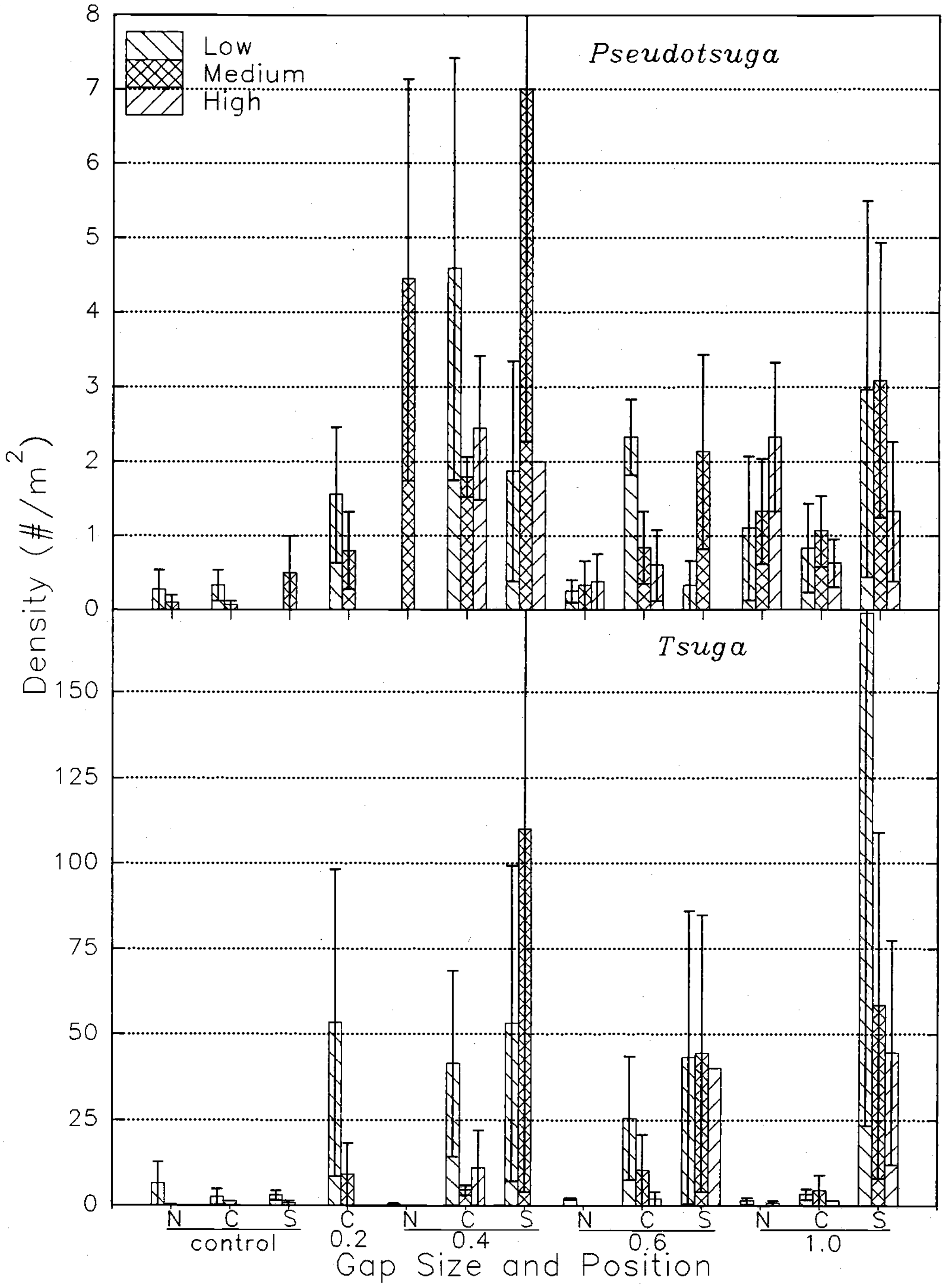

**Figure 3.15:** Density of natural regeneration by species, cover level, gap size, and within-gap position. Data are means and standard errors (weighted by number of sample plots) from all stands for *Pseudotsuga* and from old-growth stands for *Tsuga*.

Patterns of seedling density by substrate class were highly variable among gap sizes. The greatest substrate effect occurred in 0.4 gaps, where density of both species was greater on logs and skirts than on litter compared to other gaps (Figure 3.16). While class III logs appeared to be important in some gaps, sample sizes were low and variable among gaps. It is important to point out that although few *Tsuga* from the 1992 cohort established on decayed wood in controls, many of these substrates were already occupied by previous seedling cohorts, occasionally at densities as high as 200 seedlings in a .25 $m^2$ plot. In addition, although there were no *Abies* germinants in 1992, older seedlings were present on litter in most gaps and controls in stand TCO.

The pattern found in Chapter 2 (Figure 2.11) of increasing density of *Pseudotsuga* from north to south positions in old-growth stands, and the lack of pattern in mature stands appears to be due to differences in availability of substrates between age classes. Seedling density was greater in south positions in old-growth than in mature stands regardless of cover, and was lower in north positions in old-growth, even under medium cover (Figure 3.17a). The differences between age-classes for south positions become much less pronounced when considering litter plots alone, however (Figure 3.17b), suggesting that the greater abundance of class V logs and skirts in the old-growth stands (Table 3.22) may aid seedling establishment in open-shade (south) locations of gaps.

Correlations of seedling density with cover of vegetation and substrate in sample plots generally confirm the analysis above, which classified plots into cover levels and substrate categories, but are interesting due to the high correlation between cover of skirt material and seedling density (Table 3.23). The correlations also illustrate negative associations of north positions and litter with seedling density.

### Size of natural regeneration

Measurements of seedling size from the microsite survey study displayed strong patterns across the two 1.0 gaps, particularly in stand TCO, where seedling

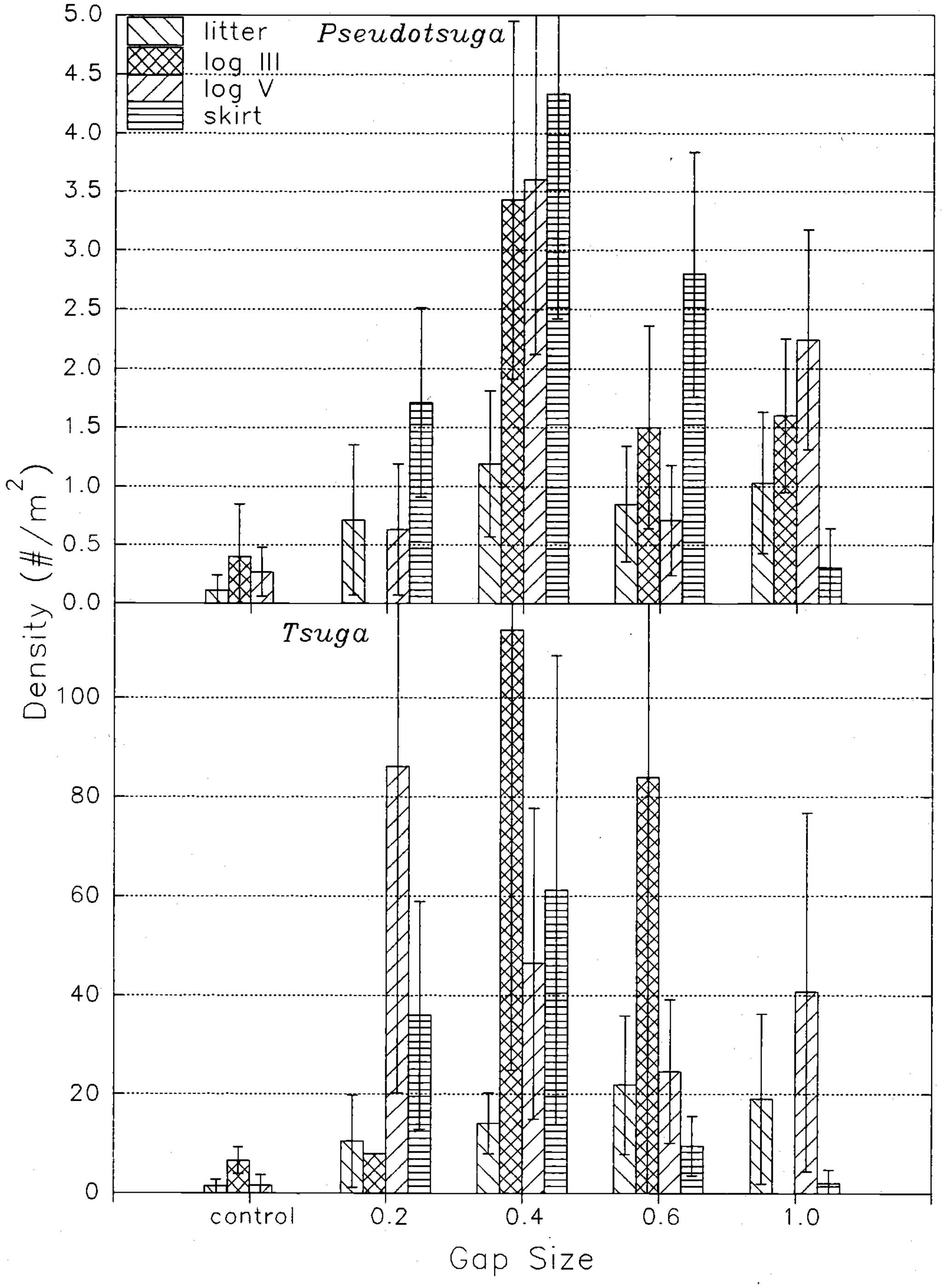

**Figure 3.16:** Density of natural regeneration by species, substrate, and gap size. Data are means and standard errors (weighted by number of sample plots) from all stands for *Pseudotsuga* and from old-growth stands for *Tsuga*.

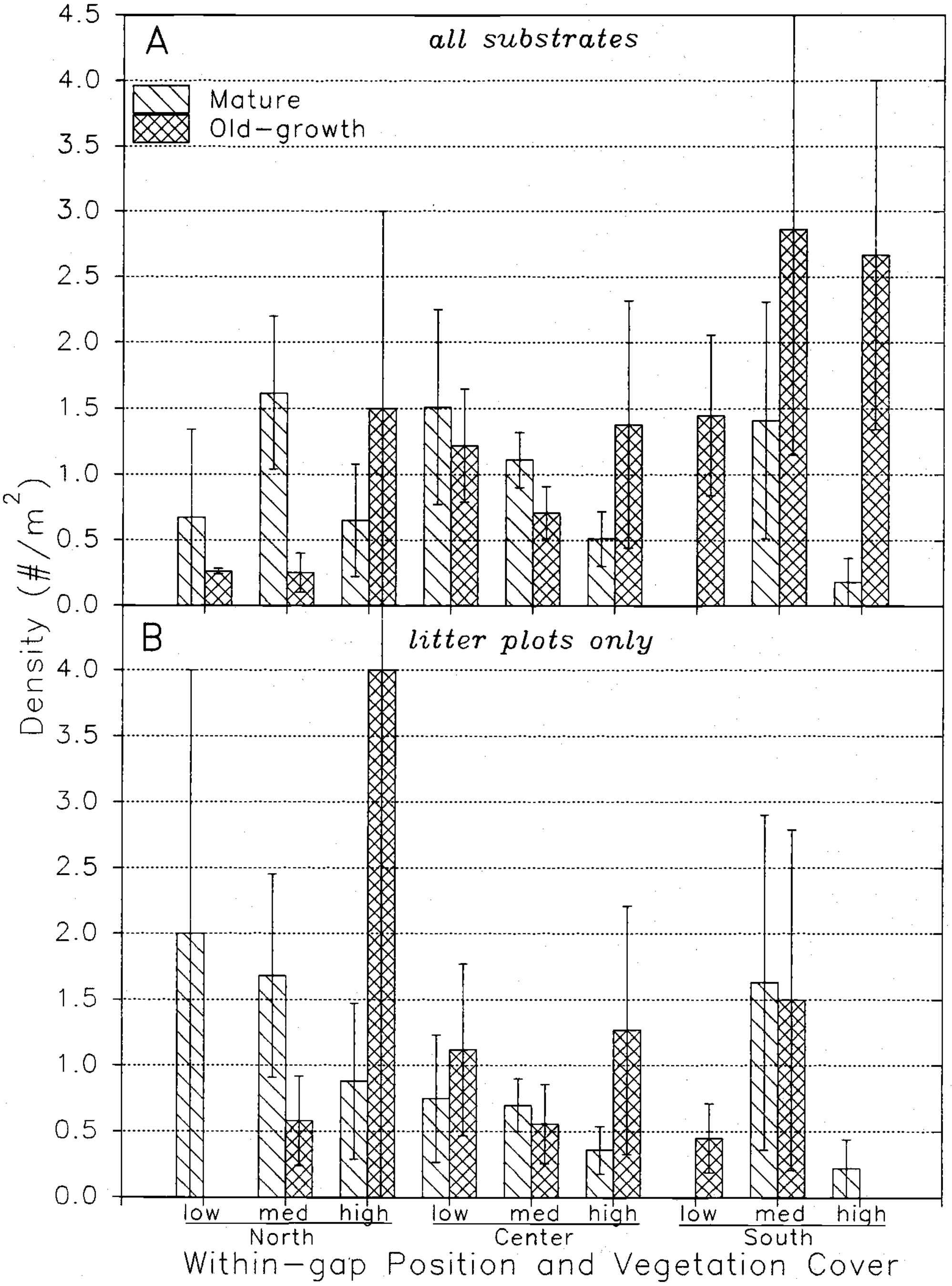

**Figure 3.17:** Vegetation cover level effects on density of *Pseudotsuga* natural regeneration by within-gap position for (a) all substrates combined, and (b) litter plots only. Data are means and standard errors for all gaps from each stand within an age class ($n \leq 2$).

**Table 3.22:** Understory vegetation density, cover of substrates, and litter depths of the four stands in the experimental gap study. Covers are sums of individual species' cover estimates, with "understory" generally referring to vegetation less than 1 m in height, and mid-story to vegetation 1-5 m in height.

| Stand name: | HJA | TCO | MCY | PCM |
|---|---|---|---|---|
| Mean vegetation cover (%) | | | | |
| Understory bryophytes | 7.3 | 8.1 | 9.6 | 5.0 |
| Understory herbs | 4.9 | 9.3 | 0.8 | 26.7 |
| Understory shrubs | 9.4 | 26.8 | 46.9 | 35.6 |
| Mid-canopy trees | 4.2 | 5.8 | 43.4 | 34.6 |
| Mean cover of substrates (%) | | | | |
| Mineral soil | 0.8 | 0.1 | 0.4 | 0.5 |
| Forest floor | 47.8 | 42.3 | 62.8 | 80.2 |
| Class III + IV logs | 9.6 | 8.5 | 12.5 | 2.4 |
| Class V logs | 24.5 | 31.4 | 14.1 | 6.2 |
| Organic "skirts" | 8.1 | 10.0 | 3.7 | 5.4 |
| Mean litter depth (cm) | | | | |
| L layer | 0.6 | 0.4 | 0.5 | 0.4 |
| F layer | 1.5 | 1.1 | 1.1 | 0.9 |
| H layer | 1.1 | 3.3 | 0.4 | 0.6 |
| Total | 3.2 | 4.8 | 2.0 | 1.9 |

height peaked just north of gap center and declined towards the north and south edges (Figure 3.18). The dampened pattern in the PCM gap may be due to the greater cover of understory vegetation in that gap compared to the TCO gap. The peak in *Pseudotsuga* height just north of gap center in stand TCO may reflect a zone of moderately high light with moderate temperatures and high soil moisture (soil moisture tended to decline near gap edges). Heights of *Tsuga* seedlings in the TCO 1.0 gap followed a similar pattern as *Pseudotsuga*, except for a marked dip and rise in height south of gap center. Examination of the data revealed no obvious differences in substrate or vegetation cover among seedlings between 4 m north and 12 m south of gap center; trampling by researchers in the high-use area around gap center may have somehow damaged seedlings in that area. *Pseudotsuga* seedlings

**Table 3.23:** Correlations between density of naturally regenerated seedlings and measured variables averaged for each position within each gap. Pearson correlation coefficients and probability of Type I error are shown for correlations with p-values less than 0.20. Factor abbreviations are: gap= gap size, pos= within-gap position, covr= cover of understory vegetation (less moss), litter= cover of forest floor, log3= cover of class III and class IV log, log5= cover of class V log, and skirt= cover of organic "skirts" around tree boles. Gap size for controls was set at 0.05, and values for north, center, and south positions were 3, 2, and 1, respectively (n= 104 for *Pseudotsuga*, n= 52 for *Tsuga*).

| | Correlation | Pr > \|R\| |
|---|---|---|
| *Pseudotsuga* | | |
| skirt | 0.423 | 0.0001 |
| gap*skirt | 0.291 | 0.0038 |
| covr*skirt | 0.288 | 0.0043 |
| litter | -0.149 | 0.1441 |
| pos | -0.141 | 0.1546 |
| gap*covr*skirt | 0.134 | 0.1893 |
| *Tsuga* | | |
| covr*skirt | 0.630 | 0.0001 |
| skirt | 0.627 | 0.0001 |
| gap*skirt | 0.493 | 0.0006 |
| gap*covr*skirt | 0.445 | 0.0022 |
| pos | -0.382 | 0.0052 |
| litter | -0.305 | 0.0416 |
| pos*covr*skirt | 0.249 | 0.0994 |
| pos*covr*litter | -0.197 | 0.1939 |

tended to be taller in the centers of the 0.2 gaps in stand TCO, while *Tsuga* seedling heights increased slightly from south to north.

## Microsite survey

Microsites occupied by seedlings differed from randomly located microsites in a variety of ways. Seedling microsites of *Tsuga* differed more frequently from random microsites than did *Pseudotsuga* microsites (Table 3.24). For *Pseudotsuga*, shrub cover was significant in PCM 1.0 Center, substrate and herb cover were

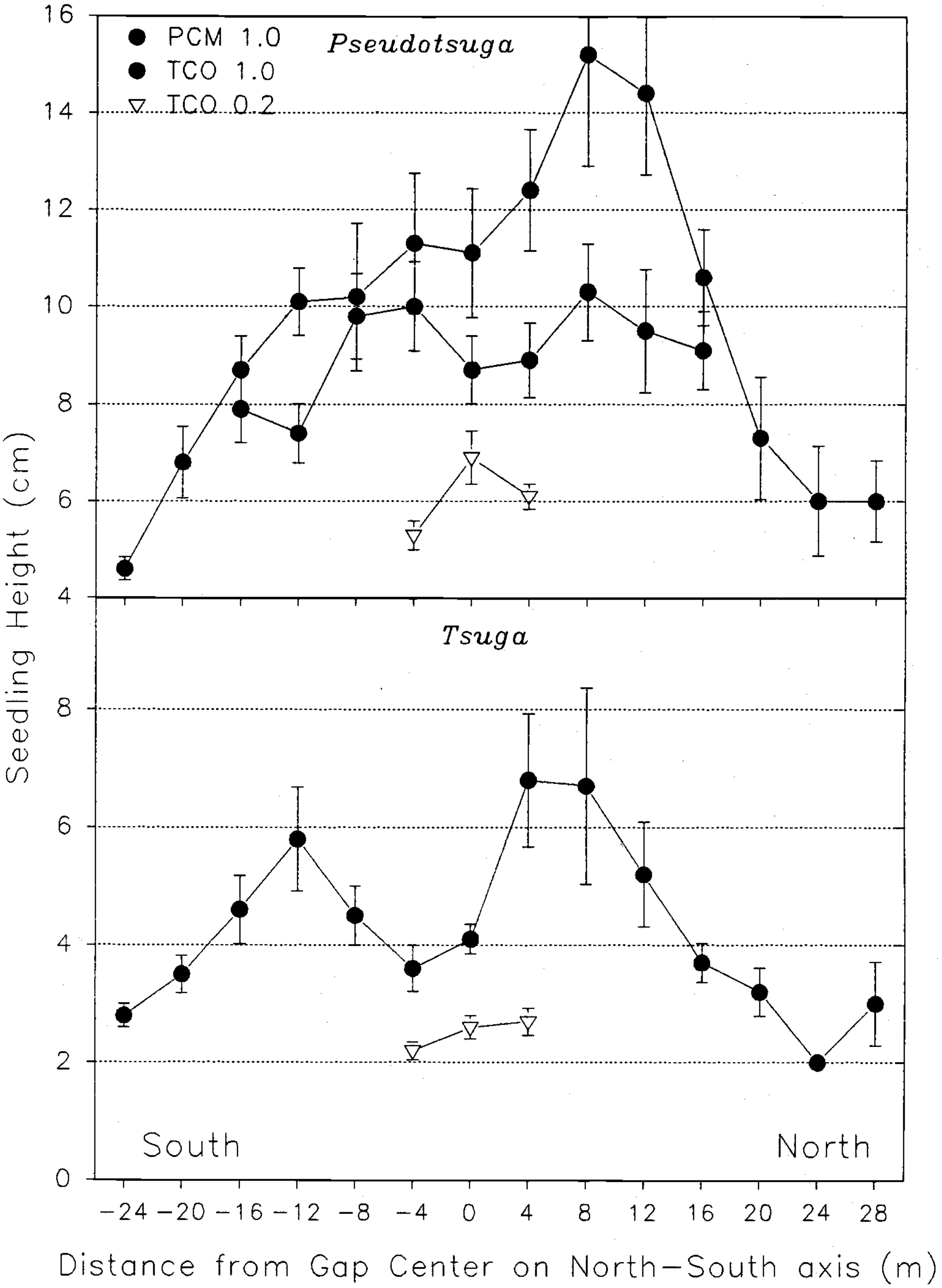

**Figure 3.18:** Heights of 1992 cohort seedlings by species and position on north-south transect in 10. and 0.2 gaps. Positions are distances in meters from gap centers, with negative numbers= south. Data are means and standard errors of seedlings at each position (n≤15 for 1.0 gaps, n≤18 for 0.2 gaps, depending on presence of seedlings.

**Table 3.24:** Comparison of microsite characteristics between naturally regenerated seedlings and randomly located plots by gap and within-gap position, using Chi-square tests for categorical variables and T-tests for numerical variables. Species abbreviations are: PSME= *Pseudotsuga menziesii*, TSHE= *Tsuga heterophylla*. Probabilities less than 0.10 are shown in bold type. Chi-square test results of "NA" were unavailable due to contingency table row or column sums equal to zero.

| | | | South shade | | Dead shade | | Substrate | | Total cover | | Herb Cover | | Shrub cover | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Gap | Spp | Pos | $X^2$ | P> $X^2$ | $X^2$ | P> $X^2$ | $X^2$ | P> $X^2$ | T | P>\|T\| | T | P>\|T\| | T | P>\|T\| |
| PCM 1.0 | PSME | North | 3.66 | 0.056 | NA | NA | 3.73 | 0.292 | 1.26 | 0.211 | -0.54 | 0.591 | 1.58 | 0.119 |
| PCM 1.0 | PSME | Center | 1.75 | 0.186 | 1.01 | 0.315 | NA | NA | -0.29 | 0.774 | 1.81 | 0.074 | -2.16 | **0.034** |
| PCM 1.0 | PSME | South | 3.63 | 0.057 | 2.09 | 0.148 | NA | NA | -1.55 | 0.126 | -0.70 | 0.489 | -0.46 | 0.644 |
| TCO 1.0 | PSME | North | 0.41 | 0.817 | 0.29 | 0.592 | 9.13 | **0.028** | -1.15 | 0.250 | -4.19 | **0.000** | 1.65 | 0.100 |
| TCO 1.0 | PSME | Center | 2.77 | 0.250 | 3.04 | 0.081 | 2.20 | 0.532 | 0.00 | 0.998 | -0.18 | 0.861 | 0.17 | 0.868 |
| TCO 1.0 | PSME | South | 5.47 | 0.065 | 0.33 | 0.568 | 5.48 | 0.140 | -0.07 | 0.946 | -1.37 | 0.174 | 1.02 | 0.308 |
| TCO 1.0 | TSHE | North | 18.90 | **0.000** | 32.59 | **0.000** | 50.03 | **0.000** | 2.30 | **0.023** | 4.58 | **0.000** | -0.57 | 0.571 |
| TCO 1.0 | TSHE | Center | 4.02 | 0.134 | 0.17 | 0.683 | 6.05 | 0.109 | -0.80 | 0.427 | 0.69 | 0.495 | -1.60 | 0.112 |
| TCO 1.0 | TSHE | South | 5.68 | 0.059 | 0.21 | 0.649 | 1.43 | 0.699 | -0.54 | 0.587 | 0.06 | 0.954 | -0.74 | 0.463 |
| TCO 0.2 | PSME | Center | 6.60 | **0.037** | 1.12 | 0.291 | 2.64 | 0.450 | -0.82 | 0.414 | -2.22 | **0.029** | 1.57 | 0.120 |
| TCO 0.2 | TSHE | Center | 12.27 | **0.002** | 0.15 | 0.696 | 1.53 | 0.675 | 0.17 | 0.867 | 2.64 | **0.010** | -2.28 | **0.024** |

significant at TCO 1.0 North, and south shade and herb cover were significantly different in the TCO 0.2 gap sizes. For *Tsuga*, all factors except shrub cover were significant at TCO 1.0 North, while south shade, herb cover, and shrub cover were significant in the 0.2 size gaps in stand TCO. *Tsuga* seedlings were more common in microsites with high levels of south shade in North positions of TCO 1.0 than would be expected from random selection, and tended to be more common in microsites with low levels of south shade in South positions of the same gap and in the TCO 0.2 size gaps (Figure 3.19). Most of the south shade for *Tsuga* in North positions of TCO 1.0 was in the form of dead shade provided by logs (as small as 10 cm in diameter), old snags, and cut stumps. *Pseudotsuga* tended to be more common in low- or no-south shade microsites than would be expected from random selection in all gap sizes and positions except for TCO 1.0 North.

Differences in vegetation cover between seedling microsites and random microsites were greatest in the most exposed and most shaded gap locations examined. Cover over *Tsuga* seedlings in the north position of TCO 1.0 was significantly lower than cover over random microsites, primarily due to differences in herb cover (Figure 3.20). Herb cover over *Pseudotsuga* seedlings in the same location was also significantly lower than herb cover over random microsites. Microsites of both species in the 0.2 gaps also had lower herb cover than random microsites (Figure 3.21). Low establishment in microsites with high herb cover may be due to competition from herb roots (which are most likely shallower than shrub roots) in hot, dry locations (1.0 North) and from shade by low herb canopies in low-light locations (0.2 gaps).

*Pseudotsuga* and *Tsuga* seedlings tended to be less common on litter than would be expected from random establishment (Figure 3.22). In the north position of TCO 1.0 in particular, *Tsuga* were found on class III logs and skirts and *Pseudotsuga* were found on class V logs and skirts more frequently than would occur from random establishment with regard to substrate. (PCM 1.0 is not shown due to low abundance of non-litter substrates.)

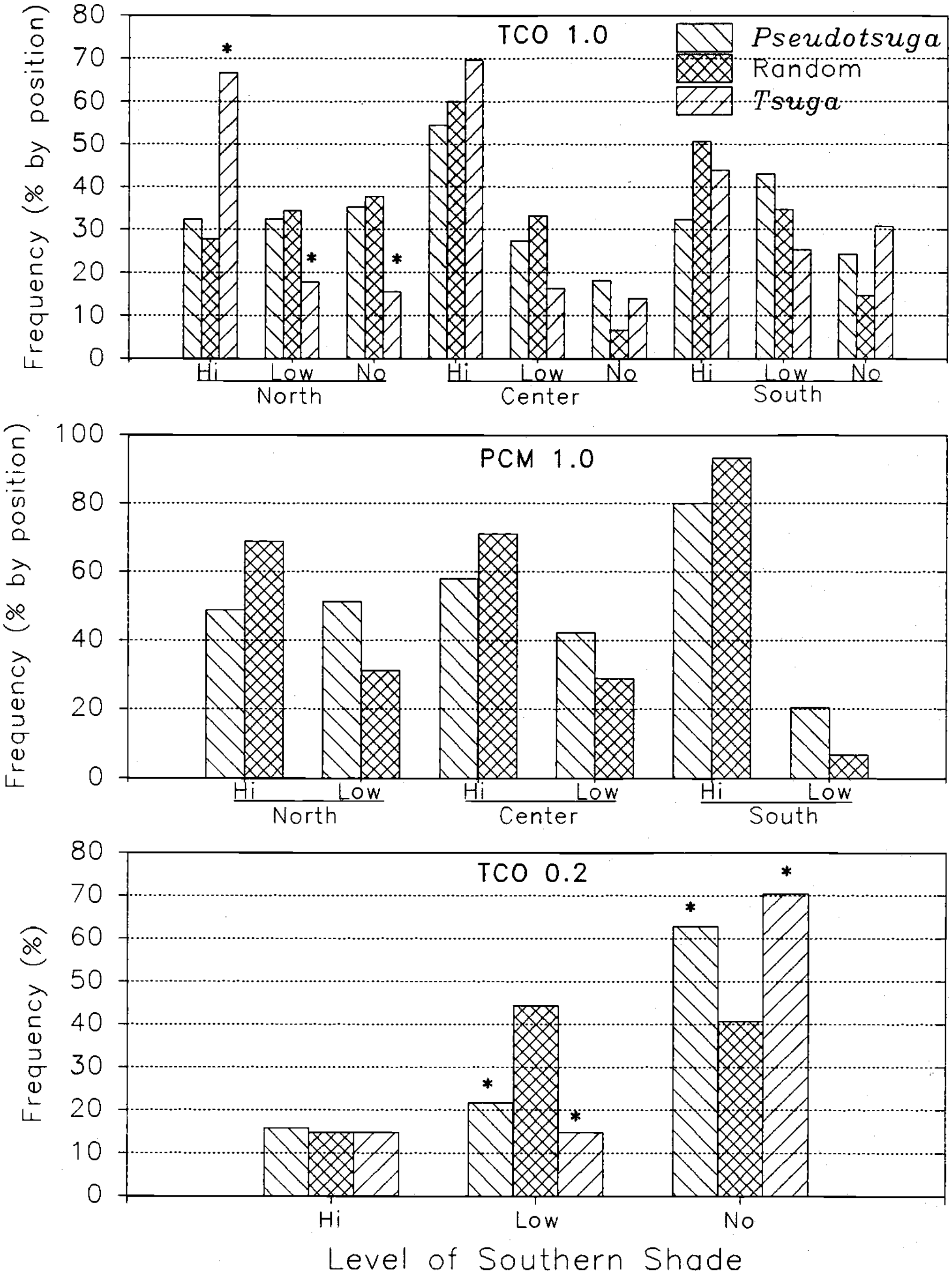

**Figure 3.19:** Frequency of occurrence of southern-shade levels for random microsites and microsites in which *Pseudotsuga* and *Tsuga* were found, in two 1.0 and 0.2 size gaps (0.2 gap data combined).

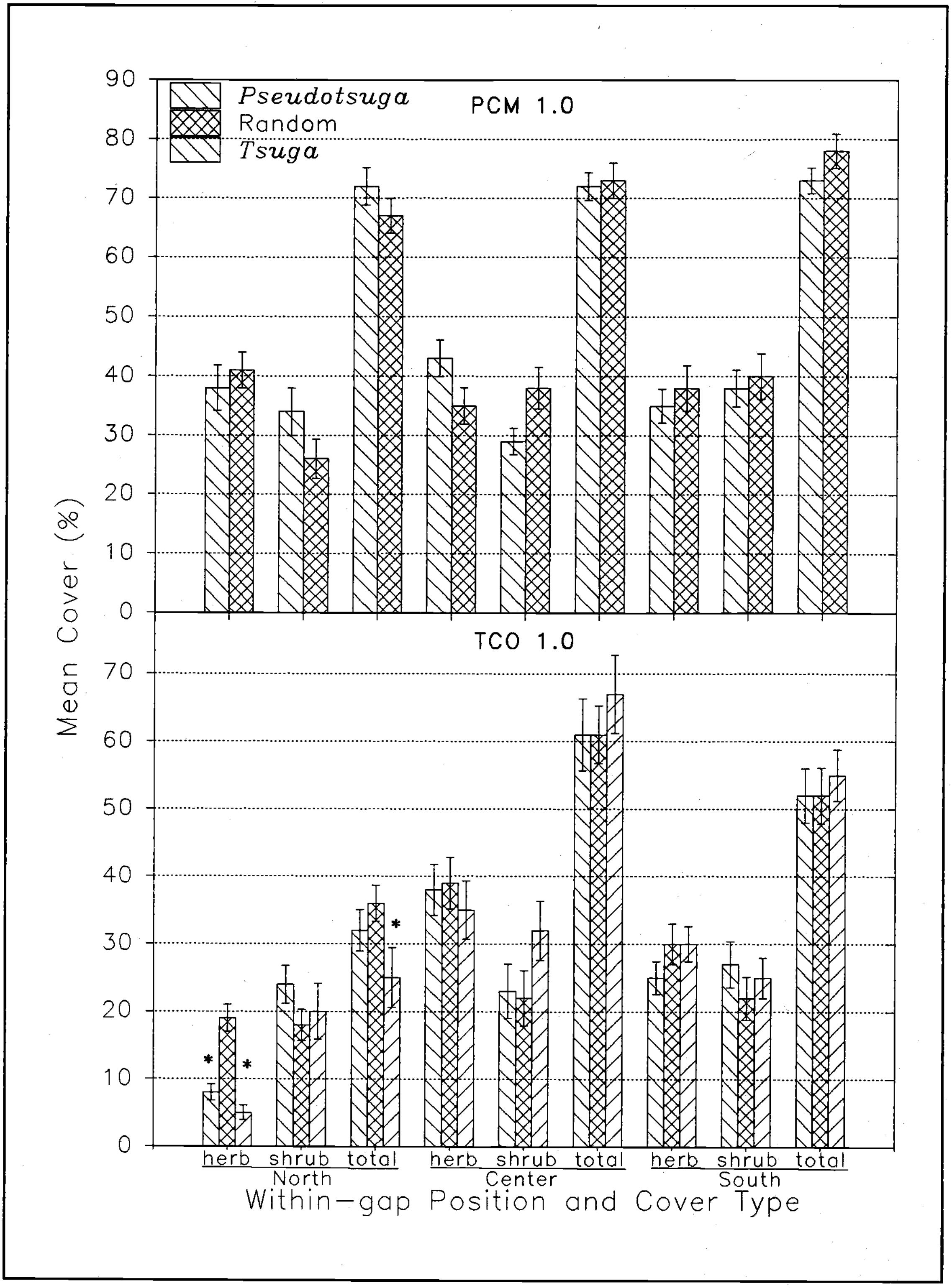

**Figure 3.20:** Mean cover of herbs, shrubs, and total herb and shrub for random microsites and microsites in which *Pseudotsuga* and *Tsuga* were found for two 1.0 size gaps.

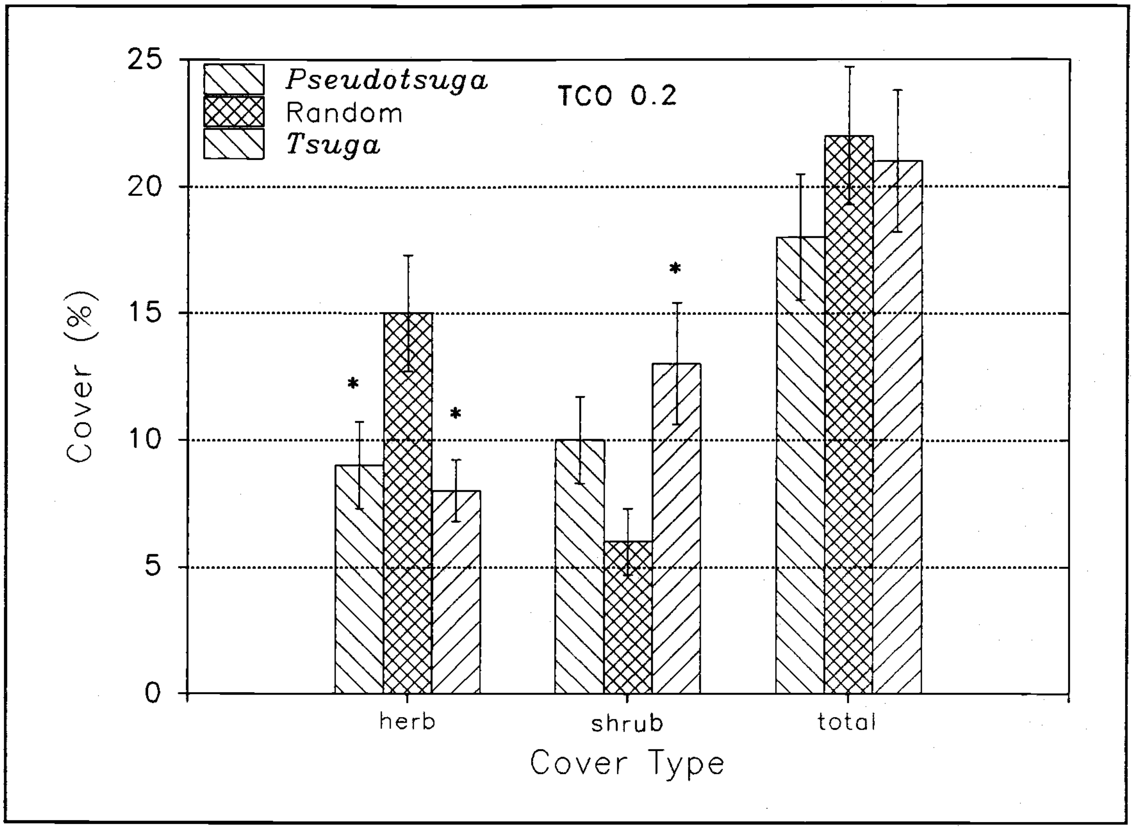

**Figure 3.21:** Mean cover of herbs, shrubs, and total herb and shrub for random microsites and microsites in which *Pseudotsuga* and *Tsuga* were found, in combined data for two 0.2 size gaps.

## Discussion

### Substrate effects

Tree seedling establishment varied dramatically with substrate type and among gap sizes in this study. Seedling establishment on decayed wood seed-plots was significantly greater than establishment on forest floor and mineral soil in closed-canopy areas and small gaps, and the difference was greatest for *Tsuga heterophylla* and least for *Pseudotsuga menziesii*. Substrate effects on establishment of naturally regenerated seedlings was more variable, however, with little or no apparent

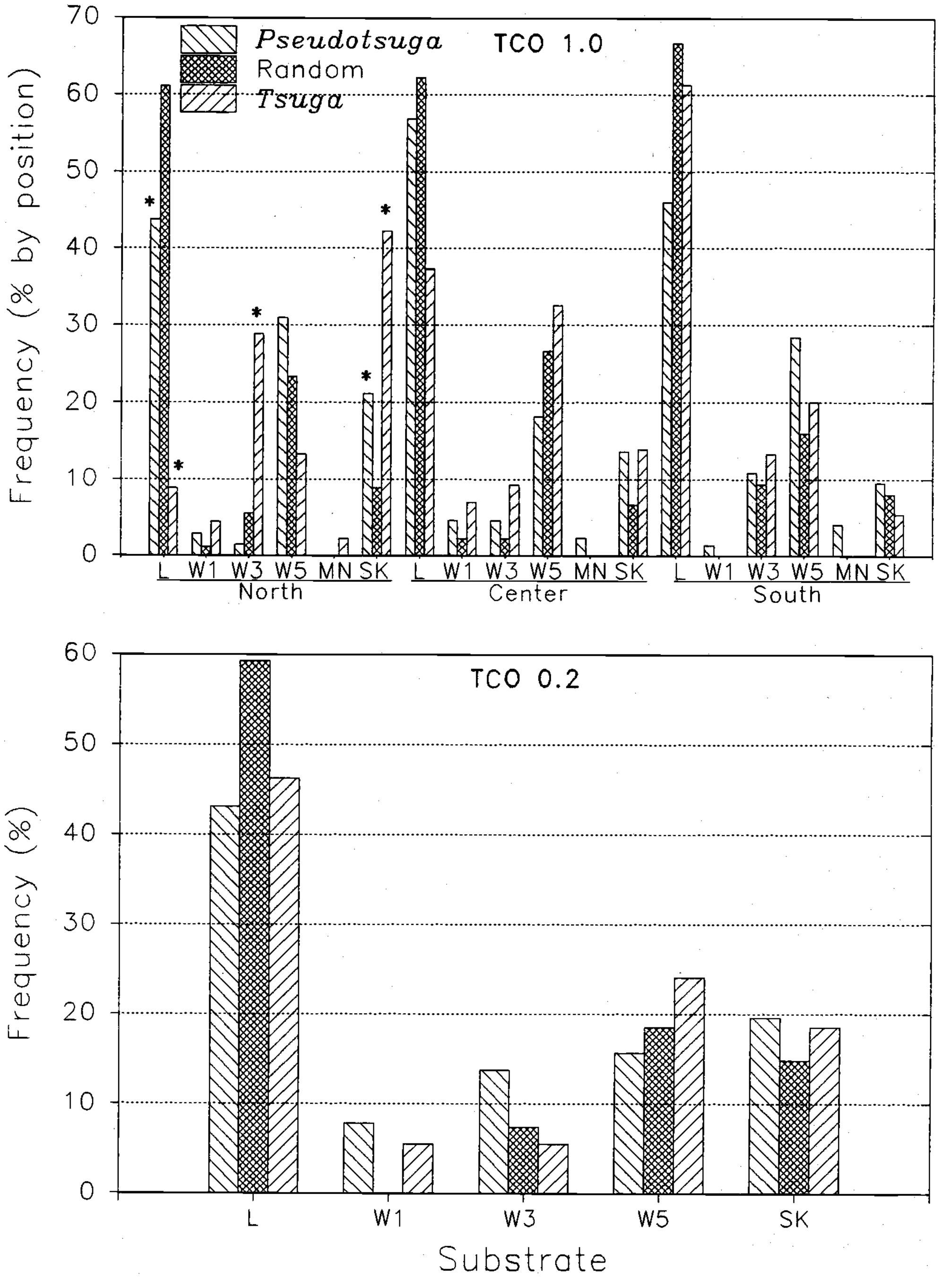

**Figure 3.22:** Frequency of occurrence of substrates for random microsites and microsites in which *Pseudotsuga* and *Tsuga* were found, in two 1.0 and 0.2 size gaps (0.2 gap data combined). Substrate types are: L=litter, W1, W3, and W5=class I, III, and V log, respectively, MN=mineral soil, and SK=skirt.

difference between establishment on decayed logs and on the forest floor in controls and 0.2 gaps (Figure 3.11, 3.16, and 3.22). These differences in establishment between experimental substrates and naturally decayed logs may be due to the uniformly soft surface of experimental seed-plots providing easy penetration for radicles of germinating seedlings, compared to the highly variable quality of decayed logs, which often had patches of hard outer "shell" and bark. The suitability of wood for establishment varies with species, decay class, and origin (*e.g.* from standing snag or blowdown) (Christy and Mack 1984, Minore 1972, Thornburgh 1969). In addition, soft areas of decayed logs were often densely occupied by previous cohorts of *Tsuga* seedlings and woody shrubs (*e.g. Vaccinium* spp.), and riddled with roots (particularly the older class IV and V logs), which may have precluded establishment of new seedling cohorts; live roots and vegetation were absent from seed-plots. Thus the experimental wood seed-plots appear to represent idealized conditions for seedling establishment on wood, while the patchy distribution of high densities of pre-1992 seedling cohorts on natural logs suggests a more variable effect on natural regeneration. Other studies indicate that decayed wood is typically the only substrate on which *Tsuga heterophylla* establishes in closed-canopy areas within forests (Minore 1972, Christy and Mack 1984, Harmon and Franklin 1989). Greater establishment on decayed wood than on the forest floor in closed-canopy areas may due to the greater moisture content of wood (Harmon *et al.* 1986, Chapter 4 [Figure 4.4]).

The effect of substrates on seedling establishment varied with gap size. Seedling establishment was lower in closed-canopy areas than in 0.2 gaps on all substrates (the 0.2 gap size appears to be the most common gap size in Cascade forests [Spies *et al.* 1990]). Differences between establishment on wood and on forest floor appeared to be greater in closed-canopy areas than in 0.2 gaps, and may be related to substrate moisture content. Forest floor moisture levels were greater in 0.2 gaps, while decayed wood moisture levels were similar between closed-canopy areas and 0.2 gaps (Table 3.1, Chapter 4 [Figure 4.4], Gray and Spies 1993). Differences between establishment on wood and on forest floor were even lower (and not significant) in 0.4 gaps than in 0.2 gaps; forest floor moisture content tended to be higher in 0.4 gaps, while wood moisture content was a bit lower. Minore (1972) also found no difference in seedling survival between wood and litter substrates (or lower survival on wood for some species) in green-house studies where moisture levels were kept high. In contrast to the apparent lack of a substrate effect for natural regeneration in controls, establishment appeared to be greater on logs than on forest floor in gaps, particularly in shaded south locations (Figure 3.11 and 3.16). Greater precipitation in gaps (Geiger 1965, Canham 1993) and higher light levels may have provided sufficient resources for new seedling establishment on logs that were already occupied by vegetation.

Thus seedling establishment in the gaps in this study was much less restricted to wood than in closed-canopy areas. The relative advantage of decayed wood over the other substrates for *Tsuga* establishment declined with increasing gap size; Minore (1972) noted a similar trend with increasing canopy openness. Other studies have found that *Tsuga* establishment in small gaps occurs primarily on logs (Stewart 1986a, Thornburgh 1969, Lertzman and Krebs 1991). This difference between studies may be due to the latter three studies being conducted at higher elevations where duration of snowpack may be a limitation on seedling germination and survival and where forest floors tend to be deeper (Thornburgh [1969] noted that *Tsuga* in gaps was not limited to logs at lower elevations).

Class V logs, which tend to be the most abundant decay class of wood in most forests (Table 3.22), are generally poor substrates for establishment in closed forests (Christy and Mack 1984), but I found them to be quite good for establishment in shaded portions of larger gaps (Figure 3.16 and 3.22). A possible reason for this change in suitability is that logs tend to be occupied by tree roots much more than by non-tree roots (Harvey *et al.* 1987, Vogt *et al. in preparation*), so buried (class V) logs that are accessible to roots of mature trees are relatively dry in closed-canopy areas (*unpublished data*). With the decrease in conifer root density associated with large gaps (Parsons *et al.* 1994), class V logs (and some of the class IV logs used in the natural regeneration survival study) may have been relatively unoccupied by roots compared to the surrounding soil, where understory vegetation response was high. The strong association I found between seedling density in gaps and skirts (Table 3.23 and Figure 3.16 and 3.22) has not been described in the literature before; it may be that the very high incidence of mycorrhizae in skirts (Vogt *et al. in preparation*) aids seedling establishment, particularly in gaps where conifer roots don't dry them out.

Establishment of all species was lower in exposed areas of the largest gap size than in smaller gaps. Seedling establishment on mineral soil and forest floor was lower in the centers of 1.0 gaps than in the centers of 0.4 gaps. Establishment of all species tended to be lower on forest floor than on mineral soil or decayed wood in 1.0 gaps, and *Tsuga* seedlings in particular were relatively rare on forest floor in north and center positions of 1.0 gaps. Lower establishment rates on forest floor in exposed locations compared to other substrates appeared to be associated with higher maximum surface temperatures on forest floor. Establishment of *Tsuga* in exposed areas was greater in the year with cooler, wetter early summer weather, possibly due to lower maximum surface temperatures.

The primary limitation on the establishment of *Tsuga heterophylla* in forests that experience summer drought (*i.e.* the Pacific Northwest in general) appears to be moisture (Chapter 4, Williamson 1976). Since summer drying of soil tends to progress downward over time, avoidance of drought mortality depends on a species' ability to establish roots below the drying front (Haig *et al.* 1941, Ruth 1976, Kotar 1972, Scott *et al.* 1976). Seedling root growth is limited by low light as well (Haig *et al.* 1941). The larger seed of *Abies amabilis* and *Pseudotsuga menziesii* (22 times and 7 times the weight of *Tsuga* seed, respectively [Schopmeyer 1974]) and their deeper rooting habit (Zobel and Antos 1991, Scott *et al.* 1976, Minore 1979) appear to give these species an advantage over *Tsuga* in establishing on the forest floor in closed-canopy areas. Drought mortality of *Tsuga* on the forest floor is common (Christy and Mack 1984), and establishment of *Abies* in deep shade and under closed canopies is usually greater than that of *Tsuga* (Minore 1972, Thornburgh 1969, Long 1976). *Pseudotsuga* also appeared to be sensitive to below-ground resources in closed-canopy areas: the lack of naturally-regenerated *Pseudotsuga* on the forest floor in closed-canopy areas and it's relatively high establishment on both mineral and forest floor seed-plots suggests that removal of live roots associated with uncovering and churning of mineral soil or with insertion of exclosures on forest floor (*i.e.* trenching) may be more important than the nature of the substrate.

Seedling establishment on the forest floor in areas exposed to high levels of solar radiation can also be low or absent. Germination of seeds of different sizes can be affected by substrates by influencing seed moisture status (Harper *et al.* 1965); moisture content in litter can fluctuate greatly, making germination difficult for small-seeded species like *Tsuga* (Haig *et al.* 1941). For seeds that do germinate, the ability to establish deep roots can be critical to survival, since litter dries out more readily than soil in the open (Hermann and Chilcote 1965, Helgerson 1990). Once dry, litter also gets hotter than mineral soil when exposed to direct sunlight. Heat is often thought to kill seedlings by killing the cambium at ground level (Silen 1960, Helgerson 1990), but little of that type of mortality was noted in this study (or in Tappeiner and Helms 1971). (It was seen in many *Taxus brevifolia* germinants, however.) Mortality in exposed areas, which was greatest for *Tsuga* and lowest for *Pseudotsuga*, was probably due to desiccation. High temperatures create greater evaporative demand and greater levels of photorespiration in seedlings (Waring and Schlesinger 1985). *Abies amabilis* and *Tsuga heterophylla* transpire more under stress than *Pseudotsuga menziesii* (Livingston and Black 1988, Hinckley *et al.* 1982), becoming prone to desiccation, and *Tsuga* also tend to close stomata later in the day than the other species (Livingston and Black 1987). Greater survival of *Abies* than *Tsuga* in the exposed areas in my study may also be due to greater rooting depth leading to better moisture status, and greater height of *Abies* foliage from the hot surface leading to lower evaporative demand. Although *Pseudotsuga* is often said to require mineral soil to establish (Ruth 1976, Stewart 1978), density of natural regeneration on forest floor seemed adequate in this study (1 seedling/m$^2$), even in exposed portions of large gaps. *Pseudotsuga*'s "requirement" for mineral soil may be an exaggeration, or may be sensitive to site conditions and annual weather; adequate regeneration on litter in exposed areas has been reported in other studies (Hermann and Chilcote 1965, Williamson 1973).

Frost heaving of soil is occasionally cited as an inhibitor of seedling establishment in forest canopy gaps (Geiger 1965) and in large clear-cuts (Isaac 1943, Brockway *et al.* 1983). Although many uprooted *Abies* and *Tsuga* were found on mineral soil plots in 0.2 gaps and southern portions of larger gaps in this study, the cause was not clear--appearances suggested that root rot or root predation were not ruled out.

Patterns of seedling growth often differed from patterns of survival on different substrates. Despite similar seedling establishment on decayed wood compared to other substrates for *Pseudotsuga* in 1.0 gaps, growth was much lower on wood. Similarly, seedling establishment was often lowest, and growth highest, on forest floor in 1.0 gaps. Other studies have found greater seedling growth on forest floor than on mineral soil (Radwan 1992, Kotar 1972 [at lower elevations]). The nitrogen content of decayed wood is usually relatively low (Minore 1972), while mineralization of nitrogen in forest floor would tend to be relatively high compared to other substrates. *Pseudotsuga* appears to be less tolerant of low nitrogen levels than *Tsuga* (Minore 1979); I am not aware of similar comparisons with *Abies*.

Substrates are important in the gap dynamics of other forest types as well. Logs are important for tree establishment in Appalachian spruce-fir forests (White *et al.* 1985), in tropical forests (Lawton and Putz 1988) and in southern temperate forests (Veblen 1985), particularly for pioneer species. Mineral soil is also important for establishment of pioneer or small-seeded species in gaps (Putz 1983, Lawton and Putz 1988, Nakashizuka 1989). The importance of these substrates for tree establishment is often tied to the exclusion of trees from the forest floor by dense vegetation (Veblen 1985, Nakashizuka 1989).

The relatively high establishment of shade-tolerant *Abies amabilis* and *Tsuga heterophylla* on forest floor as well as on wood in 0.2 gaps suggests that the slow occupation of gaps in Pacific Northwest forests by saplings (Spies *et al.* 1990, Lertzman and Krebs 1991) is not due to lack of appropriate substrates. *Abies* and *Tsuga* growth rates in the 0.2 gaps were low and only slightly greater than growth in control areas, despite slightly higher light levels and greater soil moisture. The generally low light levels in these small gaps, caused by the narrow crowns of gap-maker trees and the tall, deep crowns of gap edge trees (Canham *et al.* 1990), seems to be the primary cause of slow closure. Even in forest types that tend to reach gap closure much faster than in Douglas-fir forests, shade-tolerants seedlings may require multiple gaps to attain canopy status (Uhl *et al.* 1988, Runkle and Yetter 1987, White *et al.* 1985).

## Understory shade effects

Understory shade inhibited and facilitated seedling establishment in different gap sizes and within-gap positions. Artificial understory shade over forest floor depressed seedling establishment in closed-canopy areas and 0.4 size gaps, most likely due to low reduced light levels. Shade appeared to aid establishment in 1.0 size gaps, primarily through higher germination rates rather than survival of emerged seedlings. Greater germination rates under shade may have been caused by greater forest floor moisture content due to lower surface evaporation by direct radiation. The similarity in survival of emergents among shade treatments is probably due to the similarly high surface temperatures (greater than 55°C), which occurred on shade plots during exposure to "sunflecks" penetrating the 5 cm openings in the shade treatments. Reduced total light levels under shade apparently reduced seedling growth in all gap sizes.

Shade provided by large logs facilitated seedling survival in exposed portions of large gaps, especially for *Tsuga heterophylla*. Similar effects on natural regeneration of *Tsuga* in exposed locations were seen on north sides of small logs (*e.g.* 10 cm diameter), old snags, and cut stumps. Although the zone of enhanced survival on north sides of logs was narrow, a low amount of woody debris in exposed areas could greatly change the species composition in large openings by facilitating establishment of *Tsuga* where it might otherwise not establish. Studies in clearcuts have found that shade by coarse woody debris and stumps enhanced seedling survival, often more effectively than shade from live vegetation (Isaac 1943, Minore 1986, Thornburgh 1969).

## Understory vegetation effects

Understory vegetation creates shaded microsites on the forest floor, but locally depletes below-ground resources (moisture and nutrients) as well (Radosevich and Holt 1984). The pattern of *Pseudotsuga* establishment in relation to understory vegetation appeared to be similar to the pattern in relation to dead shade: establishment tended to decrease with increasing cover in closed-canopy areas, 0.2 gaps, and shaded portions of large gaps, and tended to increase with increasing cover in exposed portions of larger gaps. No significant differences were found between total vegetation cover on *Pseudotsuga* microsites and random microsites, however, suggesting the vegetation effect was not strong. (On the other hand, *Pseudotsuga* was found in microsites with "no" southern shade more frequently than expected from random in 0.2 gaps and southern portions of 1.0 gaps [Figure 3.19], suggesting a sensitivity to vegetation cover over a larger area than sampled in microsite plots, which were 1/4 the size of the natural regeneration density plots.) Facilitation of seedling establishment by vegetation in exposed areas has been noted anecdotally for *Pseudotsuga* (Isaac 1943) and *Abies* (Thornburgh 1969). Establishment of *Tsuga* seedlings displayed no apparent benefit from shade by vegetation: establishment tended to decline with increasing cover regardless of gap size or within-gap position. Indeed, Harmon and Franklin (1989) found that *Tsuga* seedlings in closed-canopy areas of *Picea sitchensis* Zone forests (Franklin and Dyrness 1973) were restricted from the forest floor by understory vegetation, and that establishment was similar to that on logs when vegetation was removed. Vegetation removal (in forest floor seed-plots) had no such effect in my study, probably because of limited moisture in the forest floor of closed-canopy areas (*Picea* forests receive much more precipitation than Cascade forests). Although *Tsuga* appeared to be sensitive to vegetation cover in gaps, densities under high cover in moist, shaded portions of large gaps were greater than 40 seedlings/m$^2$. Contrary to the Oregon Cascades, canopy gaps in the Coast Range do not seem to have more *Tsuga* seedlings in them than closed-canopy areas (Holah 1991), possibly due to generally greater density of understory vegetation, or a different assemblage of understory species (*e.g. Rubus spectabilis*).

The tendency of naturally-regenerated seedlings in this study to avoid herb cover more that shrub cover is not a universal pattern. A negative association with herb cover has been observed for *Abies amabilis* (Wilson 1991) and *Tsuga canadensis* (Maguire and Forman 1983). Some studies have found that shrub cover was worse than herb cover for establishment (Isaac 1943) and growth (Wagner 1989) of *Pseudotsuga*, however. Litter-fall from a dense canopied, deciduous shrub (*Vaccinium membranaceum*) may also smother establishing seedlings (Thornburgh 1969). (Observation in my study indicated that areas occupied by the shrub *Rhododendron macrophyllum*--often with dense accumulations of leaves underneath them--had no establishing seedlings.) Isaac (1943) observed that broad-leaf plants with spreading roots inhibit seedling establishment, while slender-leaved, deep-rooted plants like *Pteridium aquilinum* promote seedling establishment in clear-cuts. The conflicting results concerning the effects of herbs and shrubs probably have less to do with intrinsic differences between woody and non-woody vegetation and are instead due to characteristics of individual understory plants. The difference between exclusion and facilitation of seedlings by two different shrub species can be due to differences in depletion of moisture from upper soil layers (Tappeiner and Helms 1971).

## Microsite heterogeneity and gap dynamics

Although the importance of microsite heterogeneity for plant establishment in gaps has been recognized (Orians 1982, Denslow 1987, Veblen 1989), this is the first study that systematically examined the process of seedling establishment in different microsites over a range of gap sizes. Many interactions, or potential interactions, were found between species, substrates, coarse woody debris, vegetation cover, annual climate, gap size, and within-gap position. In the face of such complexity, it is natural to ask "so what?"; is microsite heterogeneity simply "averaged out" at the gap level, or do the details of microsite quality substantially modify species dynamics in canopy gaps? Definitive answers to these questions requires study of a much larger portion of the tree life cycle than that covered in this study. Nevertheless, results from the early stages of establishment provide several insights concerning the importance of heterogeneity for different species.

The process of seedling establishment begins with the arrival of seed in a microsite (Figure 3.23). The abundance of seed-producing adults in a landscape can therefore dramatically affect species establishment in gaps; very few *Tsuga* or *Abies* established naturally in otherwise suitable gaps in the mature stands of this study due to lack of seed. The timing of seed production can be important as well. Since none of the principal tree species in the Pacific Northwest have seed banks in the soil (Isaac 1935, Ingersoll and Wilson 1990), tree establishment depends on dispersal over the previous year. Despite an abundance of mature *Abies amabilis* in stand TCO, few seed were produced, and fewer seedlings established naturally, over the duration of this study. The results for natural regeneration in this study may have differed if the copious seed crops of *Tsuga heterophylla* and *Pseudotsuga menziesii* had not been shed one year after gap formation. The dramatic increase in understory cover and decrease in soil moisture with time since gap formation (unpublished data) suggests that the abundance of regeneration microsites decreases with time since disturbance. Timing of establishment of neighboring plants can overwhelm a given species' competitive superiority (Harper 1977). *Tsuga*, which appears to be most sensitive to understory competition and moisture, sheds at least some seed every year, which is probably an advantage for arriving in suitable microsites. *Pseudotsuga* and *Abies*, on the other hand, shed seed in mast years often separated by 3-5 years. The larger seed of these species compared to *Tsuga* may confer an advantage for establishing on less than ideal microsites. Low abundance of suitable microsites may not be critical, however, if large seed crops ensure that at least some seed arrive in suitable microsites. Thus abundance and timing of seed dispersal and seed size can greatly influence species composition in gaps.

Annual variation in the suitability of microsites for different species can occur due to differences in weather and predation. Cool, wet weather in early summer allowed *Abies* to establish with greater success in closed-canopy areas, depressed all species in shaded gap environments, and facilitated establishment in exposed gap

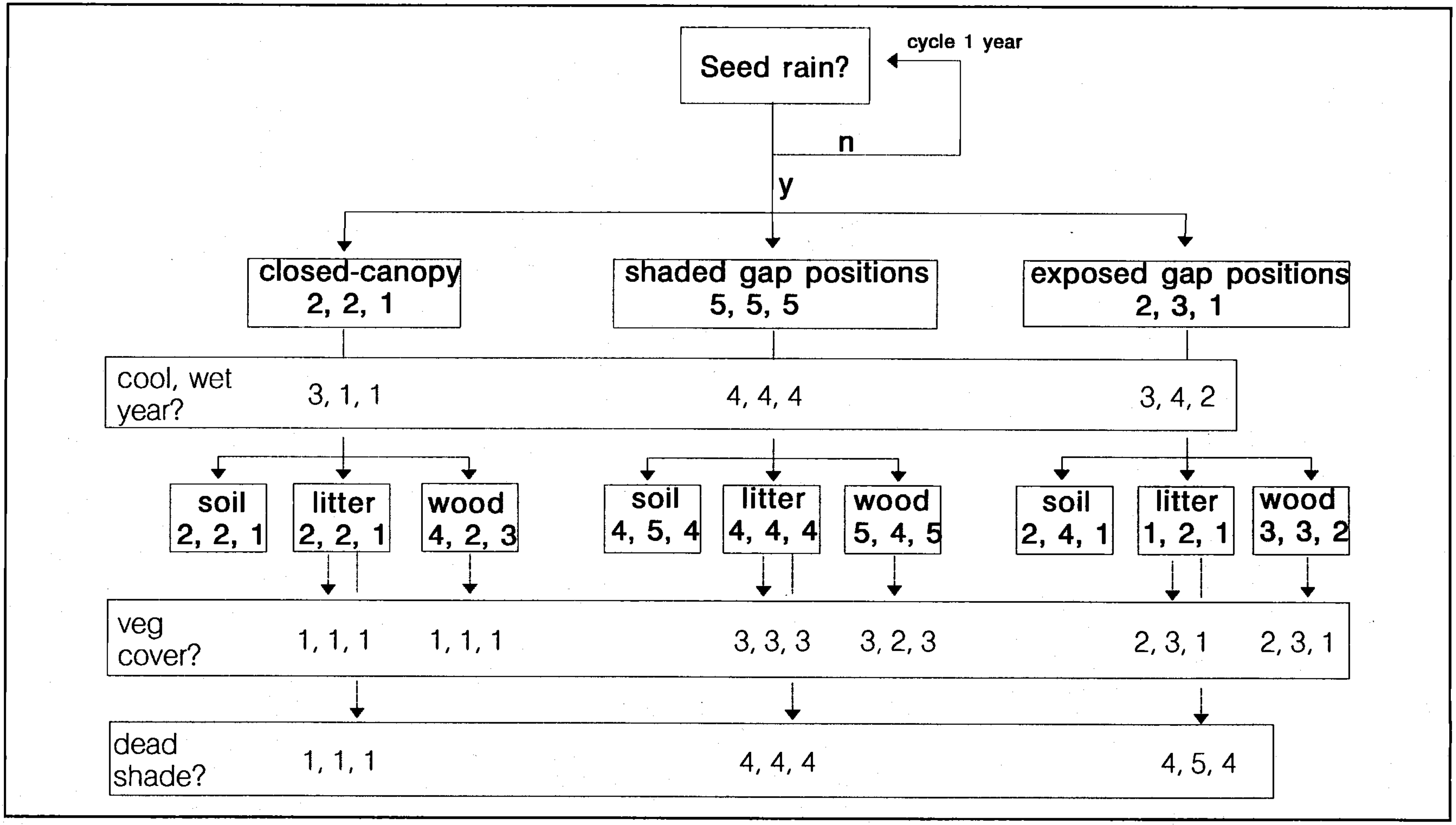

**Figure 3.23:** Summary diagram of seedling establishment in relation to structural heterogeneity in gaps. Numbers are ranks of establishment success for a given species, with 1= low and 5= high, for *Abies*, *Pseudotsuga*, and *Tsuga*, respectively.

environments compared to warmer, drier weather in early summer (Figure 3.23). Predator populations and predation can also change drastically from one year to the next in response to seed production, other food supply, or weather (Halvorson 1982, Isaac 1943). The very large *Pseudotsuga* seed crop of 1991-92 appeared to ensure sufficient seed for establishment in 1992, while the much smaller seed crop of 1992-93 seems to have led to much greater predation on seeds and seedlings in exclosures in 1993. These transient effects on establish can change the relative abundance of species in gaps, and would not be discernible by observation of established seedlings.

The abundance of different substrates in a forest may dramatically affect the species diversity of establishing seedlings (Figure 3.23). Decayed logs are typically the only microsites on which *Tsuga* becomes established in closed-canopy forests, usually only on wood of a specific species (*e.g. Pseudotsuga*) in a particular stage of decay (*e.g.* class III or IV). Not only are most *Tsuga* seedlings in dense Cascade forests found on wood, but most saplings in open forests in the "understory reinitiation stage" (Oliver 1981) of forest development are found on wood, and many adult *Tsuga* are stilt-rooted, suggesting establishment on logs (*personal observation*). Although establishment in shaded portions of gaps is abundant on forest floor, decayed log substrates and organic skirts (which are typically only found around the bases of *Pseudotsuga*) also appear to be important. Presence of logs on the forest floor also provide shaded microsites for *Tsuga* establishment in exposed areas within large openings. Similar levels of shade provided by vegetation, however, do not facilitate establishment in these hostile environments. Thus *Tsuga* appears to be particularly sensitive to the abundance of very specific types of microsites, some of which may depend on stand history and the previous establishment of another species (*e.g.* decayed wood and skirts of *Pseudotsuga*).

Establishment of *Pseudotsuga menziesii* appears to be much less sensitive to microsite heterogeneity than establishment of *Tsuga heterophylla*. *Pseudotsuga* was able to germinate regardless of light levels, survival was similar regardless of substrate, and although sensitive to understory cover, establishment in gaps was plentiful even in stands with high density of understory vegetation. Establishment of *Pseudotsuga* does appear to be limited by exposure on forest floor, however, and benefits from shade by woody debris or residual trees in large openings (Figure 3.23, Franklin 1963, Minore 1986). Sensitivity of *Abies amabilis* establishment to a broad range of microsite types is unclear due to lack of natural regeneration in the gaps, but appears to be relatively insensitive to substrate, able to establish in closed-canopy areas, and more sensitive to exposure than *Pseudotsuga*. Some of the species' sensitivity to microsite heterogeneity appears to be related to seed size; *Tsuga*, with the smallest seed, is most prone to desiccation prior to germination and has the fewest carbohydrate reserves to move roots or leaves into relatively high-resource areas.

The sensitivity of *Tsuga heterophylla* to microsite conditions implies that mature forests with few class III or IV logs due to a stand history lacking in large *Pseudotsuga* (from intensive silviculture or recurrent fire), will also have few established *Tsuga*. In addition, large openings without coarse woody debris to provide shade, or without decayed wood to allow establishment once other trees or vegetation do provide enough shade, may have no establishing *Tsuga*. Lack of early establishment following disturbance may preclude establishment for many years; *Tsuga* does not appear to establish in forests for 3-4 decades following stand closure (Gray 1990). Any strategy of accelerating stand development to the old-growth stage by encouraging establishment of *Tsuga heterophylla* (FEMAT 1993) must consider gap size and within-stand heterogeneity if it is to succeed.

Microsite heterogeneity also appears to have implications for the gap partitioning hypothesis, which predicts that different species should tend to establish and succeed on different portions of the environmental gradient from closed canopy areas into gaps (Ricklefs 1977). Thus gap partitioning is usually cast in terms of coarser scale environmental gradients than those associated with seedling regeneration microsites. Rather than simply modifying the effect of gap size and within-gap gradients, microsite heterogeneity appears to allow species to transcend the constraints of those environments. For example, given a forest with sufficient heterogeneity, *Tsuga heterophylla* is not only able to establish in dry, low-light closed-canopy forest, but may also survive in high-light areas prone to environmental extremes. Although the gap partitioning hypothesis is based on niche separation among species for regeneration in areas with different resource levels, it may be too simple to capture the many variables affecting seedling establishment. While many studies have found predictable differences in species composition with gap size and position (Runkle 1982, Phillips and Shure 1990, Minckler and Woerhide 1965, Brandani *et al.* 1988, Poulson and Platt 1989), several others have not (Uhl *et al.* 1988, Nakashizuka 1989, Denslow 1987, Spies *et al.* 1990, Ehrenfeld 1980). The concept of regeneration niche (Grubb 1977) is predicated on strong selective pressures on regeneration traits caused by high rates of seed and seedling mortality. While species establishment varies along resource gradients, differences among species in the timing and amount of seed production, seed size, spatial dispersal of seed, specific environmental requirements for germination, suitability of different substrates, effects of timing and severity of weather, susceptibility to predation, and effects of specific species of neighboring plants also define a species' regeneration niche (Grubb 1977). The interaction of microsite heterogeneity with these species-specific characteristics provide a wide array of potential outcomes for species establishment in canopy gaps that may rarely fit into one or two-dimensional categorizations of environment.

# CHAPTER 4: TREE SEEDLING ESTABLISHMENT RESPONSE TO RESOURCE GRADIENTS AND MICROCLIMATE IN CONIFER FOREST CANOPY GAPS

## Introduction

The diversity of plant species that exist in apparently stable assemblages is difficult to explain with classic ecological theory. According to 'Gause's hypothesis' no two species in a stable community may occupy the same niche (Gause 1934). It is difficult to reconcile this idea with observations of numerous species occupying the same community, particularly since all autotrophic plants require the same basic resources: light, water, carbon dioxide, and the same mineral nutrients. One response to this riddle is the idea that even communities occupied by mature vegetation are not entirely stable. The mortality of mature plants creates gaps in the vegetation, and result in a variety of environments and resource levels found within a given community (Watt 1947). The gap partitioning hypothesis (Ricklefs 1977, Denslow 1980), really an application of Gause's hypothesis, predicts that resource gradients from established vegetation into gaps is broad enough that different species will have evolved to occupy discrete niches along those gradients. In this way, the heterogeneity of resources within forests created by canopy gaps may maintain species richness in forests (Orians 1982).

In contrast, lack of partitioning of resource gradients by species within canopy gaps could arise due to the ability of many plant species to respond flexibly to different resource ratios. All plants are fundamentally constrained by the need to allocate tissue to the acquisition of both above- and below-ground resources. In areas where there is a relative abundance of one resource, another will become limiting. For example, areas with relatively high levels of soil moisture often develop dense vegetation that depletes light levels on the forest floor. Although many species appear to be able to compensate for a single limiting resource through increased allocation towards its acquisition (Chapin *et al.* 1987), success in plant establishment and growth may depend on a fundamental, physiologically determined ability to tolerate the lowest resource level in a given environment (Tilman 1988).

These ideas of plant response to environment are largely based on competition as the dominant (or sole) force in the evolution of plant "habitat selection" (Bazzaz 1991). Grubb (1977) points out, however, that once established, plants can tolerate sub-optimal resource levels through a variety of mechanisms, including physiologic, phenologic, and morphologic traits, which he considers to be niche dimensions in their own right. Grubb emphasizes the importance of the "regeneration niche" in allowing a variety of species to persist within a similar habitat. The sensitivity of germinating seedlings to the surfaces on which they land (Harper *et al.* 1965, *e.g.* desiccation inhibited germination due to a poor match between seed size and surface roughness), suggests that the presence of a given species in a habitat may have as much to do with surface environments as it does with above- and below-ground resource levels.

Resource levels and surface environments vary greatly within and among gaps. Increased availability of resources in canopy gaps occurs due to reduced consumption of light, water, and nutrients by loss of biomass and/or by increased mineralization of nutrients held in soil organic matter (Canham and Marks 1985). The abundance of plant resources can vary dramatically within and among gaps, however (Denslow 1987, Veblen 1992). Light levels within gaps vary predictably with latitude, with gap size, shape, orientation, the height of surrounding trees, and the slope of the site (Geiger 1965, Poulson and Platt 1989, Canham *et al.* 1990). In temperate latitudes, levels of diffuse light increase with gap size, but significant levels of direct solar radiation also reach the understory in northern portions of large gaps (Phillips and Shure 1990, Canham *et al.* 1990). Soil moisture levels are usually higher in canopy gaps than in closed-canopy areas (but see Collins and Pickett 1988), with little difference associated with gap size, but with decreasing moisture levels near gap edges (Denslow 1987, Minckler and Woerhide 1965, Vitousek and Denslow 1986). This soil moisture response in gaps is commonly attributed to the decrease in transpiring vegetation (Veblen 1992) and a reduction in root density (Wilczynski and Pickett 1993, Vogt *et al.* 1993, Parsons *et al.* 1994) but may also be due to increased throughfall of precipitation (Canham 1993). Differences in soil nutrient levels between gaps and non-gaps have been found in some studies (Mladenoff 1987, Canham 1993, Parsons *et al.* 1994), but not others (Uhl *et al.* 1988, Vitousek and Denslow 1986, Vogt *et al.* 1993). Thus the differing directional gradients of soil moisture (and potentially nitrogen as well) from gap edge to gap center superimposed on north-south light gradients produce an array of resource combinations associated with gap size and within-gap position.

Most gap studies tend to make general observations of plant response to resource gradients in gaps, without quantifying the relationship. Field physiological studies, on the other hand, tend to make detailed observations of short-term behavior of a few plants to light gradients. No studies that I am aware of have attempted to quantify plant response to multiple resource gradients present in gaps of different sizes and on different sites. The study of canopy gaps is commonly a patch-oriented approach. Areas are categorized into similar types of patches, whether it be gap size, location within gap size, density of vegetation, microtopography, etc. These classifications are usually based on the perception that environment and resources are similar. It is likely that understanding of plant process would be greatly enhanced by relating plant response to actual environmental measurements and relying less on often subjective and simplified classifications of environment.

The purpose of this paper is to attempt to relate tree seedling establishment and growth to measurements of above- and below-ground resources, as well as surface environments. I will also compare the relative benefits of a patch-based classification approach with the resource-based approach in terms of their ability to clarify the process of seedling establishment in canopy gaps in Pacific Northwest forests. The importance of canopy gaps to forest dynamics in this region, and their attendant effects on resource levels, are not well known. Most of the research on forest disturbance in the Pacific Northwest has focused on succession following large disturbances like fire or clear-cutting (Isaac and Meagher 1936, Agee and Huff 1981, Dyrness 1973, Halpern and Franklin 1990). The common successional sequence in the "Douglas-fir forests" of the Pacific Northwest is of young stands dominated by *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) in a single canopy layer developing into multi-layer old-growth forests containing increasing amounts of shade-tolerant *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and *Abies amabilis* (Dougl.) Forbes (Pacific silver fir) (Munger 1940, Franklin *et al.* 1981). While shade-tolerant *Tsuga heterophylla* and *Abies amabilis* seedlings are more abundant in canopy gaps than under closed canopies (Harmon 1987, Alaback and Tappeiner 1991, Thornburgh 1969, Long 1976, Stewart 1986a, Spies *et al.* 1990), many gaps are long-term features which may take 50 to 100 years to attain canopy closure (Spies *et al.* 1990, Lertzman and Krebs 1991) (indeed, some gaps may result from lack of establishment during stand initiation rather than from recent overstory mortality). In comparison, canopy closure may take as little as two years in moist tropical forests (Lorimer 1989) or five years in temperate deciduous forests (Runkle 1990). It is unclear if low resource levels are limiting seedling and sapling recruitment in these gaps, either from a lack of light caused narrow gaps and tall, deep-crowned edge trees or low levels of below-ground resources due to root encroachment by surrounding trees, or whether some other mechanism (e.g. lack of suitable regeneration microsites) precludes occupation by tree seedlings.

The specific objectives of this study are to examine the effect of light intensity, substrate moisture, and surface temperature on tree seedling establishment and growth in Douglas-fir forest canopy gaps. The studies described in Chapters 2 and 3 determined that tree species responded differently to gap size, within-gap position, and substrates within canopy gaps, but the degree of association with actual resource levels was unclear. Thus an additional objective is to determine whether information on resource levels alone explains more of the variation in tree seedling response than patch-level information does. Seedling establishment is a continuous process from seed dispersal through germination, emergence, and subsequent survival. The focus of this study is on survival of emerged seedlings, but survival as a fraction of seed rain is also examined to assess the relative importance of these stages in the process of early seedling establishment. Based on inferred resource patterns of previous results, I hypothesize that establishment and growth of all species respond positively to light and moisture, but that *Tsuga* establishment is depressed by high surface temperatures and is more sensitive to low moisture than *Abies* and *Pseudotsuga*.

# Methods

## Site description

Canopy gaps were created by cutting trees in four forest stands in the *Tsuga heterophylla* Zone (Franklin and Dyrness 1973) of the west slope of the Cascade Mountains. Two stands were in old-growth forests (approximately 500 yrs in age) dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla* in multiple canopy layers (HJA and TCO), and two stands were in mature forests (90-140 yrs in age) dominated by *Pseudotsuga* in a single canopy layer (MCY and PCM; Table 4.1). One old-growth stand was located in the H.J. Andrews Experimental Forest in the Willamette National Forest of the central Cascades of Oregon; the other three stands were located in the Wind River Experimental Forest in the Gifford-Pinchot National Forest of the southern Cascades of Washington. Additional details of stand features are provided in Chapter 2.

**Table 4.1:** Characteristics of the four stands in the experimental gap study. Soil texture from Gray and Spies (*in press*).

| | old-growth | | mature | |
|---|---|---|---|---|
| Stand name: | HJA | TCO | MCY | PCM |
| Location | 44°15'N,<br>122°15'W | 45°49'N,<br>122°00'W | 45°47'N,<br>121°57'W | 45°50'N,<br>121°49'W |
| Elevation (m) | 900 | 550 | 550 | 850 |
| Soil texture | Loam | Loam | Clay loam | Sandy loam |
| *Pseudotsuga* age (yrs) | 350-500 | 350-500 | 90 | 140 |
| Mean canopy height (m) | 50 | 50 | 35 | 50 |

Climatic regimes from meteorological stations in or near the two Experimental Forests are similar, with summer drought and high temperatures common from June through September (less than 3 cm of monthly precipitation and mean maximum temperatures greater than 25°C in July and August), a pattern characteristic of the Pacific Northwest (Chapter 2, Figure 2.1). Climate varied over the two year duration of the study, with higher precipitation, and lower maximum and minimum temperatures, from March through August of 1993 than in the same period in 1992.

Within each stand, experimental gaps were located in areas with slopes less than 20% and with relatively dense tree canopies (to minimize interactions with recent gap events). Four sizes of circular gaps were created in each stand, as well as control plots. Gap diameter (measured between tree crown edges) was scaled to the average height of trees in the stand. The gap diameter to tree height ratios for the 4 gap sizes were 0.2, 0.4, 0.6, 1.0. The control plots were equal in area to the 1.0 gap size. Gaps were created in the fall of 1990 by cutting all trees over 2 m tall (except *Acer circinatum*) within the gap perimeter. Trees were stage-felled into specific locations (usually in the northeast and/or northwest quadrants to avoid damage to southern trees which defined the gap shade pattern), and skidders situated outside of the gaps (to minimize disturbance to soils and understory vegetation) winched the fallen tree boles from the gaps with cables. Most of the branches and foliage trimmed from the felled trees were piled outside the gap perimeter. Some of the abundant *Acer circinatum* in the mid-story of the mature stands was cut to facilitate cutting and removal of tree boles.

This study of resource effects on tree seedling relied on several different seedling establishment treatments coupled with resource measurements within each treatment. Seedling establishment results are discussed in detail in Chapters 2 and 3; an overview of the studies is provided in addition to information on resource measurement techniques.

## Seedling establishment experiment

The seedling establishment study consisted of sowing known quantities of seed on plots with different treatments of within-gap position, substrate, and level of shade. The study was conducted in three of the four gap sizes and in controls, with one of each per stand (Figure 4.1); the 0.6 gap size was not used to reduce effort, and because a pilot study indicated seedling responses within this gap size were similar to those found in portions of the 0.4 and 1.0 gap sizes. Mineral soil plots were located at the centers of all gaps, and at the north and south edges of the 0.4 and 1.0 gaps and controls. Forest floor and decayed wood plots were located in the centers of all gaps and controls. Shade plots were located in the centers of the 0.4 and 1.0 gaps and controls in the two mature stands (MCY and PCM). Three 60 x 60 cm seed-plots were created for each treatment. For the mineral soil treatment, the forest floor and much of the A1 soil horizon was removed and the upper 10 cm of soil churned, removing coarse fragments and roots over 1 cm in diameter in the process. Mycorrhizal mats (Griffiths *et al.* 1991) were avoided if possible or removed. A uniform layer of B1 horizon soil was tilled at a road-side in the TCO stand and spread in a surface layer 2.5 cm deep across the mineral soil seed plots at all of the stands to further reduce effects of soil variation on the experiment. For the forest floor treatment, seed-plots were located on flat areas with an intact litter layer over mineral soil. Decayed wood plots were created by chopping up large pieces of class IV logs (Maser *et al.* 1979) and placing them in square boxes with 15 cm high boards on the sides and window screen on the bottom. Smaller pieces of wood were packed around the larger pieces and a fine wood powder spread over the top for a uniformly soft surface to retain seed. Shade levels of 40% and 90% were created over intact forest floor by stapling shade cloth to 1 m by 1 m square wooden frames set 30 cm above the forest floor (the average height of tall herb and low shrub canopies) on stakes sunk into the ground. To approximate the partial shade of understory vegetation, the 40% and 90% shade levels were attained by cutting different densities of 5 cm diameter holes at regular spacings out of the 96% opaque black shade cloth. Shade-

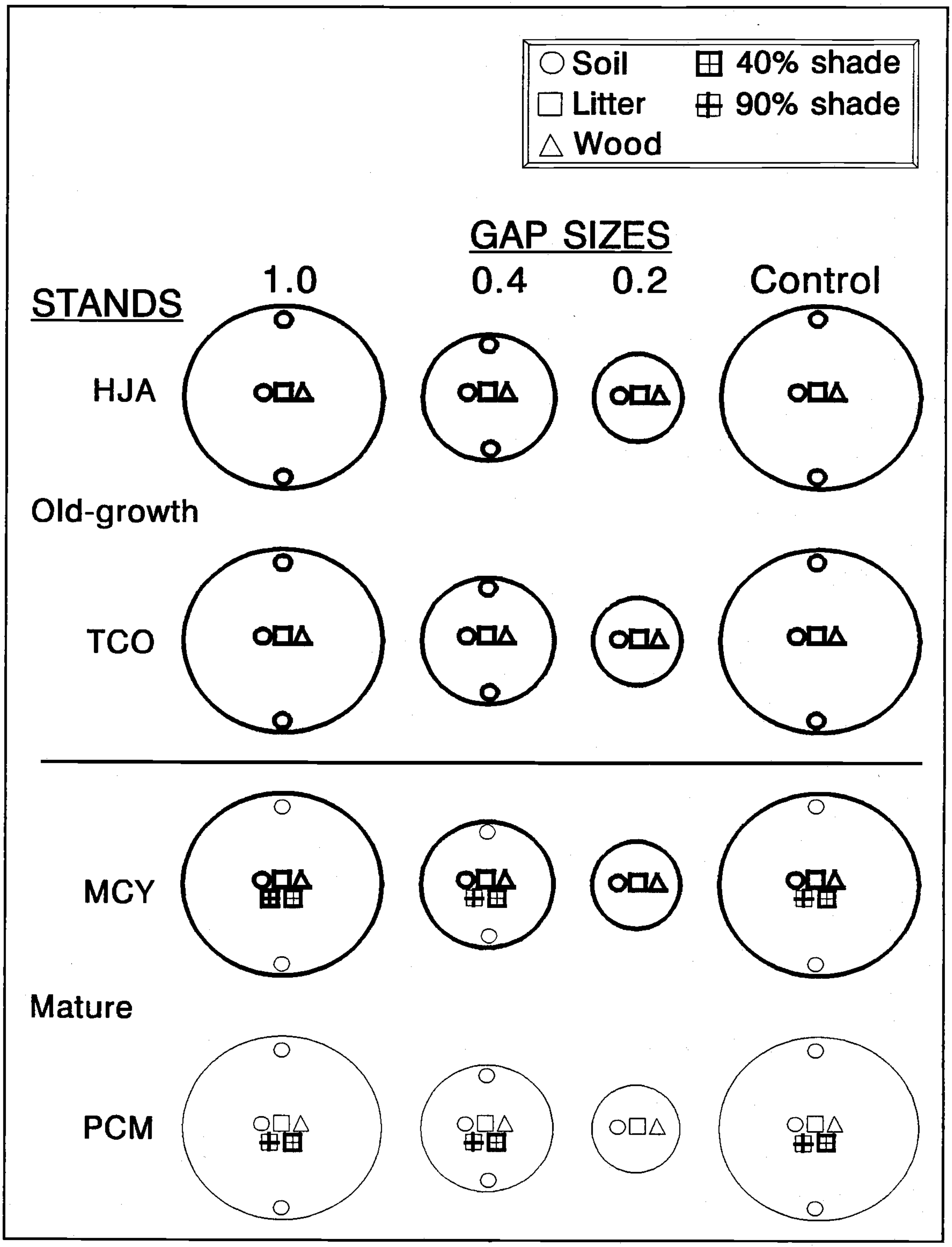

Figure 4.1: Schematic of experimental design for seedling survival and growth study. Each symbol represents three seed-plots.

cloth frames were removed over winter (November to April) to avoid destruction from snow loads.

Exclosures were placed over each seed-plot to deter seed and seedling predation by rodents and birds, which can deplete seedling populations by more than 60% (Gashwiler 1967). Exclosures were made of galvanized metal hardware cloth (12 mm mesh). Exclosures for the mineral soil, forest floor, and decayed wood treatments consisted of a 15 cm tall cylinder sunk 7-10 cm into the substrate, covered with a removable cone about 40 cm tall at the peak. The cylinder was 56 cm in diameter, enclosing an area of 0.25 $m^2$. Exclosure bottoms for the shaded plots were similar to those described above, but were square in shape, and exclosure tops were flat pieces of hardware cloth (shade cloth could not be placed at a low enough height over the cone-shaped tops). Both types of exclosures reduced PAR quantum levels a tan exposed site in a gap by 17.5%, but had no detectable effect on surface temperatures. Potentially competing understory vegetation in and around the seed plots (growing above a 45° line projecting from the base of the exclosures) was clipped or uprooted at regular intervals throughout the course of the study. Seed-plots were either located away from potentially shading mid-story trees, or trees were tied back to minimize shading. Seed-plots were created during the summer and fall of 1991 and seed was sown in the late fall of 1991 (one year after gap creation). Seed-plot surfaces were roughened slightly with a hand rake to discourage seed movement by raindrops (Lawrence and Rediske 1962).

One hundred *Abies amabilis*, 100 *Pseudotsuga menziesii*, and 500 *Tsuga heterophylla* seeds were divided evenly between the three seed-plots of each treatment. All seeds were sown during the first three weeks of November 1991. The seeds used at the HJA stand were from a local seed zone, and those used at the other three stands were from a Wind River seed zone (all seedlots were from the Wind River Nursery). Germination tests conducted by the Wind River nursery estimated seedlot viability for *Abies* at 95 and 93%, *Pseudotsuga* at 94 and 70%, and *Tsuga* at 76 and 76% for the Wind River and H.J. Andrews seed zones, respectively. Natural seed rain also added large numbers of seed in the fall of 1991, primarily *Pseudotsuga* in the mature stands (MCY and PCM), and both *Pseudotsuga* and *Tsuga* in the old-growth stands (HJA and TCO). Seed rain was monitored with seed traps placed in the north, center, and south of each gap size and control in each stand. Since seed sowing and placement of exclosure tops occurred after natural seed dispersal had started, seeds which had already been shed at the time of sowing were more exposed to predation than seeds which were shed later.

Seedlings were counted in the seed-plots once each month from late April to October of 1992 and in June and October of 1993. Seedlings were considered emerged and counted if they were erect and rooted and had mostly shed their seed-coats. If the total number of live and dead seedlings on a plot exceeded the previous month's count of live seedlings, the number of dead seedlings in excess (*i.e.* which had never been counted as live) was recorded as "new mortality" (*e.g.* if there were 20 live seedlings $t_1$, and 18 live and 6 dead seedlings at $t_2$, then 4 seedlings were recorded as "new mortality"). Seedlings were considered dead when they were missing, cut at the stem, or entirely lacking green color. At the end of the 1993 growing season, basal diameter and height were measured on up to five randomly selected seedlings of each species from each seed-plot. Seedling growth began to be restricted by exclosure tops in 1993, so the tops were removed from all seed-plots in July 1993. Measurements from seedlings which had clipped or browsed tops was noted. *Tsuga* seedlings were removed and counted from some plots in stand TCO to make room for a study of annual variation in seedling establishment (Chapters 2 and 3).

## Microclimate measurements

Measurements of photosynthetically active radiation (PAR), surface temperature, and soil moisture were made in or next to the seed-plots. PAR photon flux density was measured with calibrated quantum sensors (LI-190SZ, LI-COR Inc., Lincoln, Nebraska, USA) and galium arsenide photodiodes (G1738, Hamamatsu Corporation, Hamamatsu City, Japan) placed 1.5 m above the forest floor at the centers and north and south edges of each gap and control. Sensors in the 1.0 gaps and controls of the old-growth stands (HJA and TCO) ran continuously through the summer of 1992. Mobile microclimate stations were used to sample the rest of the gaps, with measurements taken in all gaps over 6-14 relatively sunny days in each stand during July and August of 1992. Data-loggers sampled each light sensor at 10 second intervals and stored measurements as 2 hr means. Light sensors were within 1 to 6 m of the seed-plots in each within-gap position.

Volumetric soil water content was estimated from Time Domain Reflectometry (TDR) using regressions that were developed for decayed wood and the soils in each stand (Gray and Spies, *in press*). One pair of thirty cm long TDR probes were placed in one seed-plot of each treatment (*e.g.* in one of the three mineral soil seed-plots in each gap center) at a 30° angle to sample the 0-15 cm depth. Measurements were taken at monthly intervals between May and September 1992.

Soil surface temperature was measured using temperature-sensitive paints (Omegalaq, Omega Engineering Inc., Stamford, Connecticut, USA) applied to toothpicks that were laid on the surface of one seed-plot per treatment (the same plots in which the TDR measurements were made). Four paints, which congealed when temperatures exceeded 48, 55, 62, or 69°C, were used. Laboratory tests using heat lamps and thermocouples indicated the painted toothpicks responded rapidly and accurately to surface temperature changes.

## Statistical Analysis

The response variable for the analysis of seedling establishment was the fraction of the maximum number of emerged seedlings counted (plus all "new mortality" counts) that were still alive at the end of the experiment (termed "establishment"). This measure could potentially under-estimate seedling survival by missing seedlings that died and were replaced by new emergents; comparisons with individually marked seedlings (Chapters 2 and 3) suggest that the effect was slight, and occurred primarily in exposed locations of 1.0 size gaps. An alternative measure of establishment was calculated as the fraction of total seed shed on a treatment (sown plus seed rain) alive at the end of the experiment. Since *Tsuga* seedlings were removed from 38 out of the 108 TCO seed-plots to make room for sowing more seed in the fall of 1992 (for a study of annual effects on seedling establishment), final seedling counts were adjusted under the assumption that the original number of seedlings would have followed the same survival trajectory as those left after thinning did (*i.e.* final count/post-thin count = adjusted/pre-thin count). Final counts on the thinned plots were adjusted with the formula: adjusted count = (pre-thin count * final count)/post-thin count.

All seedling counts were summed across the three seed-plots (as experimental sub-plots) comprising a treatment within a gap, and establishment calculated on those sums. As is common with binomial data, establishment percentages exhibited non-uniform variance and non-normality, and were transformed prior to analysis with an arcsin-square root equation specifically designed for data with several values close to zero (Zar 1984, eq. 14.5):

$$p' = 0.5 * \{\arcsin([N_f / (\max + 1)]^{1/2}) + \arcsin([(N_f + 1) / (\max + 1)]^{1/2})\}$$

where:
$p'$ = transformed value
$N_f$ = number of seedlings alive at final count
max = maximum number of seedlings found on a treatment

Regression models were used to evaluate the association between seedling survival and resource levels. Polynomial regressions were not able to fit both the steep initial rise in establishment with increasing light and the more gradual decline in establishment at higher light levels. A non-linear method fitting gaussian ("bell-shaped") curves for the response of each species to multiple resource gradients (modified from Gauch and Whittaker 1976) was used instead (NLIN procedure in SAS 6.10 [SAS Institute Inc. 1987]). Many species tend to follow a gaussian distribution in abundance along resource gradients (Gauch 1982), and the gaussian models fit species establishment data along resource gradients better than the polynomial models did. Predicted establishment values from the models were back-transformed ($\sin(p')^2$) before plotting.

The relative importance of moisture and light differences in seed-plots was investigated with separate regressions of seedling establishment on each resource individually. The residuals for the light models were examined, and linear regressions of the residuals on moisture content were calculated to get a sense of how of the much residual variance from the light models could be accounted for by moisture content.

Split-plot analyses of variance were used to evaluate the association between seedling establishment and patch-type information (*i.e.* stand age, gap size, within-gap position, substrate and shade). Inclusion of all treatments into one model resulted in spurious linear contrasts generated by SAS due to the great lack of balance (only one position in gap size 0.2, only one substrate in north and south positions, and shade plots were present only in mature stands). Thus the position, substrate, and shade experiments were modelled separately, similar to the analyses in Chapters 2 and 3, but species were analyzed separately to match the structure of the non-linear model. The ANOVAs used the same establishment response variable as the regressions, and were weighted by the denominator used to estimate establishment (the maximum number of emerged seedlings). ANOVAs were also run on the residuals and predicted values from the non-linear models (*e.g.* covariance analysis) to assess whether the different models were explaining different aspects of the same dataset.

The analysis of seedling size used second-order polynomial regressions for each species. The response variable was the mean size of the seedlings measured in a treatment (*i.e.* three seed-plots), where size was calculated as seedling height multiplied by basal area. Measured seedlings with damaged tops (from animal browsing) were included in the analysis (their presence had no effect on results). The size data were log-transformed ($\log(y+1)$) prior to analysis. The sample size for this analysis was smaller than that for the analysis of establishment due to treatments without surviving seedlings. Predicted seedling size values from the models were back-transformed ($\log(y')-1$) before plotting.

Since light measurements using the roving stations were taken at different times in different stands, light measurements were adjusted for the seasonal decline in light intensity following the summer solstice and for differences in cloudiness among sample periods. Data from quantum and radiometer sensors at the Wind River nursery and at the primary meteorological station at the H.J. Andrews experimental forest were used to make the adjustments. Since only radiometer measurements were available from the H.J. Andrews, both the radiometer and quantum data are plotted for the Wind River nursery, illustrating that the relative values and trends are very similar (Figure 4.2). The mean solar radiation values from these "reference stations" were calculated for the entire sample period (July 1 to August 31), and for the periods during which the roving stations were operating in the different stands. Quantum flux data from the Wind River station was used for stands TCO, PCM, and MCY and radiometer data from the H.J. Andrews station was used for stand HJA. A correction factor for the stand measurements was calculated using the reference station data by dividing the mean values for the entire period by the mean values for the period when stands were sampled. The mean daily flux values for the roving station data from each stand were then adjusted using this correction factor; data from the permanent stations in the stands were not adjusted. All subsequent presentation of light data uses these adjusted values. Actual light levels were most likely greater in the summer of 1992 (when seedlings emerged) than the levels measured in the summer of 1991 due to generally sunnier weather. The relative differences among stands, and among gaps within stands, were probably very similar between years, however.

The monthly volumetric water content data was examined for seasonal trends, and the data from the driest period in 1992 was used. This seemed appropriate because most of the seedling mortality occurred in 1992, and relative differences between treatments were greatest at the driest time of the summer. The driest and hottest time of the summer is presumably when moisture becomes the most limiting factor to seedling survival and growth. The data from early August 1992 were used for the analyses.

Means of the maximum surface temperatures exceeded on a seed-plot were calculated for the three sample periods in the summer of 1992. Since the lowest temperature recorded by the temperature-sensitive paints was 48°C, temperatures for sample periods that did not exceed this level were estimated based on maximum surface temperatures recorded with thermocouples by the permanent and roving

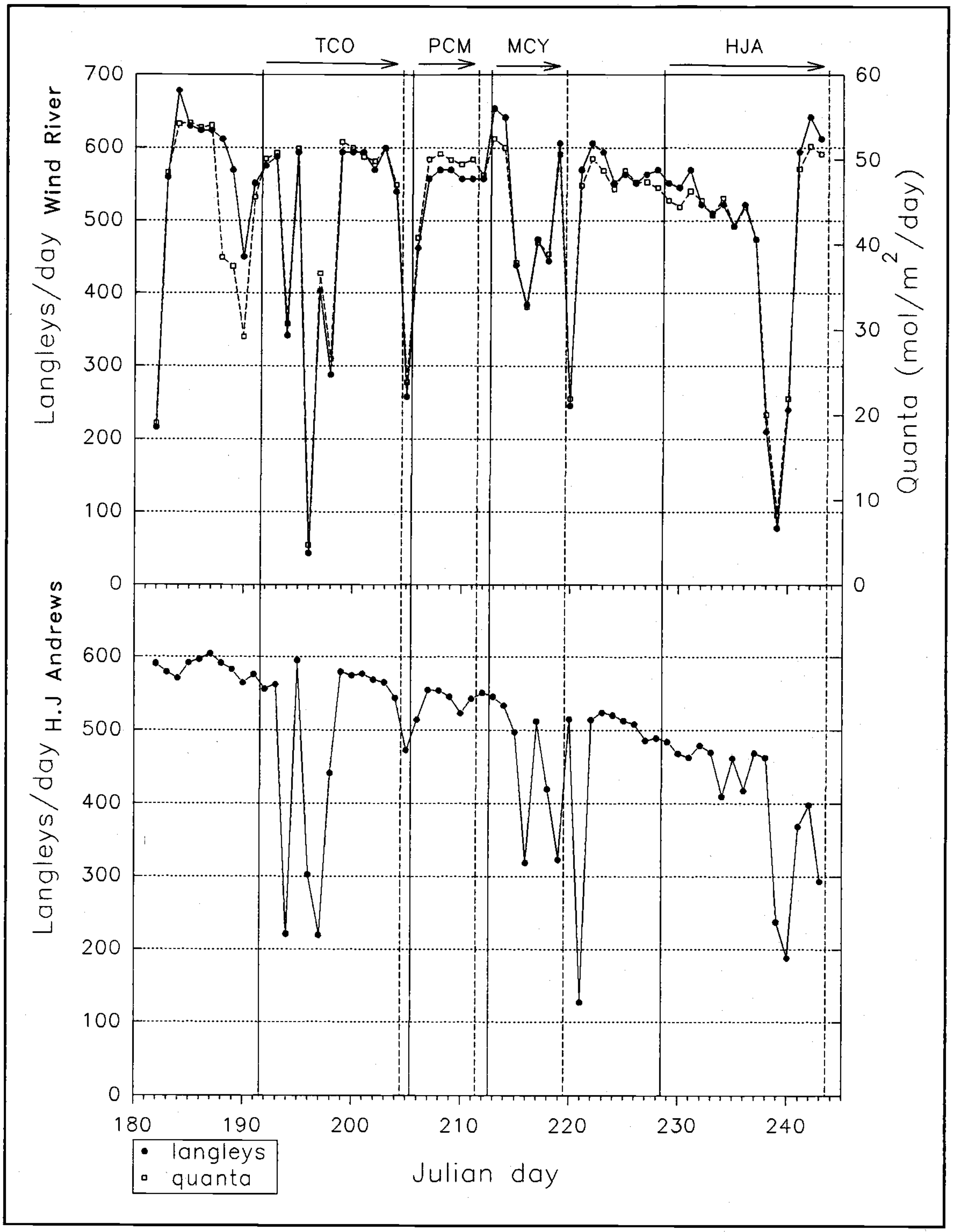

**Figure 4.2:** Daily light measurements between July 1 and August 31, 1991 at (a) Wind River nursery and (b) H.J. Andrews headquarters. Light intensity and photosynthetically active quantum flux were both measured at Wind River. Days during which roving gap light sensors were in each stand are marked with vertical lines (start= | , finish= ¦) and stands designated at the top of the graph.

microclimate stations. Thus surface temperatures for sample periods without data in controls, 0.2 gaps, and the south ends of 0.4 and 1.0 gaps were set at 30°C, and those in other positions in 0.4 and 1.0 gaps were set at 40°C (shade plots in 0.4 gaps were set at 35°C).

## Results

### Microclimate patterns on seed-plots

Levels of PAR quantum flux varied predictably with gap size and within-gap position. Light levels were about twice as high in 0.2 gaps as in controls and increased dramatically with gap size (Figure 4.3). Light levels tended to be greater at north positions than center positions, with relatively low light levels at south positions of gap sizes 0.4 and 1.0. Given a mean daily flux of 42.8 mol/m$^2$/day during July and August at the Wind River Nursery meteorological station, light measurements in the gaps ranged from 1.5 to 56% of full sunlight.

Seed-plot moisture levels tended to differ with gap size, within-gap position, substrate, and level of shade. A split-plot ANOVA for mineral soil plots indicated differences among positions ($F_{[2,18]}=8.70$, $p=.002$) and suggested an interaction between gap size and position ($F_{[4,18]}=2.64$, $p=.068$), but least-square means were not estimable for separation of position means due to the unbalanced design. Moisture levels in the mineral soil seed-plots tended to be higher in gap size 0.2 than in controls and were similar in gap centers across different gap sizes (Figure 4.4a). Moisture levels tended to increase from north to south across the larger gaps. (Larger sample sizes from across the gaps indicated moisture in gaps was similarly higher than in controls, and north positions were significantly drier than south [Gray and Spies 1993].) An ANOVA on substrate plots detected a significant effect for substrate type ($F_{[2,24]}=43.05$, $p=.0001$) and separation of least-square means indicated wood plots were significantly different from litter and soil plots ($p < .0001$).

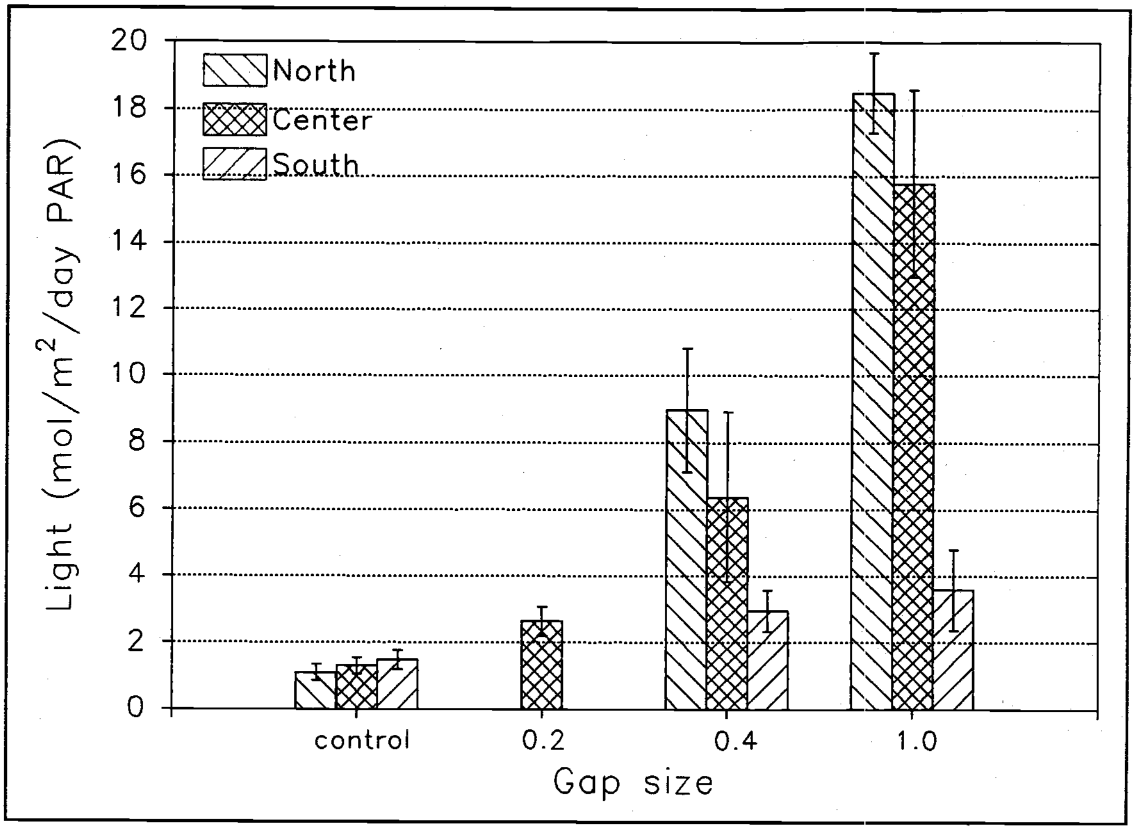

**Figure 4.3:** Mean levels of photosynthetically active radiation (PAR) by gap size and within-gap position. Data were adjusted for seasonal trends (see Methods).

Moisture was greatest in wood seed-plots, and tended to be slightly higher in litter plots than in mineral soil plots (Figure 4.4b). There were few consistent effects of shade treatment in the mature stands on moisture levels (shade: $F_{[2,6]}=1.81$, $p=.243$, shade* gap:$F_{[4,6]}=2.69$, $p=.134$), although moisture tended to decrease with shade level in controls and increase with shade level in 1.0 gaps (Figure 4.4c). The 90% shade cloth treatment may have intercepted filtered precipitation in controls, while shade may have reduced evaporation from the forest floor in 1.0 gaps.

Maximum surface temperature also varied among gap sizes and seed-plot treatments. Temperature patterns for the mineral soil seed-plots tended to mirror light patterns, with decreasing temperature from north to south in the larger gaps, although temperatures were relatively high in north positions of 0.4 gaps, probably due to a

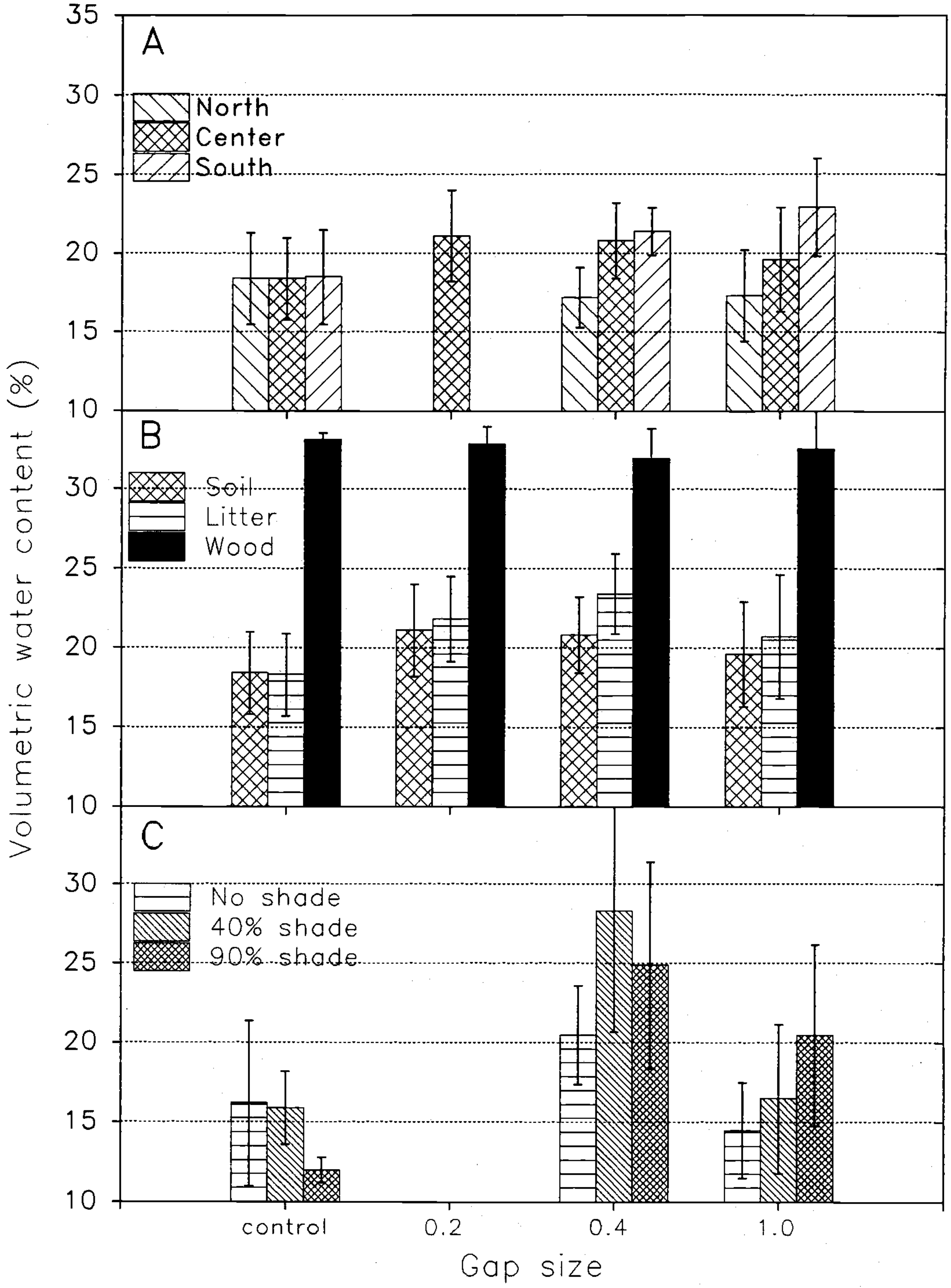

**Figure 4.4:** Volumetric water content in seed-plots by gap size and (a) within-gap position, (b) substrate, and (c) understory shade level. Data are means and standard errors of measurements taken in early August 1992 (n=4 stands for (a) and (b), n=2 stands for (c)).

temperature response to the incidence, rather than the amount, of direct radiation (Figure 4.5a). Mineral soil seed-plots tended to be cooler than the other substrates, and wood was only slightly cooler than litter, probably due to the similarly dark color but higher moisture content of wood (Figure 4.5b). Maximum surface temperatures on litter tended to decrease with level of shade, although temperatures still exceeded 55°C under shade in 1.0 gaps (Figure 4.5c). The 5 cm openings in the shade cloth apparently allowed sufficient duration of direct radiation "sunflecks" to increase surface temperatures dramatically.

The resource patterns discussed above provided an array of interacting levels of resources on the different seed-plots. There were a range of moisture levels present with increasing light levels, although high-moisture plots were relatively rare at high light levels (represented exclusively by wood seed-plots) (Figure 4.6a). The north positions of the 1.0 gaps tended to have the greatest light levels, although the highest light levels (24 mol/m$^2$/day) were recorded at the center of the 1.0 gap in stand PCM. Light levels between 5 and 10 mol/m$^2$/day were rare, with north and center positions of 1.0 gaps and north positions of 0.4 gaps in two stands above this zone, and with all other positions having light levels below this zone. Maximum surface temperatures did not vary as greatly with light as moisture did, with the highest temperatures tending to occur at the highest light levels (Figure 4.6b). The highest maximum surface temperatures at low light levels are represented exclusively by the shaded seed-plots.

### Microclimate effects on seedling establishment

Seedling establishment was primarily associated with light intensity, although moisture and surface temperature were also important. The relative importance of these three environmental factors varied among species. The raw data is shown before the regression results to display the variability within interacting resource levels and to compare trends for establishment of emerged seedlings with those for establishment from seed. Establishment of *Abies* emergents tended to increase with

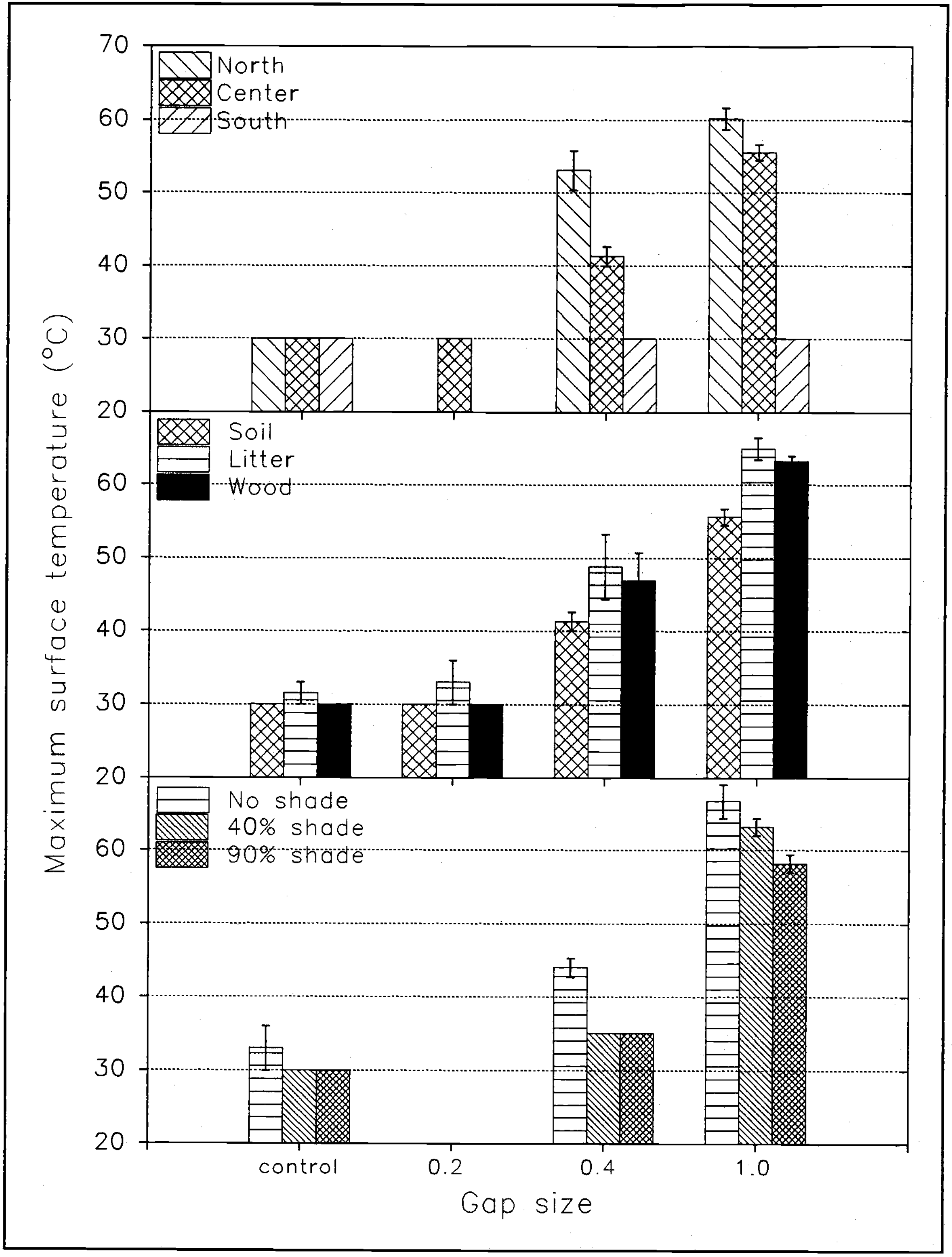

**Figure 4.5:** Maximum surface temperatures on seed-plots by gap size and (a) within-gap position, (b) substrate, and (c) understory shade level. Data are means and standard errors of the mean maxima (of three sample periods) per seed-plot (n=4 stands for (a) and (b), n=2 stands for (c)).

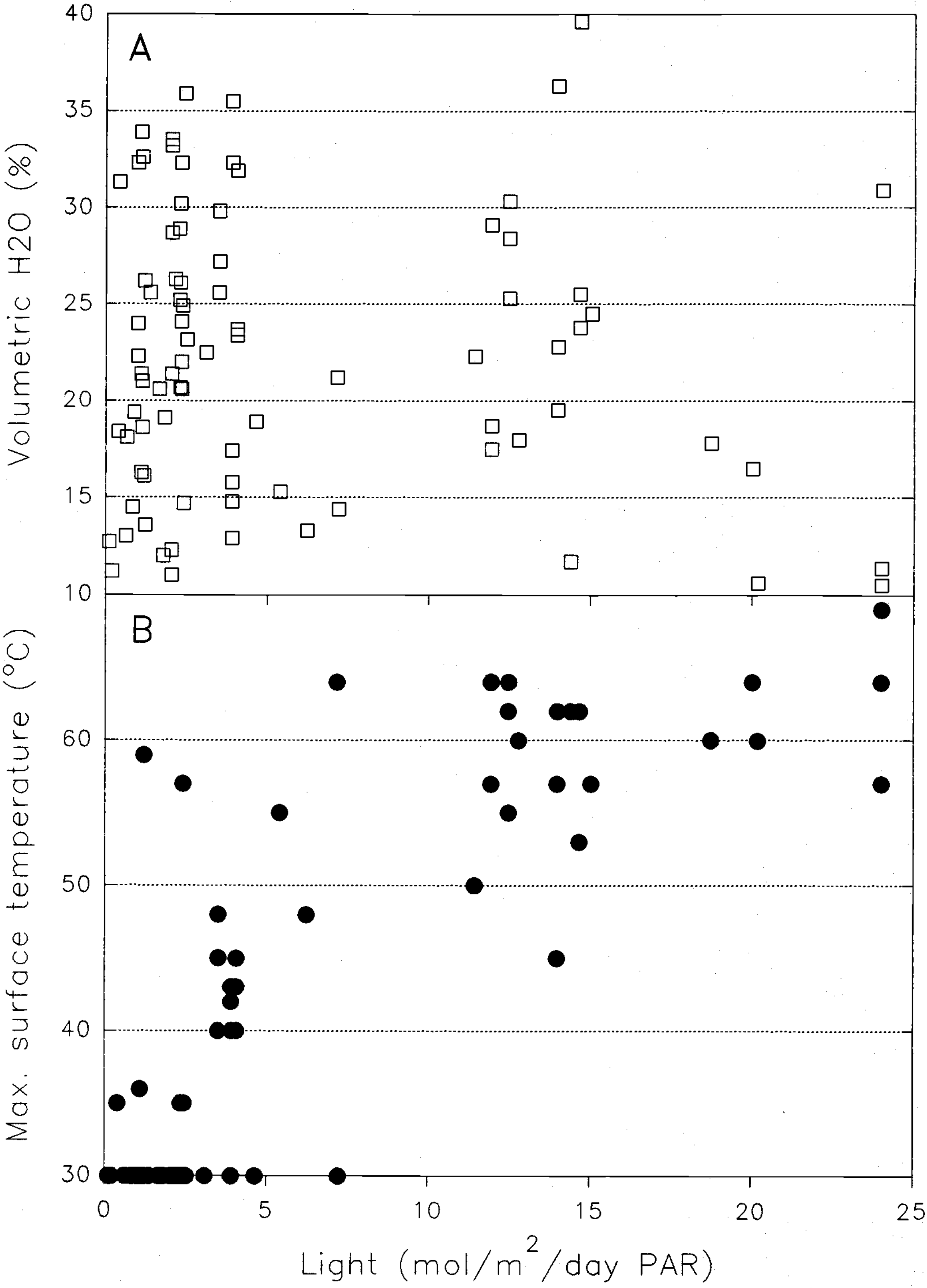

**Figure 4.6:** Patterns of (a) volumetric water content and (b) maximum surface temperature in relation to light levels (photosynthetically active radiation). Data are from each seed-plot treatment in each stand.

moisture content, particularly at low light levels (Figure 4.7). Few trends are evident with temperature, except for perhaps a slight decrease in establishment with increasing temperature at moderate and high moisture levels. The beneficial effect of moisture at low and moderate light levels appeared to be more pronounced for establishment of *Abies* as a fraction of seed (Figure 4.8), suggesting that seed germination was aided by surface layer moisture content. Establishment of *Pseudotsuga* emergents tended to increase with light, with little evidence of a decline at the highest light levels (Figure 4.9). Establishment did not appear to be very sensitive to moisture content or surface temperature at the highest light levels, but moisture did appear to aid establishment under low light conditions. Establishment of *Pseudotsuga* from seed, on the other hand, tended to increase with moisture content at both low and high light levels (Figure 4.10). Establishment of *Tsuga* tended to be more sensitive to moisture and light than establishment of the other species. Establishment at low light was greater on plots with high moisture, and establishment under high light was very low, although moisture also appeared to be beneficial in those conditions (Figure 4.11). Most of the decline in *Tsuga* numbers occurred early in the first summer, coincident with declining soil moisture levels in controls (Gray and Spies 1993). Soil moisture measurements in the seed plots, which integrated over a depth of 15 cm, probably over-estimate the moisture levels available to *Tsuga* seedlings; even *Tsuga* that survived the first summer in the controls had mean root lengths of less than 2.0 cm. In the few instances where different temperatures occurred at similar light and moisture levels, establishment tended to be lower where surface temperatures were highest. As with the other species, establishment of *Tsuga* from seed (Figure 4.12) was more sensitive to moisture content than establishment of emergents.

Seedling establishment of all species was correlated with light levels to a much greater degree than with moisture content. Much less of the variation in establishment was accounted for by regressions on moisture content than by regressions on light levels, with $r^2$ = .086, < .0001, and .166 for moisture regressions and $r^2$ = .190, .204, and .362 for light regressions for *Abies*, *Pseudotsuga*, and *Tsuga*, respectively. Predicted values for the light models are

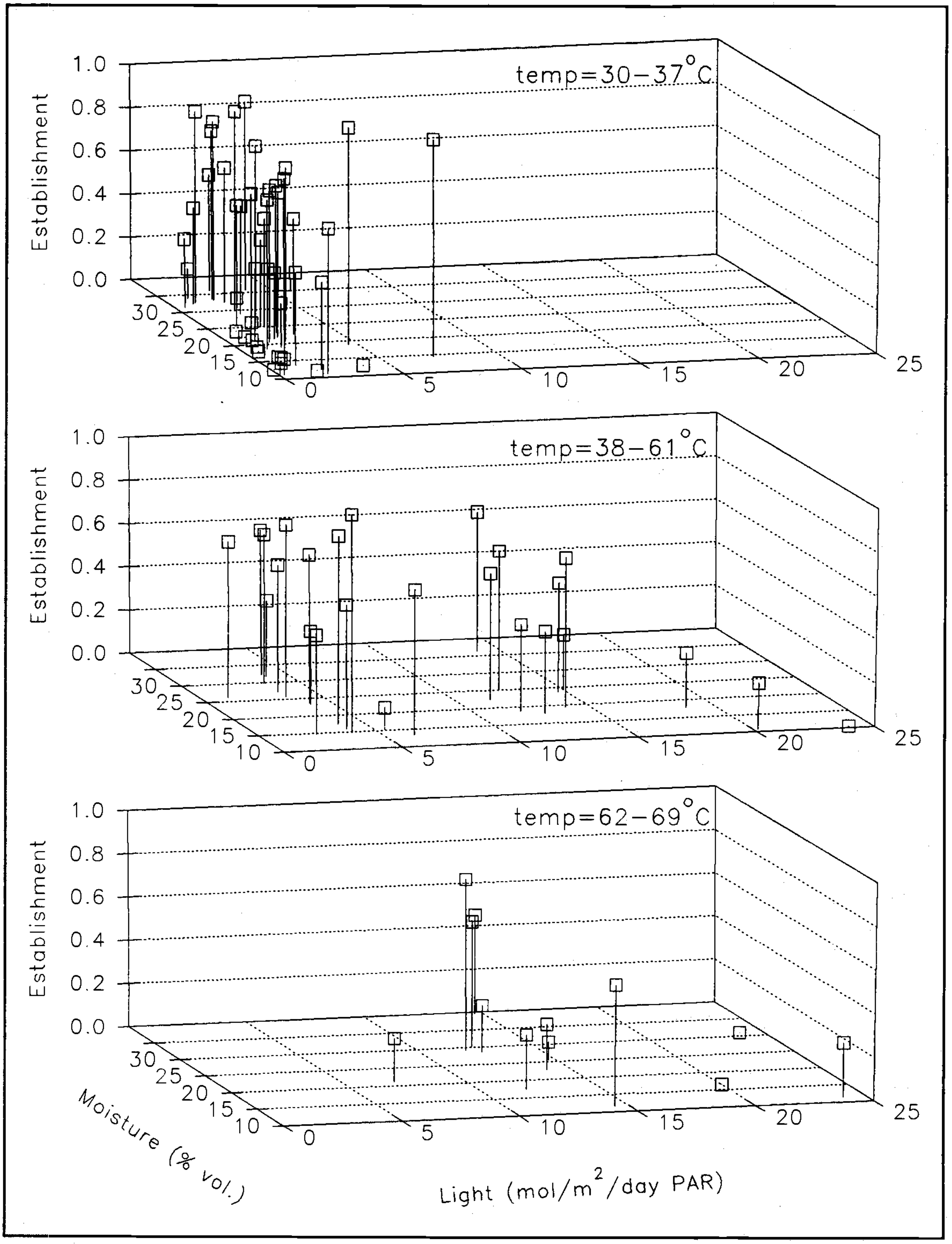

**Figure 4.7:** Establishment of *Abies amabilis* seedlings as a fraction of maximum number emerged in relation to light and volumetric moisture content at three levels of maximum surface temperatures.

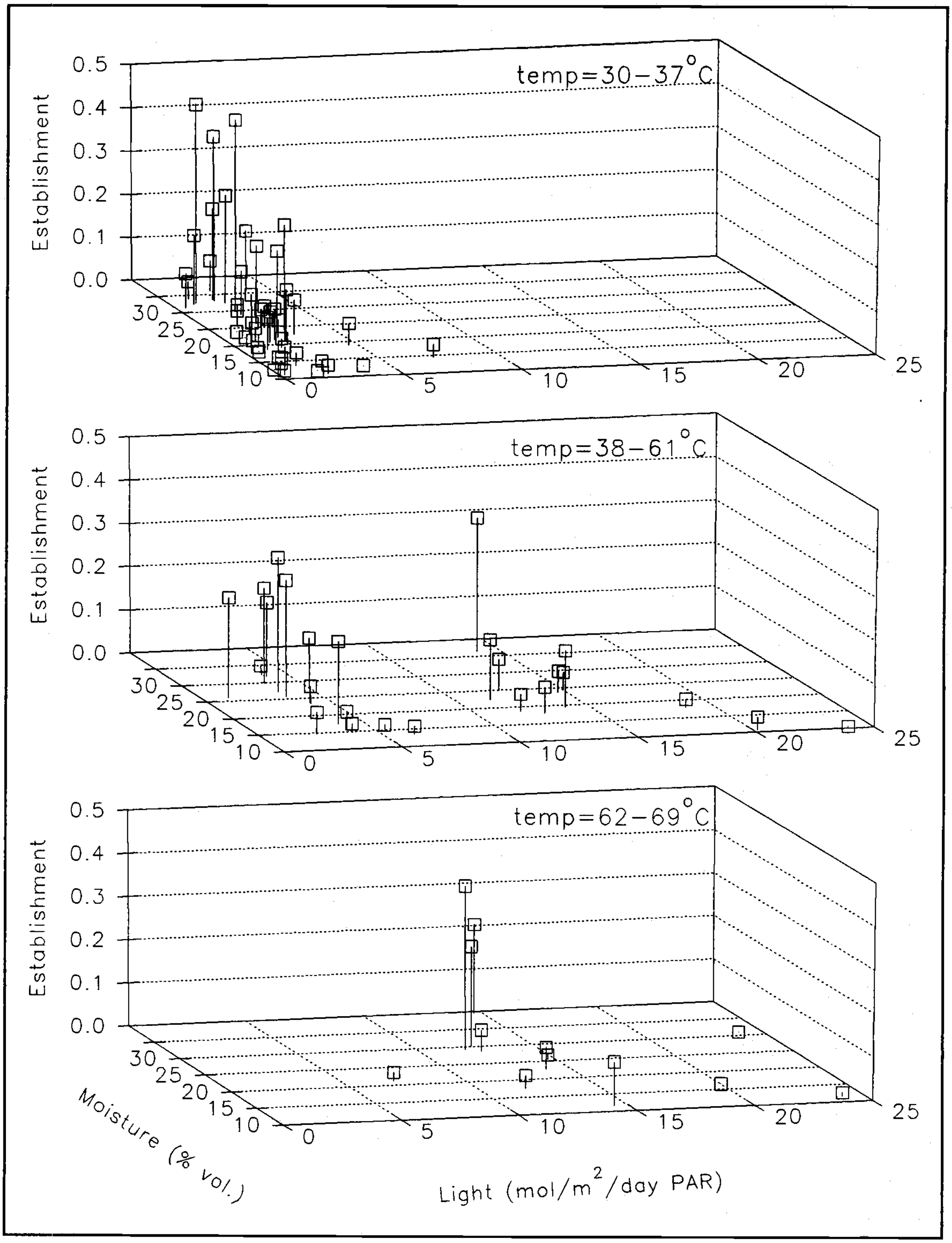

**Figure 4.8:** Establishment of *Abies amabilis* seedlings as a fraction of total seed in relation to light and volumetric moisture content at three levels of maximum surface temperatures measured.

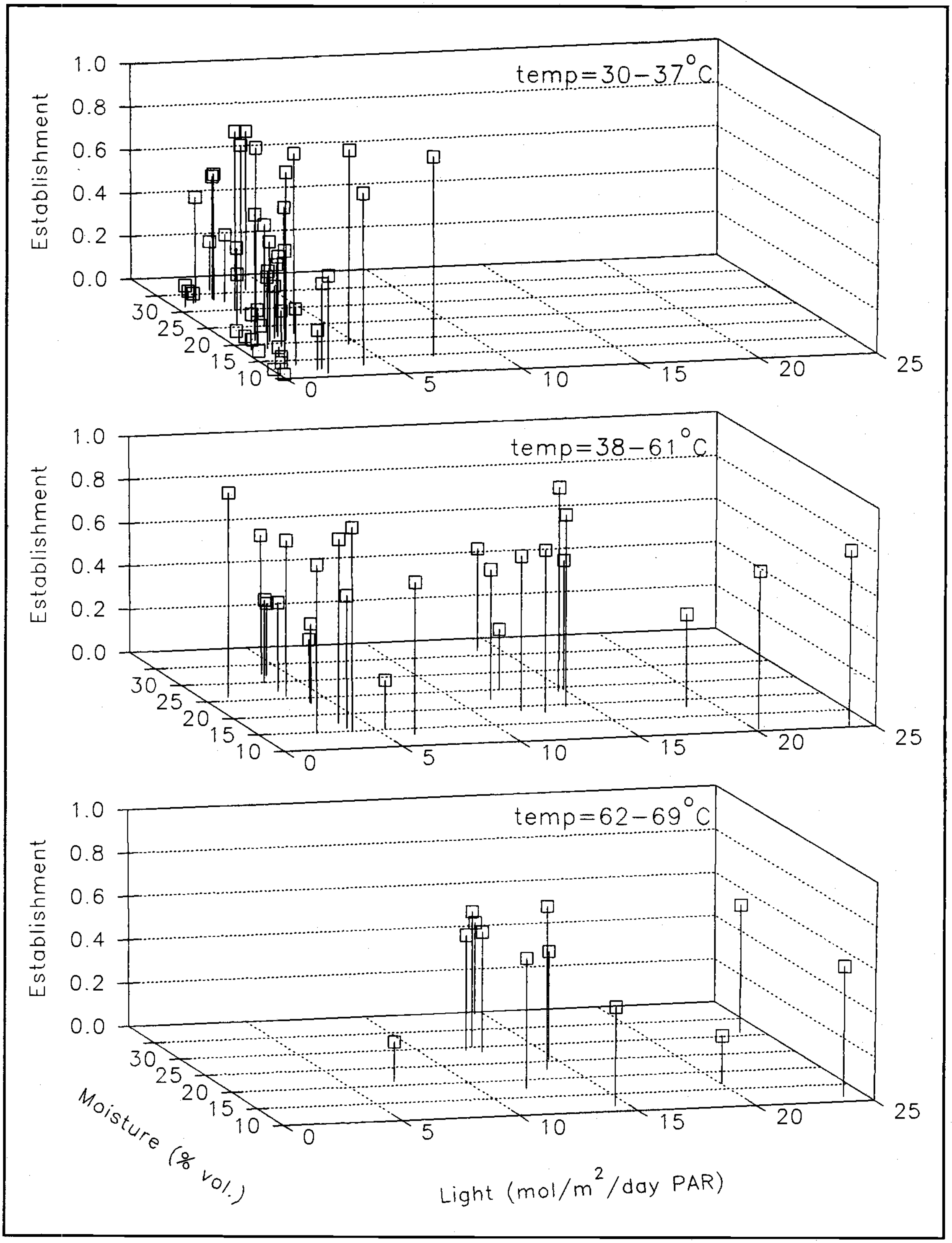

**Figure 4.9:** Establishment of *Pseudotsuga menziesii* seedlings as a fraction of maximum number emerged in relation to light and volumetric moisture content at three levels of maximum surface temperatures.

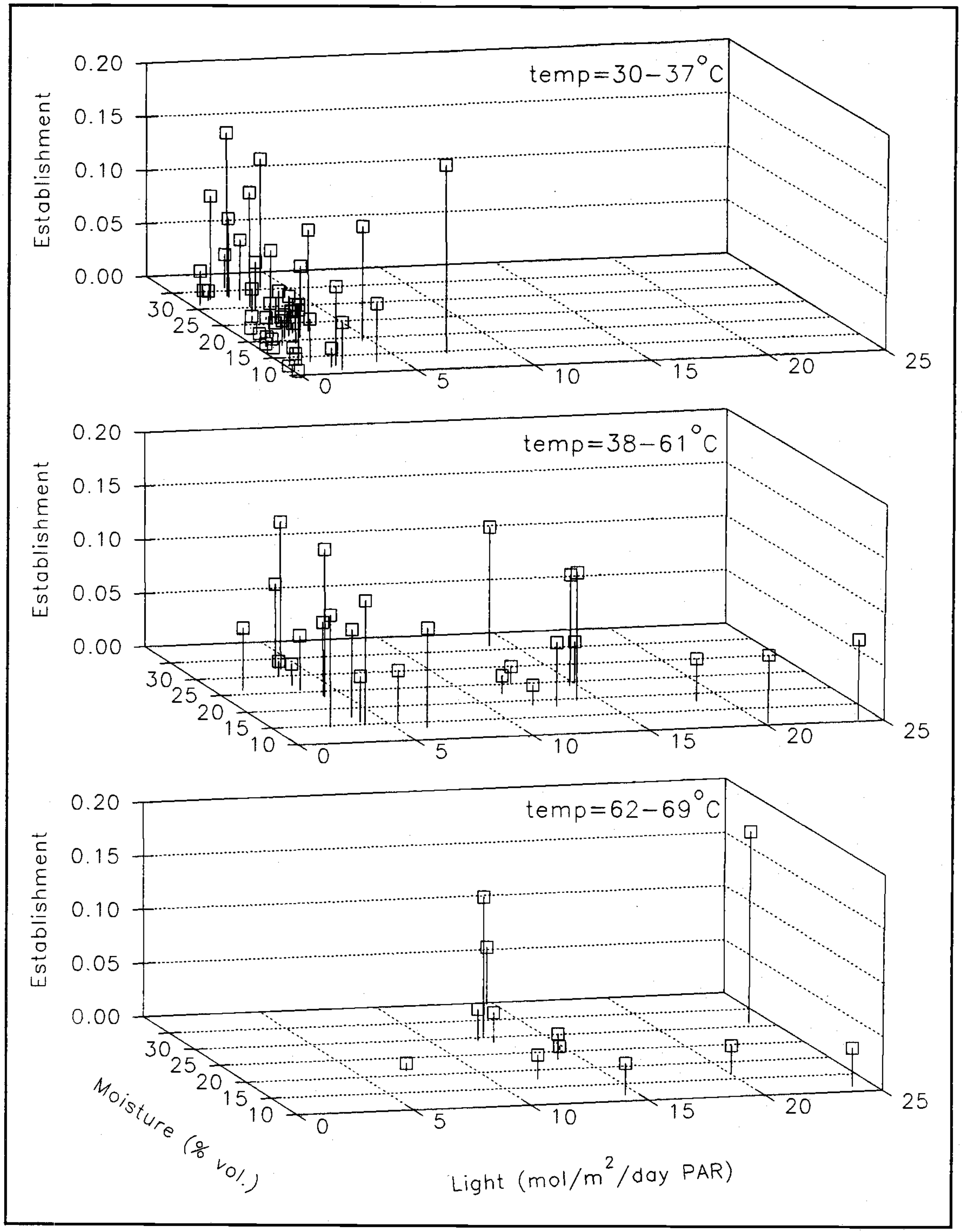

**Figure 4.10:** Establishment of *Pseudotsuga menziesii* seedlings as a fraction of total seed in relation to light and volumetric moisture content at three levels of maximum surface temperatures.

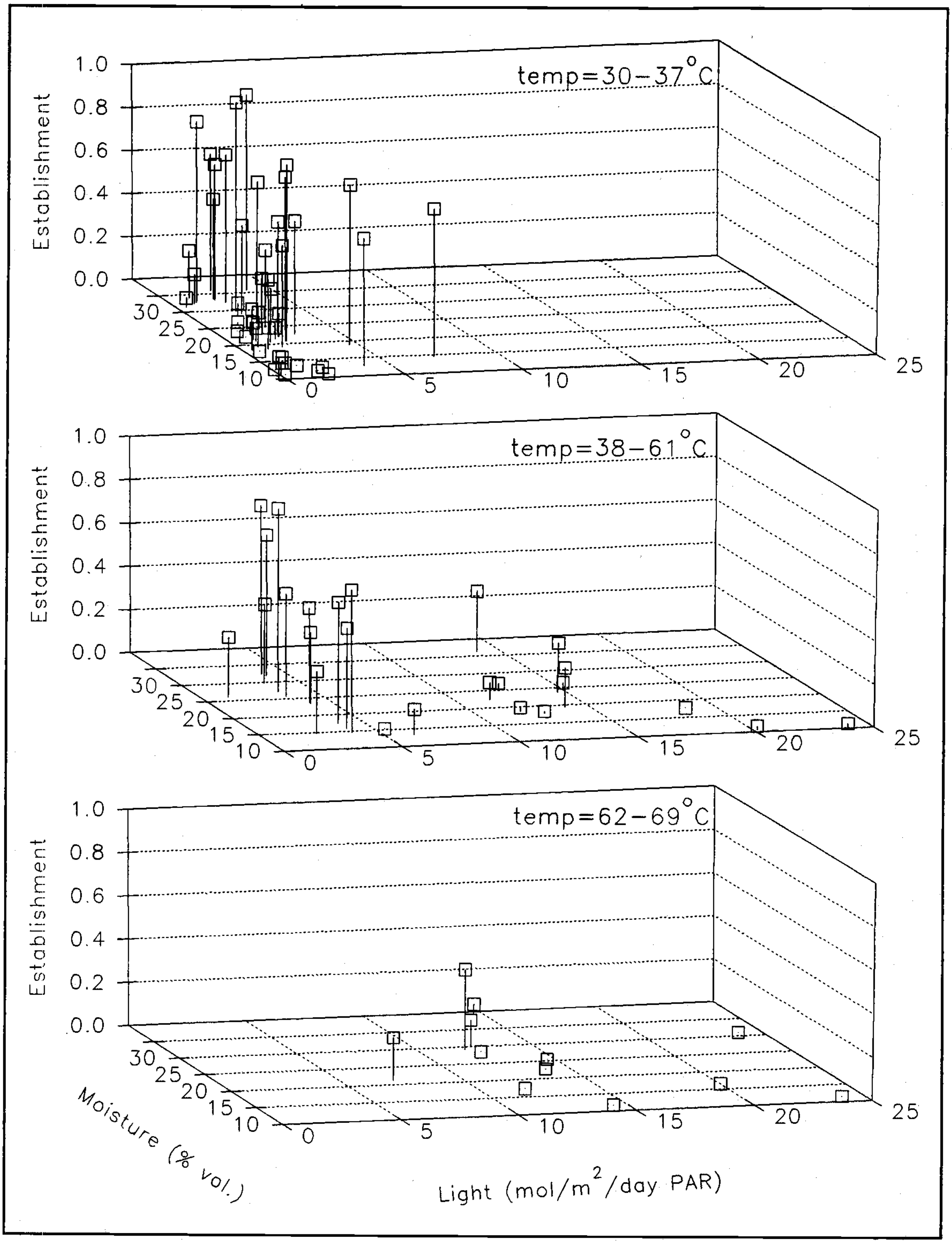

**Figure 4.11:** Establishment of *Tsuga heterophylla* seedlings as a fraction of maximum number emerged in relation to light and volumetric moisture content at three levels of maximum surface temperature.

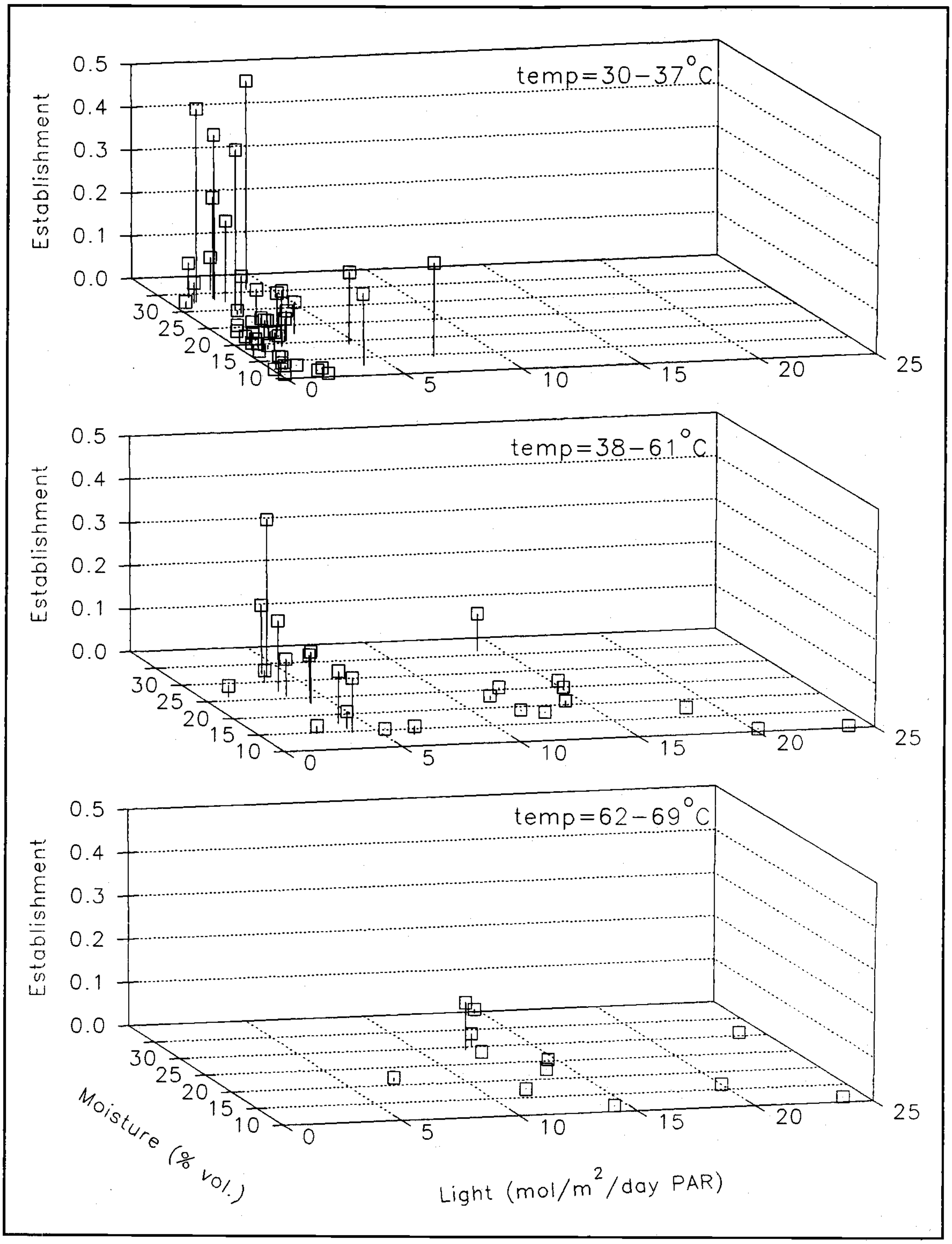

**Figure 4.12:** Establishment of *Tsuga heterophylla* seedlings as a fraction of total seed in relation to light and volumetric moisture content at three levels of maximum surface temperature.

plotted with the establishment data in Figure 4.13. Moisture content accounted for a relatively high portion of the variance in the residuals from the light models for *Tsuga*, much less for *Abies*, and basically none for *Pseudotsuga* (Table 4.2). The negative intercepts for the analysis of residuals for *Tsuga* and *Abies* indicate a relationship that treatments on which establishment was lower than predicted by light alone tended to have low moisture content.

Not surprisingly, the significance of models using all three variables to predict establishment were higher than when using light alone (Table 4.3). The increase in the coefficient of determination was very low for *Pseudotsuga* and relatively high for *Tsuga*. The modes of the predicted gaussian distributions for light and temperature were highest for *Pseudotsuga* and lowest for *Tsuga*. The pattern was reversed for moisture, with *Tsuga* having the highest predicted mode and *Pseudotsuga* the lowest. These patterns are evident in the surfaces generated from these models (Figures 4.14, 4.15, and 4.16). The figures suggest that *Pseudotsuga* establishment increases gradually with increasing light and is relatively insensitive to moisture and surface temperature, that *Abies* establishment increases more rapidly with light, decreases at high light, and is more sensitive to moisture and temperature, and that *Tsuga* establishment is severely limited at high light levels and is the most sensitive to moisture and temperature.

### Comparison of structural and microclimate models of establishment

The regressions of seedling establishment on light, moisture, and surface temperature accounted for less of the variation in seedling establishment than ANOVAs on gap size, within-gap position, substrate, and shade level, regardless of whether all factors or only significant factors were considered. Coefficients of determination from the ANOVAs (Table 4.4) tended to be highest for *Tsuga* and lowest for *Pseudotsuga*, as was the case for the coefficients of determination from the regression models (Table 4.3). These results suggest that patch-type categorizations account for more factors important to seedling establishment (*e.g.* biotic interactions)

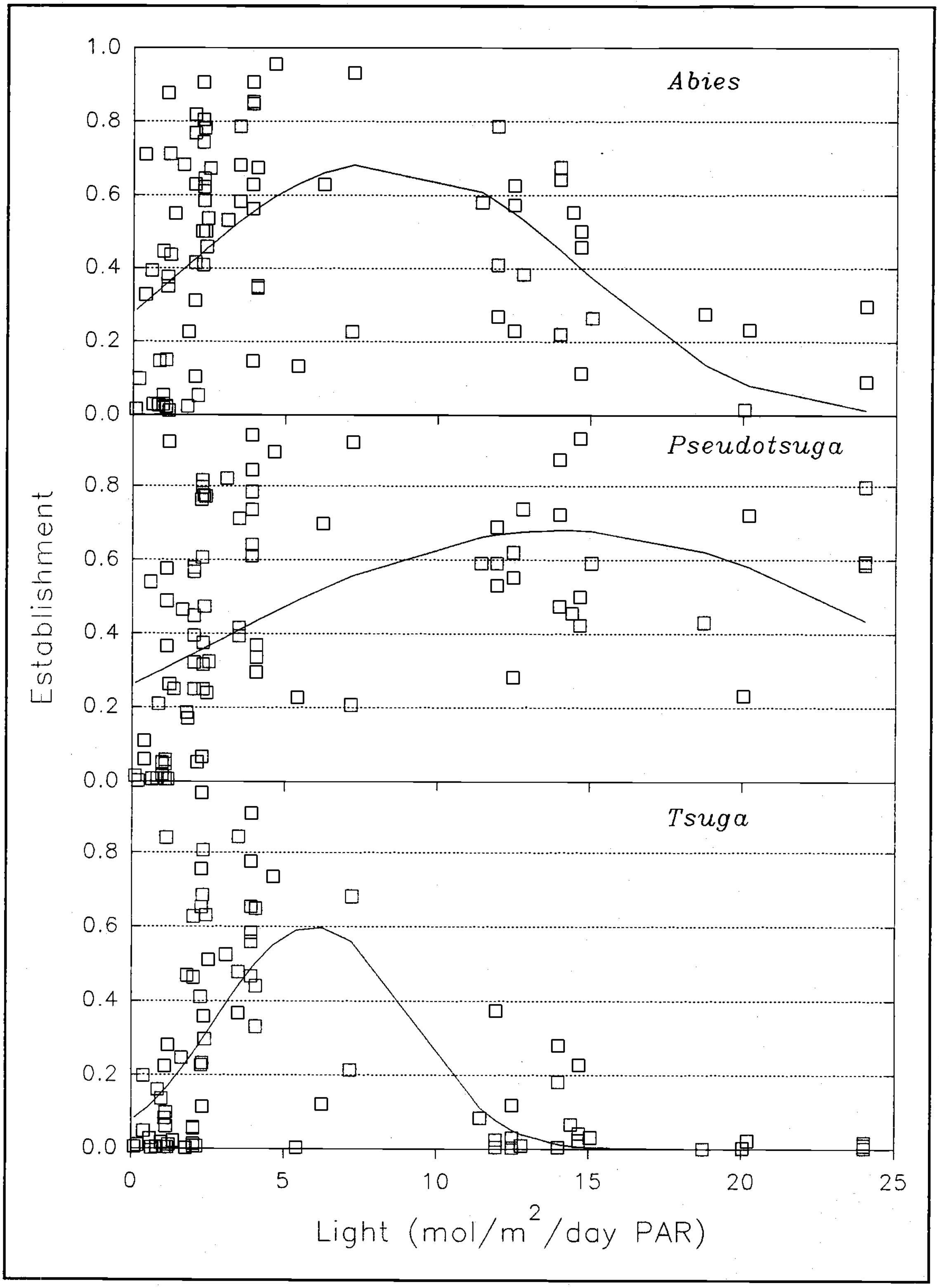

**Figure 4.13:** Non-linear model of seedling establishment (% of maximum emerged) for *Abies*, *Pseudotsuga*, and *Tsuga* in relation to light.

**Table 4.2:** Non-linear regression results for seedling establishment ("Est", % of maximum emerged) as a function of PAR quantum flux (mol/m$^2$/day). Symbols are: A= maximum establishment, $\mu_f$= mode of distribution, and $\sigma_f$= standard deviation of distribution with respect to light. Lower portion of table are results of linear regression of residuals of light model on volumetric water content.

$$\arcsin\sqrt{Est}=A*\exp\left(-\left(\frac{\mu_f-flux}{\sigma_f}\right)^2\right)$$

| | *Abies* | *Pseudotsuga* | *Tsuga* |
|---|---|---|---|
| A | 0.98 (±0.09) | 0.97 (±0.07) | 0.89 (±0.10) |
| $\mu_f$ | 8.17 (±0.57) | 14.1 (±1.88) | 5.99 (±0.44) |
| $\sigma_f$ | 10.9 (±1.56) | 18.2 (±3.40) | 5.58 (±0.58) |
| n | 84 | 84 | 84 |
| MSE | 0.0898 | 0.0927 | 0.0877 |
| $r^2$ | 0.190 | 0.204 | 0.362 |
| **resid = ß0 + ß1 * %H2O** | | | |
| ß0 | -0.191 (±0.291) | 0.021 (±0.302) | -0.397 (±0.262) |
| ß1 | 0.878 (±0.438) | -0.103 (±0.456) | 1.83 (±0.394) |
| $r^2$ | 0.0467 | 0.0006 | 0.209 |

than environment alone. Alternatively, environment may not have been measured at the precise scales (in time or space) appropriate for seedling establishment, although they were apparently more appropriate for *Tsuga* than for *Abies* or *Pseudotsuga*. Another possible interpretation is that *Abies* and *Pseudotsuga* are not as sensitive to environment over the range of levels found in this study.

Analysis of variance on the residuals from the full non-linear resource model accounted for less of the variation in seedling establishment (Table 4.5) than ANOVAs on the original establishment data (Table 4.4). Although fewer factors were significant in the analysis of residuals, the coefficients of determination for all factors were still quite high (greater than .25). This counter-intuitive result is not

**Table 4.3:** Non-linear regression results for seedling establishment ("Est") as a function of PAR quantum flux (mol/m$^2$/day), volumetric moisture content ("H2O", in %), and maximum surface temperature ("temp", in °C). Asymptotic standard errors for parameter estimates in parentheses. Symbols are: A= maximum establishment, $\mu$= mode of distribution, $\sigma$= standard deviation of distribution, and the f,h, and t subscripts refer to flux, moisture, and temperature distributions, respectively.

$$\arcsin\sqrt{Est}=A*\exp\left(-\left[\left(\frac{\mu_f-flux}{\sigma_f}\right)^2+\left(\frac{\mu_h-H2O}{\sigma_h}\right)^2+\left(\frac{\mu_t-temp}{\sigma_t}\right)^2\right]/3\right)$$

| | *Abies* | | *Pseudotsuga* | | *Tsuga* | |
|---|---|---|---|---|---|---|
| A | 1.45 | (±3.49) | 1.37 | (±1.04) | 2.95 | (±4.34) |
| $\mu_f$ | 10.0 | (±1.02) | 17.9 | (±7.47) | 7.45 | (±0.528) |
| $\sigma_f$ | 6.11 | (±0.836) | 11.0 | (±3.26) | 3.30 | (±0.296) |
| $\mu_h$ | 48.9 | (±646) | 30.2 | (±10.8) | 61.3 | (±80.8) |
| $\sigma_h$ | 45.0 | (±477) | 45.5 | (±81.9) | 25.1 | (±27.8) |
| $\mu_t$ | 34.9 | (±7.41) | 38.7 | (±6.83) | 25.7 | (±16.3) |
| $\sigma_t$ | 21.5 | (±6.57) | 21.7 | (±6.60) | 22.4 | (±11.1) |
| n | 84 | | 84 | | 84 | |
| MSE | 0.0823 | | 0.0926 | | 0.0623 | |
| $r^2$ | 0.293 | | 0.243 | | 0.570 | |

because the resource model didn't reduce variance (the total sums of squares for the ANOVAs on residuals were much smaller than for the ANOVAs on establishment), but because the resource regressions reduced the variance of the error terms in the ANOVA model (due to stands as replicates within age classes) as well as the variance of the fixed effects. Interestingly, while the sums of squares of effects such as gap size, within-gap position, substrate, and their interactions tended to be large relative to other factors in the ANOVA on establishment (Table 4.4), the sums of squares of interactions with age class tended to increase in importance in the ANOVA on the residuals from the resource models (Table 4.5). (For example, while the sums of squares square for gap and age*gap for *Abies* in the ANOVA on position are 2.8 and 0.3 in Table 4.4, the sums of squares for the same effects are .22 and .24 in Table 4.5.) Examination of the age class by gap size interaction indicated that the resource

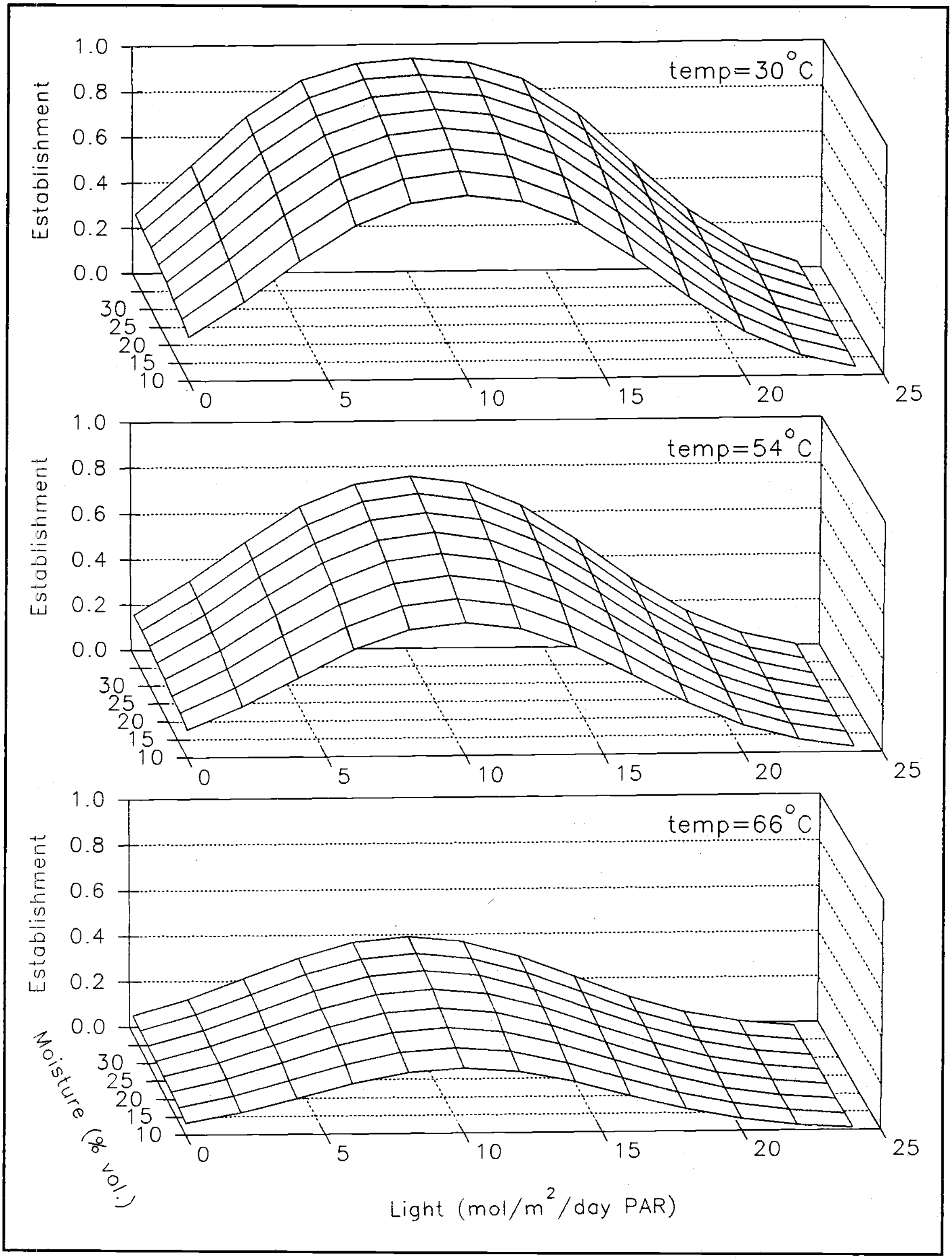

**Figure 4.14:** Non-linear model results of establishment of *Abies amabilis* (% of maximum emerged) by light and volumetric moisture content for three selected levels of maximum surface temperature (increasing temperature from top to bottom).

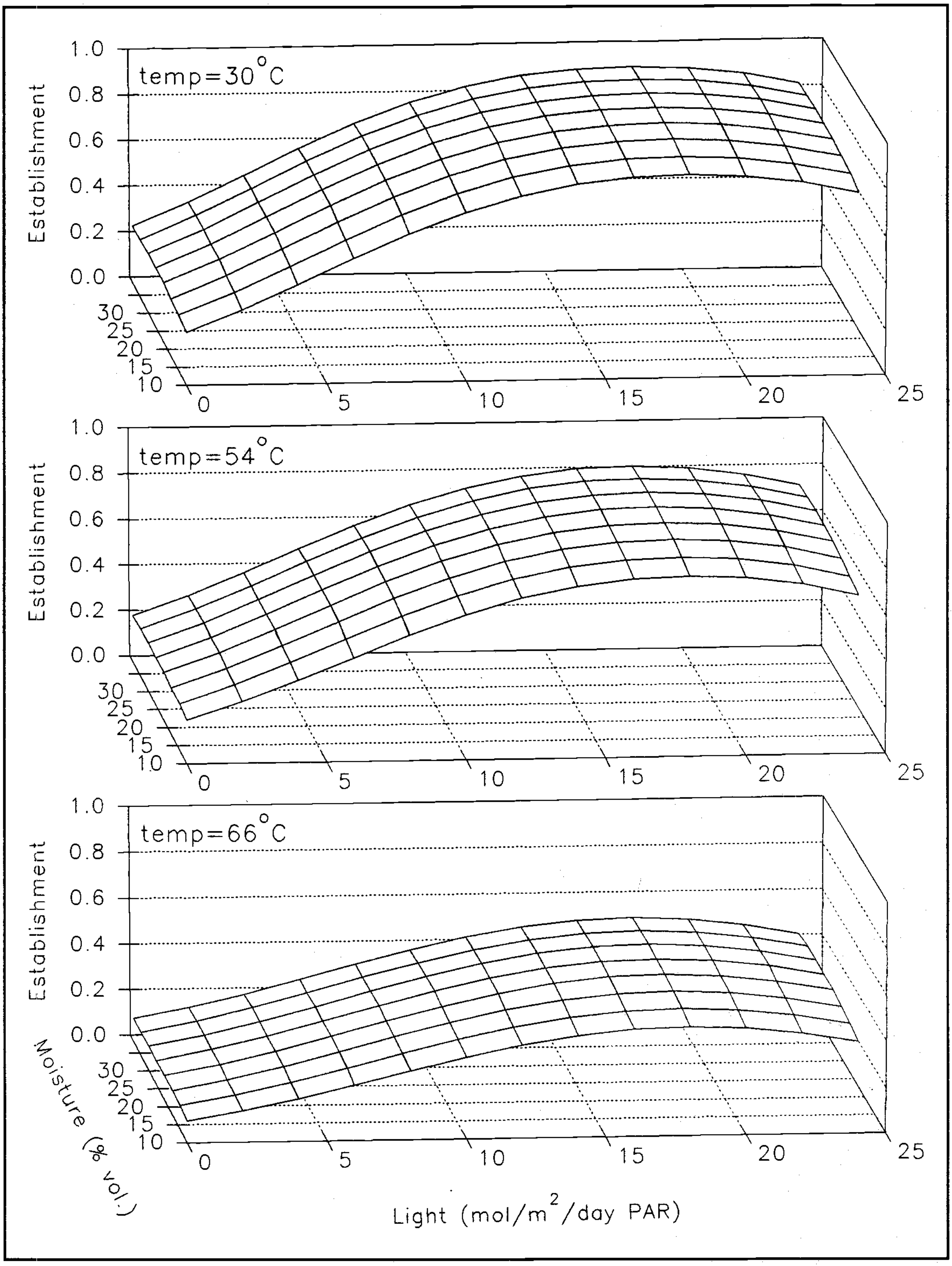

**Figure 4.15:** Non-linear model results of establishment of *Pseudotsuga menziesii* (% of maximum emerged) by light and volumetric moisture content for three selected levels of maximum surface temperature (increasing temperature from top to bottom).

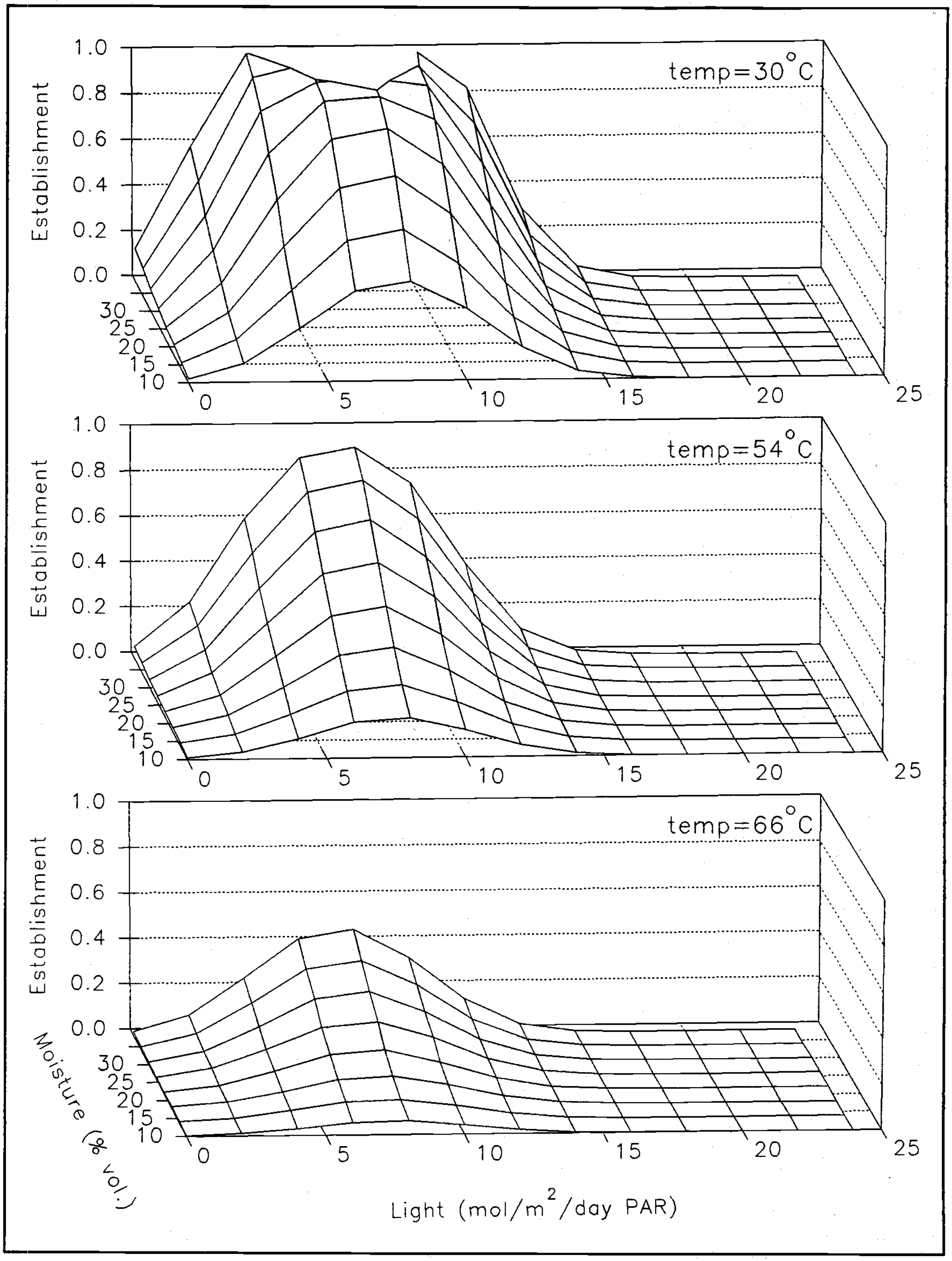

**Figure 4.16:** Non-linear model results of establishment of *Tsuga heterophylla* (% of maximum emerged) by light and volumetric moisture content for three selected levels of maximum surface temperature (increasing temperature from top to bottom).

**Table 4.4:** Proportion of variance (sums of squares) accounted for by separate ANOVAs on seedling establishment, by experiment and species, where Abam= *Abies amabilis*, Psme= *Pseudotsuga menziesii*, and Tshe= *Tsuga heterophylla*. Factors are: age= age class, gap= gap size, pos= within-gap position, subs= substrate, and shade= shade level. Asterisks (*) indicate factors significant at $p < .10$ level.

| Source | DF | Abam | Psme | Tshe |
|---|---|---|---|---|
| age | 1 | 0.991 | 0.132 | 0.342 |
| Error: stand(age) | 2 | 0.648 | 10.295 | 4.822 |
| gap | 3 | 2.794* | 7.833* | 13.388* |
| age*gap | 3 | 0.282 | 0.161 | 1.145 |
| Error: stand*gap(age) | 6 | 1.071 | 0.343 | 3.816 |
| pos | 2 | 0.245 | 0.527 | 10.426* |
| age*pos | 2 | 0.612* | 0.130 | 0.311 |
| gap*pos | 4 | 2.968* | 1.131 | 9.648* |
| age*gap*pos | 4 | 0.358 | 0.070 | 1.068 |
| Error: stand*gap*pos(age) | 12 | 0.951 | 2.679 | 0.206 |
| | | | | |
| Corrected total | 39 | 13.189 | 28.239 | 46.019 |
| Sum all factors | | 8.250 | 9.983 | 36.329 |
| **R-square** | | **0.6255** | **0.3535** | **0.7894** |
| *R-square sig. factors* | | *0.4833* | *0.2774* | *0.7271* |
| | | | | |
| age | 1 | 0.272 | 0.006 | 0.027 |
| Error: stand(age) | 2 | 0.992 | 8.640 | 3.142 |
| gap | 3 | 3.325 | 8.098* | 33.027* |
| age*gap | 3 | 0.382 | 0.015 | 3.348 |
| Error: stand*gap(age) | 6 | 4.180 | 2.297 | 20.713 |
| subs | 2 | 2.631* | 0.503 | 21.995* |
| age*subs | 2 | 0.387 | 0.038 | 0.215 |
| gap*subs | 6 | 1.989* | 1.356 | 5.236* |
| age*gap*subs | 6 | 1.442* | 0.189 | 1.554 |
| Error: stand*gap*subs(age) | 16 | 1.428 | 2.411 | 5.553 |
| | | | | |
| Corrected total | 47 | 17.793 | 25.604 | 103.106 |
| Sum all factors | | 10.428 | 10.205 | 65.403 |
| **R-square** | | **0.5861** | **0.3986** | **0.6343** |
| *R-square sig. factors* | | *0.3407* | *0.3163* | *0.5844* |
| | | | | |
| gap | 2 | 11.040 | 40.229 | 54.046* |
| Error: gap(stand) | 3 | 4.438 | 17.204 | 3.578 |
| shade | 2 | 0.100 | 8.235 | 3.203* |
| gap*shade | 4 | 3.979 | 19.588 | 35.165* |
| Error: gap*shade(stand) | 6 | 2.216 | 11.780 | 1.329 |
| | | | | |
| Corrected total | 17 | 26.591 | 111.503 | 108.660 |
| Sum all factors | | 15.119 | 68.052 | 92.414 |
| **R-square** | | **0.5686** | **0.6103** | **0.8505** |
| *R-square sig. factors* | | *0.0000* | *0.0000* | *0.8505* |

**Table 4.5:** Proportion of residual variance from full non-linear model accounted for by separate ANOVAs on seedling establishment, by experiment and species. Abbreviations are described in Table 4.4.

| Source | DF | Abam | Psme | Tshe |
|---|---|---|---|---|
| age | 1 | 0.154 | 0.000 | 0.001 |
| Error: stand(age) | 2 | 0.224 | 1.341 | 0.570 |
| gap | 3 | 0.223 | 0.252 | 0.340 |
| age*gap | 3 | 0.235 | 0.075 | 0.008 |
| Error: stand*gap(age) | 6 | 0.401 | 0.084 | 0.174 |
| pos | 2 | 0.043 | 0.043 | 0.043 |
| age*pos | 2 | 0.032 | 0.050 | 0.056 |
| gap*pos | 4 | 0.578 | 0.374 | 0.323 |
| age*gap*pos | 4 | 0.036 | 0.075 | 0.070 |
| Error: stand*gap*pos(age) | 12 | 0.341 | 0.650 | 0.361 |
| | | | | |
| Corrected total | 39 | 2.536 | 3.231 | 1.940 |
| Sum all factors | | 1.301 | 0.870 | 0.842 |
| **R-square** | | **0.5131** | **0.2691** | **0.4339** |
| *R-square sig. factors* | | *0.2279* | *0.0780* | *0.3418* |
| | | | | |
| age | 1 | 0.015 | 0.059 | 0.100 |
| Error: stand(age) | 2 | 0.633 | 1.126 | 0.770 |
| gap | 3 | 0.089 | 0.450 | 0.187 |
| age*gap | 3 | 0.554 | 0.153 | 0.129 |
| Error: stand*gap(age) | 6 | 0.744 | 0.661 | 0.306 |
| subs | 2 | 0.241 | 0.007 | 0.278 |
| age*subs | 2 | 0.105 | 0.002 | 0.128 |
| gap*subs | 6 | 0.347 | 0.167 | 0.075 |
| age*gap*subs | 6 | 0.315 | 0.019 | 0.244 |
| Error: stand*gap*subs(age) | 16 | 0.479 | 0.436 | 0.670 |
| | | | | |
| Corrected total | 47 | 3.524 | 3.081 | 2.887 |
| Sum all factors | | 1.667 | 0.858 | 1.141 |
| **R-square** | | **0.4731** | **0.2783** | **0.3952** |
| *R-square sig. factors* | | *0.0684* | *0.0000* | *0.0963* |
| | | | | |
| gap | 2 | 0.513 | 0.947 | 0.288 |
| Error: gap(stand) | 3 | 0.617 | 0.307 | 0.313 |
| shade | 2 | 0.057 | 0.066 | 0.048 |
| gap*shade | 4 | 0.162 | 0.963 | 0.168 |
| Error: gap*shade(stand) | 6 | 0.336 | 0.336 | 0.051 |
| | | | | |
| Corrected total | 17 | 1.686 | 2.619 | 0.869 |
| Sum all factors | | 0.732 | 1.976 | 0.504 |
| **R-square** | | **0.4343** | **0.7546** | **0.5801** |
| *R-square sig. factors* | | *0.0000* | *0.3677* | *0.1933* |

models were under-estimating establishment in 0.4 and 1.0 gaps in mature stands and over-estimating establishment in old-growth stands (Table 4.6). Establishment of *Abies* and *Tsuga* in 0.2 gaps, on the other hand, tended to be underestimated in old-growth stands.

Analysis of variance on the predicted values from the full non-linear resource model tended to account for similar, or greater, amounts of the variation in seedling establishment (Table 4.7) than ANOVAs on the original establishment data (Table 4.4). Coefficients of determination were increased for *Pseudotsuga* in particular. These results suggest that there was a fairly strong relationship (greater than 55% correlation) between resource effects on establishment and patch-type categorizations of seedling microsites.

**Table 4.6:** Means of residuals from full non-linear resource models by age class, gap, and species, where Abam= *Abies amabilis*, Psme= *Pseudotsuga menziesii*, and Tshe= *Tsuga heterophylla*. Gap size "ctl"= controls.

| | | **Age Class** | |
|---|---|---|---|
| gap | species | mature | old-growth |
| ctl | Abam | -0.1571 | -0.0186 |
| 0.2 | Abam | -0.0891 | 0.2484 |
| 0.4 | Abam | 0.0693 | -0.0278 |
| 1.0 | Abam | 0.1658 | -0.0672 |
| ctl | Psme | -0.2206 | -0.1045 |
| 0.2 | Psme | 0.1299 | 0.1598 |
| 0.4 | Psme | 0.0461 | -0.0025 |
| 1.0 | Psme | 0.1496 | -0.0327 |
| ctl | Tshe | -0.1463 | -0.0834 |
| 0.2 | Tshe | -0.0299 | 0.2024 |
| 0.4 | Tshe | 0.0349 | 0.0097 |
| 1.0 | Tshe | 0.1177 | 0.0001 |

**Table 4.7:** Proportion of variance from full non-linear model predicted values accounted for by separate ANOVAs on seedling establishment, by experiment and species. Abbreviations are described in Table 4.4.

| Source | DF | Abam | Psme | Tshe |
|---|---|---|---|---|
| age | 1 | 0.068 | 0.020 | 0.017 |
| Error: stand(age) | 2 | 0.029 | 0.054 | 0.056 |
| gap | 3 | 0.493 | 0.665* | 0.518 |
| age*gap | 3 | 0.036 | 0.065 | 0.116* |
| Error: stand*gap(age) | 6 | 0.073 | 0.037 | 0.062 |
| pos | 2 | 0.161 | 0.121* | 0.581* |
| age*pos | 2 | 0.122 | 0.103 | 0.004 |
| gap*pos | 4 | 0.346 | 0.086 | 0.510* |
| age*gap*pos | 4 | 0.146 | 0.056 | 0.059 |
| Error: stand*gap*pos(age) | 12 | 0.583 | 0.268 | 0.375 |
| | | | | |
| Corrected total | 39 | 2.086 | 1.447 | 2.406 |
| Sum all factors | | 1.372 | 1.117 | 1.804 |
| **R-square** | | **0.6579** | **0.7716** | **0.7498** |
| *R-square sig. factors* | | *0.0000* | *0.1285* | *0.5016* |
| | | | | |
| age | 1 | 0.042 | 0.031 | 0.078 |
| Error: stand(age) | 2 | 0.078 | 0.081 | 0.243 |
| gap | 3 | 0.599 | 0.514* | 2.076* |
| age*gap | 3 | 0.382 | 0.112 | 0.293 |
| Error: stand*gap(age) | 6 | 0.686 | 0.232 | 0.532 |
| subs | 2 | 0.085* | 0.097* | 0.485* |
| age*subs | 2 | 0.028* | 0.006 | 0.147* |
| gap*subs | 6 | 0.065* | 0.090* | 0.150 |
| age*gap*subs | 6 | 0.012 | 0.020 | 0.070 |
| Error: stand*gap*subs(age) | 16 | 0.063 | 0.045 | 0.205 |
| | | | | |
| Corrected total | 47 | 2.040 | 1.226 | 4.279 |
| Sum all factors | | 1.213 | 0.869 | 3.299 |
| **R-square** | | **0.5946** | **0.7084** | **0.7709** |
| *R-square sig. factors* | | *0.0874* | *0.5716* | *0.6327* |
| | | | | |
| gap | 2 | 0.194 | 0.018 | 0.508 |
| Error: gap(stand) | 3 | 0.071 | 0.007 | 0.153 |
| shade | 2 | 0.120 | 0.124* | 0.115* |
| gap*shade | 4 | 0.093 | 0.044 | 0.162* |
| Error: gap*shade(stand) | 6 | 0.131 | 0.079 | 0.059 |
| | | | | |
| Corrected total | 17 | 0.609 | 0.271 | 0.997 |
| Sum all factors | | 0.407 | 0.185 | 0.785 |
| **R-square** | | **0.6672** | **0.6827** | **0.7871** |
| *R-square sig. factors* | | *0.0000* | *0.4572* | *0.1743* |

## Seedling growth

Seedling size varied with resource levels among substrates and gap sizes, and was sensitive to both light and moisture (Figure 4.17). Size of *Abies* seedlings tendedto increase with light, with the largest seedlings at lower light levels found at higher moisture levels. Size of *Pseudotsuga* seedlings increased more dramatically with light than *Abies*, and although the largest seedlings at lower light were also found at higher moisture levels, the variability of this trend was much greater. Size of *Tsuga* seedlings tended to increase more rapidly with light levels than size of the other species, and also tended to respond more favorably to moisture levels, although the largest *Tsuga* seedlings were found at moderate moisture levels.

The results of the regression analysis reflect the patterns discussed above, with seedling size positively affected by light and moisture (Table 4.8). The negative quadratic terms in the model reflect a damping of the linear increase in size with these resource levels. Surface temperature was not included in this model; in preliminary step-wise regressions, temperature often precluded inclusion of light in the models, and since temperature and light were highly correlated, and surface temperature is a much less obvious factor for growth than light, it was excluded from the final model. The surfaces predicted for the three species by this model were surprising in a few respects. Seedling size for *Pseudotsuga* and *Tsuga* was predicted to decline at high light levels regardless of moisture content (Figure 4.18). This unusual response is partly due to the generally low moisture contents present in high light environments (in north positions of large gaps and the center of the 1.0 gap in stand PCM); since there was insufficient data to model a moisture response at high light, the model may have adjusted the parameter for light to reflect decreased growth. The predicted decline in seedling size with increasing moisture content appears to be a substrate effect--high moisture contents (particularly at light levels above about 10 mol/m$^2$/day) were almost exclusively represented by decayed wood seed-plots, where seedlings were usually smaller than on soil and litter plots. Removing the wood plots from the regression analysis tended to reduce the negative effect of high light as well as any

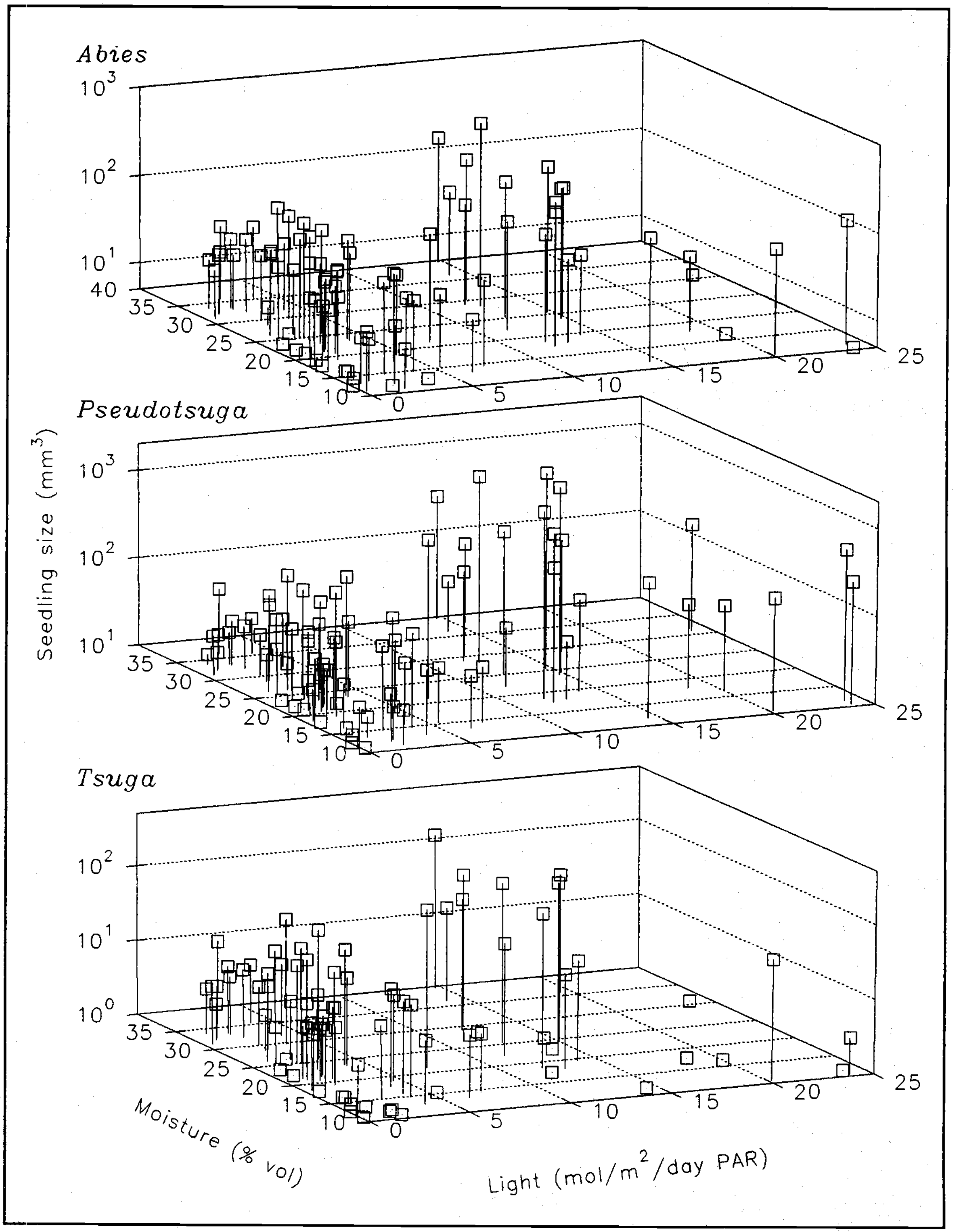

**Figure 4.17:** Size of *Abies amabilis*, *Pseudotsuga menziesii*, and *Tsuga heterophylla* seedlings (basal diameter*height) in relation to light and volumetric moisture content.

**Table 4.8:** Regression results for seedling size as a function of PAR quantum flux (mol/m$^2$/day) and volumetric moisture content ("H2O", in %). Standard errors for parameter estimates in parentheses.

log(size+1) = ß0 +ß1*flux +ß2*H2O +ß3*flux$^2$ +ß4*H2O$^2$ +ß5*flux*H2O

| | *Abies* | | *Pseudotsuga* | | *Tsuga* | |
|---|---|---|---|---|---|---|
| ß0 | 1.46 | (±0.637) | 1.072 | (±1.01) | -1.06 | (±1.08) |
| ß1 | 0.149 | (±0.0702) | 0.296 | (±0.0780) | 0.268 | (±0.104) |
| ß2 | 0.143 | (±0.0557) | 0.198 | (±0.0863) | 0.235 | (±0.0877) |
| ß3 | -0.00393 | (±0.00251) | -0.00780 | (±0.00265) | -0.0106 | (±0.00363) |
| ß4 | -0.00286 | (±0.00118) | -0.00431 | (±0.00178) | -0.00489 | (±0.00177) |
| ß5 | 0.00110 | (±0.00157) | -0.000452 | (±0.00188) | 0.00310 | (±0.00227) |
| n | 68 | | 74 | | 60 | |
| MSE | 0.358 | | | 0.675 | | 0.419 |
| $r^2$ | 0.598 | | | 0.5470 | | 0.645 |

negative effect of high moisture on seedling size (Figure 4.19--predicted size at high light and high moisture are not shown due to lack of data). The negative effect of decayed wood on growth has been noted by Minore (1972), and may be associated with low nutrient content in decayed wood.

## Discussion

### Resource and environment effects

Establishment and growth of tree seedlings depends primarily on their ability to extract above- and below-ground resources from a given microsite. The establishment phase is usually the most precarious period of a plant's existence, when seeds must pass through an "environmental sieve" to become established (Harper 1977). The effect of one environmental factor (*e.g.* light) can be significantly modified by the availability of another (*e.g.* water), however. Seed size and physiological tolerance of environmental extremes can also profoundly affect seedlings' ability to succeed in a given environment.

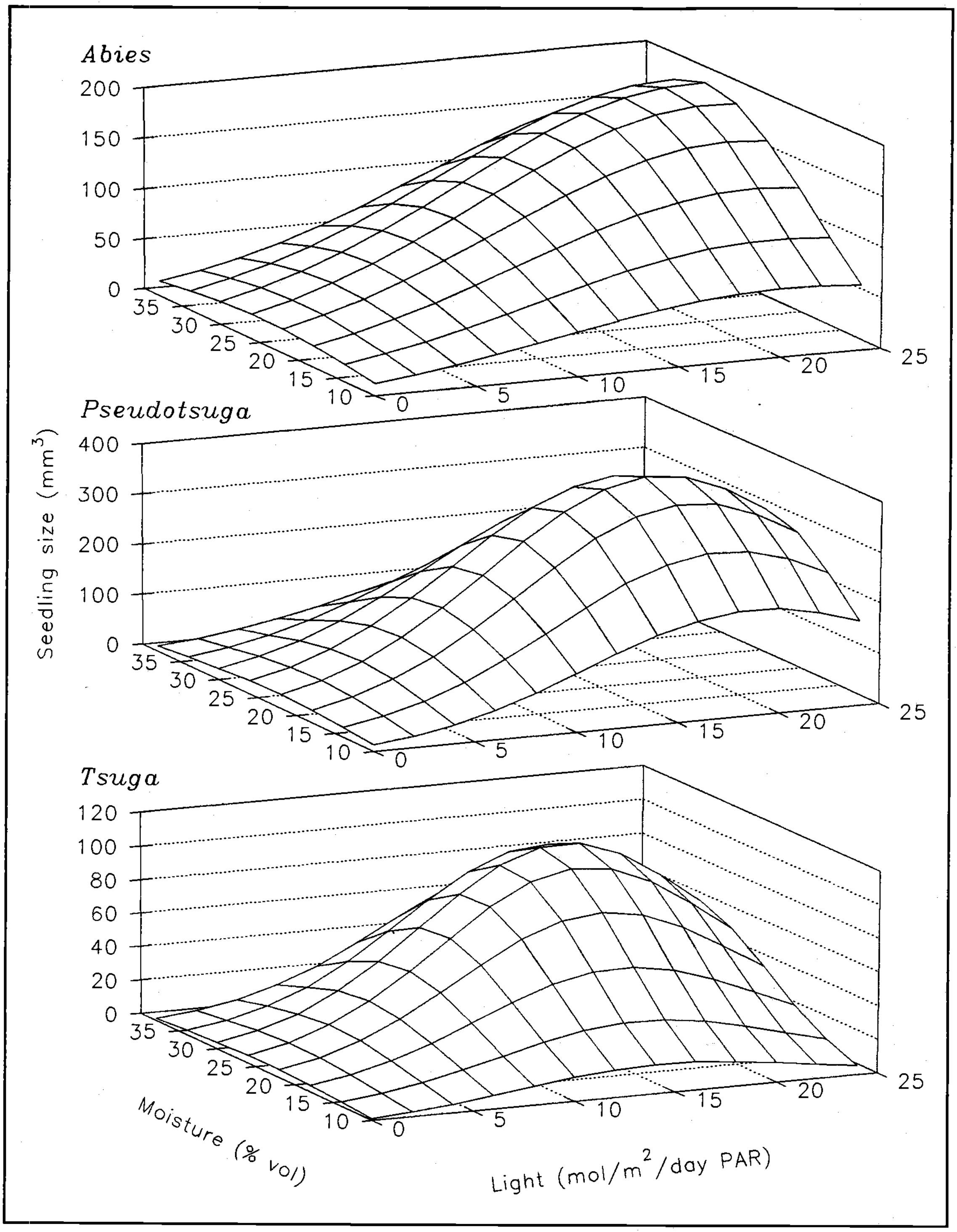

**Figure 4.18:** Polynomial regression model of seedling size (basal diameter*height) on all seed-plots by light and volumetric moisture content for *Abies amabilis*, *Pseudotsuga menziesii*, and *Tsuga heterophylla*.

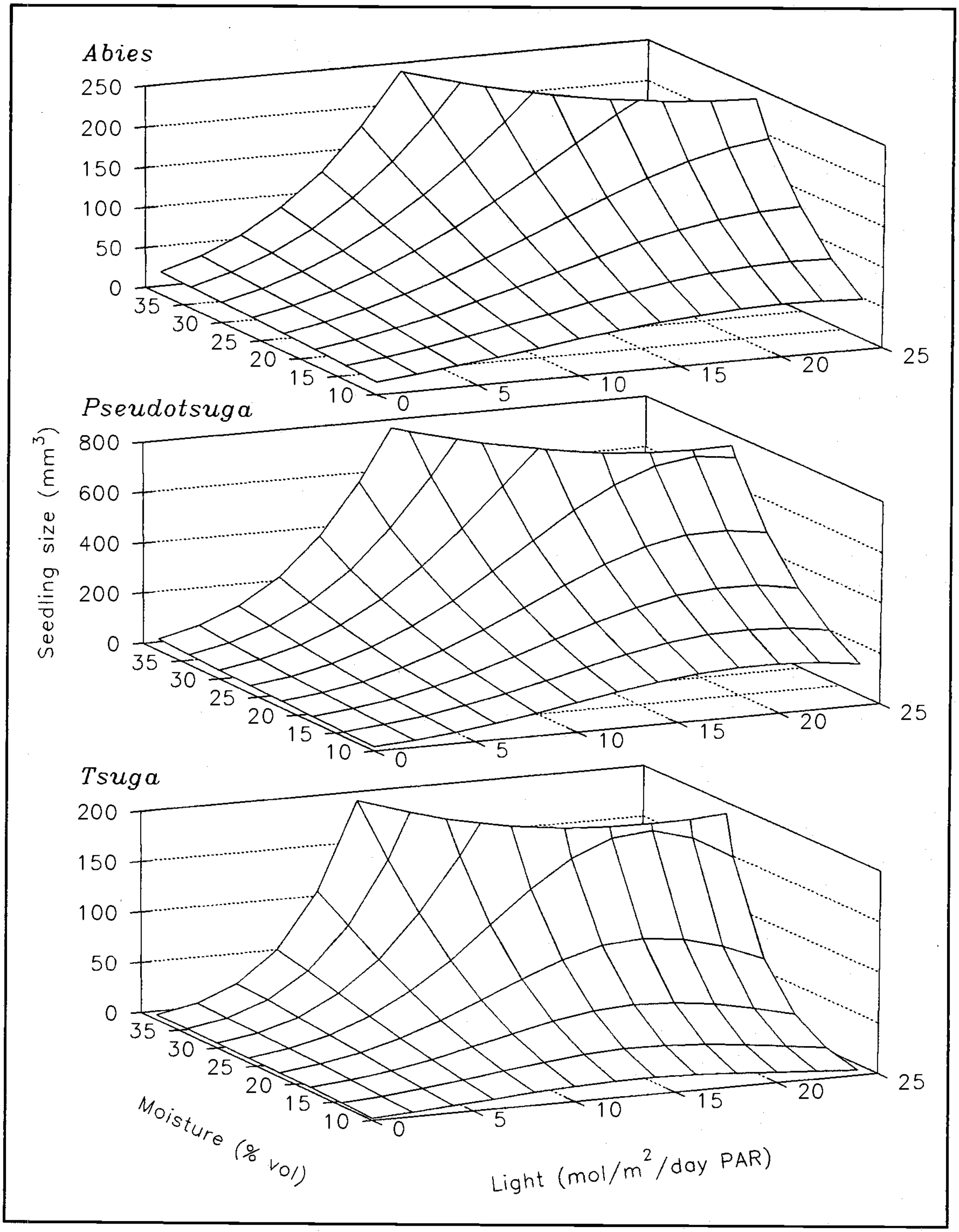

**Figure 4.19:** Polynomial regression model of seedling size (basal diameter*height) on forest floor and mineral soil seed-plots by light and volumetric moisture content for *Abies amabilis*, *Pseudotsuga menziesii*, and *Tsuga heterophylla*.

Soil moisture is a potentially limiting resource for establishing seedlings in the Pacific Northwest due to the characteristic summer droughts which often set in within a few weeks of seedling germination. The ability of establishing seedlings to survive the annual summer drought depends largely on their ability to develop root systems into progressively deeper soil layers as upper layers dry out (Haig *et al.* 1941). The forest floor of closed-canopy areas in the Douglas-fir forests in this study were areas not only of low light, but of low moisture levels as well, most likely due to transpiration by established trees and understory vegetation. Establishment of *Tsuga heterophylla* in low-light, low-moisture conditions tended to be much lower than that of *Pseudotsuga menziesii* and *Abies amabilis*. Seedling establishment is a continuous process from which includes seed dispersal, seed germination, and seedling survival. The greater ability of the relatively large-seeded *Abies* and *Pseudotsuga* to establish in low resource areas compared to *Tsuga* (seed weights are 22 and 7 times that of *Tsuga*, respectively [Schopmeyer 1974]) is most likely related to the supply of carbohydrates available to establish a sufficiently deep root system for extraction of moisture. *Tsuga* generally develops shallower roots than *Abies* or *Pseudotsuga* (Scott *et al.* 1976, Zobel and Antos 1991, Minore 1979). Since soil moisture in the seed-plots was measured at a single depth, I was unable to determine the effective moisture levels for each species (which would also require destructive sampling to determine actual rooting depths). It is well known, however, that species that are successful in closed and shaded communities, as well as those of drier habitats, tend to have larger seeds, and that large seeds confer an advantage in initial establishment and subsequent growth (Salisbury 1942, Harper 1977, Grubb 1977).

Although large seeds confer an advantage for seedling establishment in low-moisture conditions, larger seeds are also more sensitive to desiccation prior to germination due to greater seed surface area and smaller zone of contact with substrates compared to smaller seeds (Harper *et al.* 1965, Harper 1977), which appeared to be the case for *Abies* in this study. Although survival of germinated *Abies* in this study was relatively insensitive to moisture levels, establishment as a fraction of seed was much lower at low moisture levels due to lower germination rates. This relationship between germination and moisture suggests that moisture patterns among treatments measured in early August reflect surface moisture patterns that were present during germination in early June.

Decayed wood provided high-moisture microsites in low-light environments within closed-canopy areas, however. Seedling establishment tended to increase substantially with moisture in low-light areas, particularly for *Tsuga*. *Tsuga* establishment in closed canopy areas in the Cascades is almost exclusively limited to decayed wood microsites, where populations can be quite dense (Chapter 3, Christy and Mack 1984, Stewart 1986a). Moisture levels of mineral soil and forest floor plots were greater in shaded portions of gaps than in closed-canopy areas in this study, which provided additional areas for successful establishment of *Tsuga*, despite relatively low light levels.

The moderate increase in light levels associated with canopy gaps was associated with greater seedling establishment, even in relatively low-moisture conditions. Higher light levels probably increased seedling photosynthesis relative to closed-canopy areas, allowing seedlings to develop roots into deeper soil layers before upper soil layers dried out (Haig *et al.* 1941). Even at moderate light levels, *Tsuga* was more sensitive to low moisture than the other species, probably due to smaller seeds and the tendency of *Tsuga* towards shallower rooting (Scott *et al.* 1976, Zobel and Antos 1991, Minore 1979).

Differential establishment among species also occurred at the highest light levels, found in the largest gap sizes, most likely due to differences in rooting depth and physiological tolerance of extreme temperatures. *Tsuga* seedlings were extremely intolerant of high surface temperatures, even when they occurred under relatively low-light conditions (*e.g.* shade treatments). Heat is often thought to kill seedlings by killing the cambium at the ground line (Silen 1960, Helgerson 1990), but little of that type of mortality was noted in this study (or in Tappeiner and Helms 1971). Instead, mortality appeared to be due to desiccation. High temperatures create greater evaporative demand and greater levels of photorespiration in seedlings (Waring and Schlesinger 1985, Larcher 1980). *Abies amabilis* and *Tsuga heterophylla* transpire more under stress than *Pseudotsuga menziesii* (Livingston and Black 1988, Hinckley *et al.* 1982), making them more prone to desiccation, and *Tsuga* also tend to close stomata later in the day than the other species (Livingston and Black 1987). The greater establishment of *Abies* in high light, high temperature environments compared to *Tsuga* may be due to greater rooting depth leading to better moisture status, and possibly due to the greater height of *Abies* foliage from the hot surface leading to lower evaporative demand. Root development and plant water status can be critical to survival. In summary, *Tsuga* appears to be the most sensitive to the range of microsite environments in these gaps and *Pseudotsuga* the least of the three species studied.

Plants characteristic of different successional stages tend to respond differently to resource abundance (Table 4.9). The relatively flat growth response of *Abies* relative to other species (Figure 4.18) is suggestive of the lack of responsiveness to resources attributed to stress-tolerant species (Grime 1979). This characterization may be premature, however; *Abies* commonly has lower initial growth rates than *Tsuga* (Harrington and Murray 1982, Herman 1967, Kotar 1972, Long 1976, Thornburgh 1969), but it commonly exceeds *Tsuga* in height after several decades (at least in the *Abies amabilis* Zone [Herman 1967, Brockway *et al.* 1983]). Most of the other traits common to *Abies* also suggest a stress-tolerant strategy (*e.g.* seed size, stress response, seedling bank). Species also tend to differentiate based on their ability to compete for different resources (Tilman 1988). *Pseudotsuga*, which is more drought-tolerant than *Abies* or *Tsuga* (Minore 1979), had relatively suppressed growth except at the highest light levels in this study. Most of *Pseudotsuga*'s traits are suggestive of a competitive-ruderal strategy; *Pseudotsuga* tends to be highly successful in early-seral, high-light environments (Munger 1940, Franklin and Dyrness 1973). Periodic seed production by *Pseudotsuga* may be due to high predator preference of its seed, compared to other species (Moore 1940, Gashwiler 1967). The traits characteristic of *Tsuga* do not fit into generalized successional models very well, however (*e.g.* Grime 1979, MacArthur and Wilson 1967). It is a highly shade-tolerant species which tends to increase in abundance in late-successional forests, yet its growth responded dramatically to a modest increase in light, contrary to Grime's (1979) prediction for stress-tolerant species. *Tsuga heterophylla* also has relatively small seeds and tends to produce at least moderate amounts of seed on an

**Table 4.9:** Life history traits of *Abies*, *Pseudotsuga*, and *Tsuga* in relation to Grime's (1979) predictions for competitive (**C**), stress-tolerant (**S**) and ruderal (**R**) species. Relative categorization of traits are taken from various sources in cited in the text (primarily Minore [1979]) and results from this study.

| | *Pseudotsuga* | *Tsuga* | *Abies* |
|---|---|---|---|
| Tree longevity | very long<br>C/S | relatively long<br>C/S | long<br>C/S |
| Leaf longevity | medium<br>C | long<br>S | very long<br>S |
| Flowering early in life cycle? | yes<br>C | yes<br>C | yes<br>C |
| Flowering frequency | periodic<br>S | annual/periodic<br>C/S | v. periodic<br>S |
| Regenerative strategies | wind<br>C | wind/sdling bank<br>C/S | wind/sdling bank<br>C/S |
| Seed size | medium<br>C/S | small<br>R | large<br>S |
| Invasibility | high<br>R | medium/high<br>C/R | low<br>S |
| Maximum growth rate | high<br>C | medium<br>C/S | medium/low<br>C/S |
| Response to drought | fast<br>C | slow<br>S | slow<br>S |
| Response to shade | height increase/ slow growth<br>C/S | slow growth<br>S | slow growth<br>S |

annual basis, contrary to MacArthur and Wilson's (1967) predictions for late-successional species and the observations of Salisbury (1942) for species which establish in closed communities. Perhaps *Tsuga*'s low tolerance of moisture stress, at least in early life stages, would exclude it from Grime's stress-tolerator category. Despite its ability to establish in closed-canopy forests, perhaps *Tsuga* can be considered to be a gap specialist, especially if logs are considered as high-resource gaps in the forest floor. Due to copious seed production (Ruth 1976) and relatively long dispersal distances (Isaac 1930), *Tsuga* appears to be well adapted to find and establish in relatively rare, high-moisture microsites (*e.g.* logs and the gaps in this study). Salisbury (1942) identified a class of gap-invading species which also tended to produce relatively small seed at frequent intervals.

The lack of regeneration found in the many of the forest canopy gaps in the Northwest (Spies *et al.* 1990, Lertzman and Krebs 1991) does not appear to be due to lack of early seedling establishment. Seedlings were able to establish on a variety of substrates in the low-light conditions present in small gaps (which are by far the most common size in mature forests), although below-ground moisture content appeared to be a controlling factor in those conditions. Perhaps the soil moisture response is not as great in natural gaps as it was in these experimental gaps, or only a small number of seed are able to disperse into gaps soon after gap formation, when soil moisture appears to be greatest (Gray and Spies 1992). Alternatively, the low growth rates of seedlings in the low-light environments found in small gaps may contribute to low long-term survival due to competition from understory plants, predation, or mortality from pathogens or suppression. The tall, deep crowns of edge trees tend to lead to lower light levels within gaps in the Northwest than in gaps in the eastern hardwood or tropical forests, despite similar gap sizes (Canham *et al.* 1990).

## Resource versus patch-level descriptions

The analyses in this study suggest that patch-type categorizations of microsites and community structure are useful predictors of seedling establishment. Although there was a strong relationship between predicted seedling establishment of resource and patch-type models (Table 4.7), the patch-type models accounted for greater portions of the variability in establishment (Table 4.4). Some of the greater explanatory power of the patch-type models appeared to be related to age class effects that were not captured by resource models (Table 4.6). Greater establishment in large gaps in mature stands and lower establishment in large gaps in old-growth stands than predicted by resource models may have been caused by unmeasured biotic effects on seedling establishment (*e.g.* greater mortality from predators or pathogens in old-growth stands).

Although environment and resource levels arguably are prime determinants of plant survival, regressions of seedling establishment on measurements of light, moisture, and surface temperature in this study were not very high and varied among species. One reason for the lack of stronger relationships is probably the spatial and temporal scales at which measurements were taken. Survival over the two years of this study was a continuous process, and even though most mortality occurred in the first summer, measurements were taken over only a portion of that time period. For example, seedling establishment in some environments may greatly benefit from periods of cloudy weather in early summer (e.g. May); light measurements in July cannot capture such an effect. In addition, soil moisture was measured over a single increment of depth, which cannot capture the effective environment of both shallow- and deep-rooted species. Germination in particular is sensitive to surface moisture (Harper *et al.* 1965), which may be correlated with soil moisture to a limited extent. Of course, biotic factors affecting seedling survival (*e.g.* mold and insect predation--seedlings in this study were generally protected from rodents) can be relatively independent of, or at least much more variable than, the physical environment.

The variation in seedling growth in this study was correlated with resource measurements to a greater degree than the variation in survival was (Table 4.8), which seems logical, given that growth is more directly tied to resources than survival. The strong negative effect of decayed wood on seedling growth was only captured in a surrogate fashion however, since decayed wood was associated with high moisture levels. The lack of stronger relationships is probably due to missing variables that are important for plant growth; nitrogen content in particular would be important, and may explain the effect of wood on seedling growth (Minore 1972) as well as the greater growth of seedlings on forest floor than on mineral soil (Chapter 3). Similar to regressions on survival, regressions of seedling growth on resources were fit best for *Tsuga heterophylla*, possibly due to a greater correspondence between the depth at which moisture was measured and its rooting depth, relative to the other species.

Measurements of more resources at appropriate temporal and spatial scales for each species would doubtless improve predictions of seedling establishment and growth. The effort required to accomplish this would make sampling across broad gradients or differing microsites very difficult. Determining the appropriate scales at which to measure resources would necessarily be somewhat arbitrary, and would be complicated by plant growth, which continually changes the effective environment the plant is experiencing. Determining effective rooting environment, however, requires destructive sampling which further complicates experimental design. Relating resources to temporal trends may also be difficult since different resources may change in importance at different times in a season or at different stages of a plant's life cycle.

Since it is difficult to measure all relevant resources, especially at the precise time and scale relevant to seedling survival and growth, patch-level descriptions may capture important patterns (*e.g.* the detrimental effect of logs on growth) that aren't reflected by measurement of a few environmental variables (*e.g.* light and moisture) alone. The quantification of seedling response to resource levels, however, allows for more accurate description of potential mechanisms of seedling establishment. Description of resource patterns may also allow for extrapolation and comparison of patch-type results from one study to sites with different combinations of resources. For example, one might expect greater success of *Tsuga* establishment in both closed-canopy and exposed sites on sites where soil moisture is higher, or greater success of *Pseudotsuga* at higher light levels within a broad range of soil moisture contents.

# CHAPTER 5: SUMMARY

## Introduction

The objective of this dissertation was to determine the extent to which structural and environmental heterogeneity within and among canopy gaps affected tree seedling establishment in mature Douglas-fir forests. The focus of the study was on the variety of microsites present within and among gaps and closed-canopy areas and the effect of resource abundance associated with those microsites on tree seedling establishment and growth. Forests are structurally complex in the vertical and horizontal (and temporal!) dimensions. Each structural element can affect the environment of a newly establishing seedling, either directly (*e.g.* by casting shade or depleting soil moisture) or indirectly (*e.g.* by harboring predators and pathogens) (Figure 5.1). Given the large number of interacting factors that can affect plant survival and growth, the plant ecologist is forced to restrict the bounds of inquiry to a few specific processes and/or those believed to be the most important in determining plant response. Knowledge gained from prior research is invaluable in choosing which factors to study, and when and where to study them.

Three basic approaches were pursued in this study on seedling establishment in Douglas-fir forest canopy gaps:

1. Experimental approach: sow known quantities of seed or germinated seedlings in plots on which substrate variability was controlled and small mammal and bird predation was excluded that represented discrete combinations of important factors. Track germination and survival of seedling populations.
2. Monitoring approach: track survival and monitor seed rain and abundance of tree seedlings across the range of microsite conditions present in experimental gaps.
3. Resource approach: measure resource and environmental factors and model seedling survival and growth in relation to them.

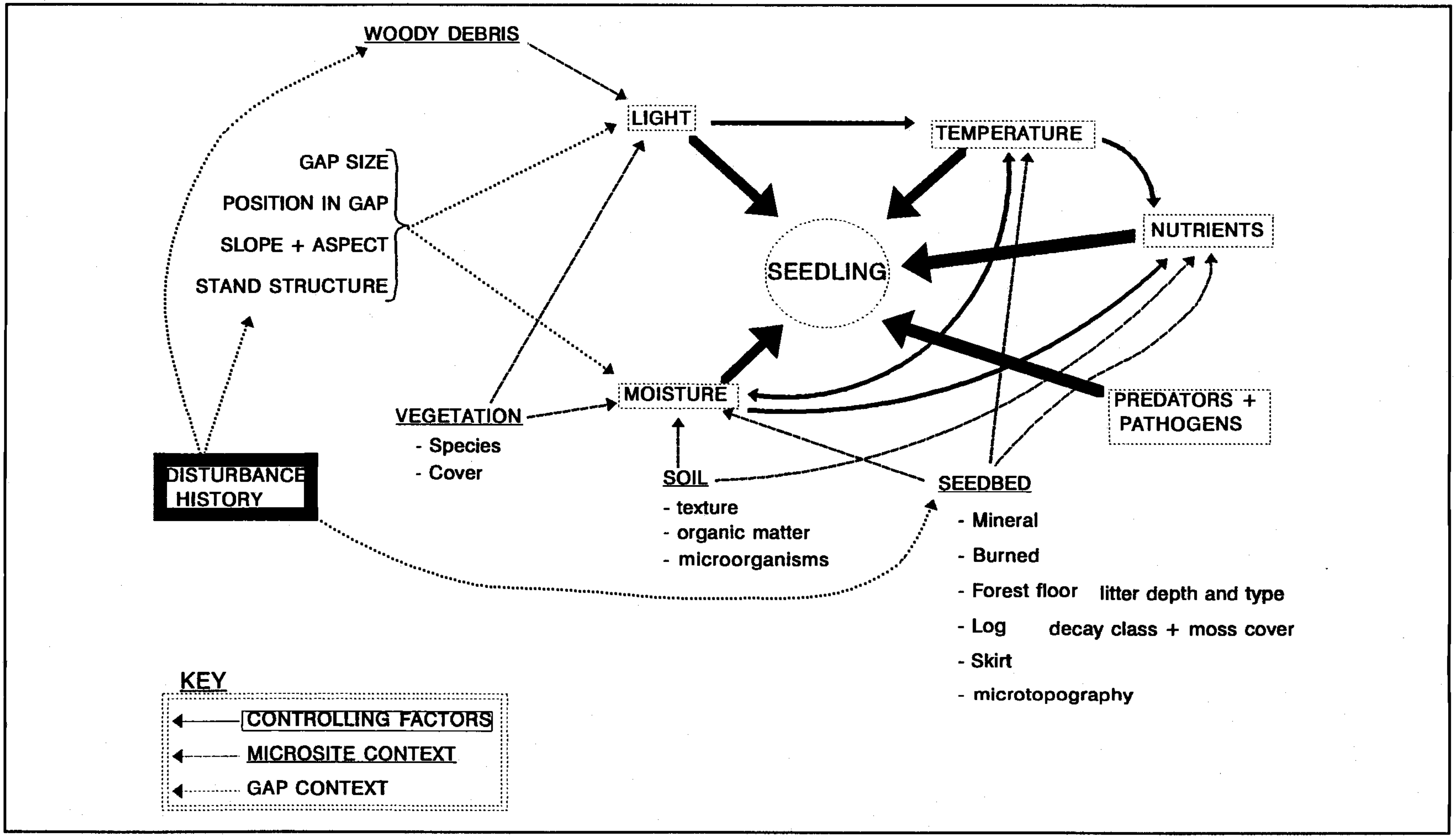

**Figure 5.1:** Controlling factors on seedling establishment in canopy gaps, focussing on direct physical factors and the influence of stand, gap, and microsite structure on them.

No single ecological study can maximize precision, realism, and generality at the same time (Levins 1966). The experimental approach in my study allowed for precise characterization of seedling response to well-defined structural features, while the monitoring approach provided greater realism by characterizing response to uncontrolled natural variation. Greater generality could only be gained by observing seedling response in a greater number of stands and gap conditions. Nevertheless, the resource approach, by correlating simple environmental measurements with seedling establishment, provides some basis on which to extrapolate results to different sites. The three approaches combined provide powerful insight into the process of seedling establishment in mature Douglas-fir forests.

## Gap size and within-gap position

Establishment of *Abies amabilis*, *Pseudotsuga menziesii*, and *Tsuga heterophylla* after two growing seasons following germination was significantly greater in gaps than in closed-canopy ("control") areas. Establishment of *Abies* and *Pseudotsuga* on mineral soil seed-plots in control areas was similar and greater than that of *Tsuga*, with most mortality occurring by the end of the first summer. Establishment of *Tsuga* and *Pseudotsuga* in controls compared to gaps tended to be greater in disturbed seed-plots than in natural microsites. Establishment of *Abies* and *Tsuga* was similar in shaded environments in 0.2 gaps and southern portions of the larger gaps, but lower in high-light portions of larger gaps, while establishment of *Pseudotsuga* on mineral soil seed-plots was the same across gap environments, but tended to be lower in natural microsites in high-light portions of larger gaps. Growth of all species increased with gap size, particularly in gap center positions. Species' growth response appeared to differ by gap size, however, with *Pseudotsuga* growth relatively low in all locations except for the centers of the 1.0 gap size, *Tsuga* growth increasing substantially with gap size, and *Abies* growth responding the least to gap size. At the end of two growing seasons, *Pseudotsuga* seedlings tended to be largest and *Tsuga* seedlings the smallest in all gap locations.

## Seedling substrates

Tree seedling establishment varied dramatically with substrate type and among gap sizes in this study. Seedling establishment on decayed wood seed-plots was significantly greater than establishment on forest floor and mineral soil in controls and 0.2 gaps, and the difference among substrates tended to be greatest for *Tsuga heterophylla* and least for *Pseudotsuga menziesii*. Differences between establishment on wood and forest floor seed-plots were lower in 0.4 gaps than in 0.2 gaps and controls. Seedling establishment on mineral soil and forest floor was significantly lower in the centers of 1.0 gaps than in the centers of 0.4 gaps, and tended to be lower on forest floor than on mineral soil or decayed wood in 1.0 gaps. Seedling growth tended to be lower on wood than on other substrates for *Pseudotsuga* in 1.0 gaps and tended to be greatest on forest floor for all species in 0.4 and 1.0 gaps.

Substrate effects on establishment of naturally regenerated seedlings were more variable, with little or no apparent difference between establishment on decayed logs and on the forest floor in controls and 0.2 gaps, possibly due to substrate variability and high density of older seedlings and shrubs on decayed logs. Establishment of natural regeneration tended to be greater on logs than on forest floor in gaps, particularly in shaded south locations. Establishment of natural regeneration in gaps tended to be relatively high on organic accumulations around tree stumps ("skirts") compared to other substrates.

## Understory shade and vegetation

High levels of artificial understory shade (90%) significantly depressed establishment of germinated seedlings in relation to moderate shade (40%) or no shade in closed-canopy areas and 0.4 size gaps, but appeared to have a slightly beneficial effect on establishment in 1.0 size gaps. Seedling germination rates in 1.0 gaps tended to be greater under shade, however, leading to greater numbers of seedlings (as a fraction of seed) becoming established under shade than without it.

Large logs (50 cm diameter) also provided shaded environments in exposed portions of large gaps, in which seedling survival was greater than in nearby unshaded areas, especially for *Tsuga heterophylla*. Similar effects on establishment of *Tsuga* were seen on the north sides of smaller logs (as small as 10 cm diameter), old snags, and cut stumps at the north end of a 1.0 gap.

The pattern of *Pseudotsuga* establishment in relation to understory vegetation appeared to be similar to the pattern in relation to "dead" shade (*i.e.* shade cloth and logs): establishment tended to decrease with increasing cover in controls, 0.2 gaps, and shaded portions of large gaps, and tended to increase with increasing cover in exposed portions of larger gaps. Establishment of *Tsuga* seedlings displayed no apparent benefit from shade by vegetation: establishment tended to decline with increasing cover regardless of gap size or within-gap position. Microsites of both *Tsuga* and *Pseudotsuga* tended to have lower herb cover, and similar or greater shrub cover, than randomly located microsites in 1.0 and 0.2 gaps.

## Stand structure

Seedling establishment within canopy gaps was affected by forest age class, although patterns differed between establishment on seed-plots and establishment on natural microsites. Establishment on mineral soil seed-plots in exposed locations of large gaps (0.4 North, 1.0 North and Center) tended to be greater in old-growth stands than in mature stands, while establishment on mineral soil seed-plots in shaded locations of large gaps (0.4 Center and South, 1.0 South) tended to be lower in old-growth than in mature stands, primarily for *Abies amabilis* and *Tsuga heterophylla*. Greater soil moisture content in the old-growth stands may account for greater establishment in exposed locations, as well as for the significantly greater size of seedlings in the old-growth stands.

Establishment of *Pseudotsuga menziesii* on natural microsites in exposed north positions, however, was greater in mature stands than in old-growth stands, while establishment in shaded south positions was greater in old-growth stands than in mature stands. This pattern appeared to have resulted from differing effects of vegetation cover across positions between age classes, and greater availability of decayed wood and skirts in old-growth stands. The greatest effect of age class on establishment of natural regeneration appeared to be on availability of seed, with few *Tsuga* establishing in mature stands, where seeds and mature *Tsuga* were rare, and many in old-growth stands, where seeds and mature *Tsuga* were abundant.

Seedling establishment on seed-plots in control areas appeared to be related to structural differences among stands that were not consistent by age class. The lowest seedling establishment rates were associated with the lowest light levels, which were found in mature stand MCY, which had the shortest overstory trees (resulting in dense packing of crowns) and the highest cover of mid-story trees, and in old-growth stand HJA, which had a high density of *Tsuga* in a relatively uniform mid-canopy layer (which established following a fire about 150 years ago). In contrast, stand PCM, which had the highest light levels, was dominated by widely spaced crowns of relatively tall *Pseudotsuga* and a moderate cover of mid-story trees, while stand TCO had trees in a broad distribution of size classes and a heterogenous, multi-layered canopy. Despite greater light levels in controls in stand PCM, seedling establishment rates in stand TCO were generally higher than those in stand PCM, possibly due to greater levels of soil moisture.

## Annual differences

Seedling establishment after one growing season differed between 1992 and 1993, possibly due to cooler temperatures and greater precipitation in the summer of 1993. Establishment of *Tsuga heterophylla* on seed-plots exposed gap locations tended to be greater, while establishment in shaded gap locations and controls tended to be lower, in 1993 than in 1992. Establishment of *Abies amabilis*, on the other hand, tended to be greater in controls in 1993 than in 1992. Predation of *Abies* and *Pseudotsuga* seeds and seedlings in gaps (despite exclosures) appeared to be much greater in 1993 than in 1992, possibly due to less food availability from the much smaller seed crop of 1992-93.

## Resource levels and environment

Seedling establishment was strongly correlated with measurements of light, substrate moisture content, and surface temperature in experimental seed-plots. Although seedling establishment increased with light levels, establishment of *Abies amabilis* and *Tsuga heterophylla* declined at the highest light levels, where maximum surface temperatures were also highest. Establishment of *Tsuga* increased greatly with moisture content, while *Abies* establishment displayed a much smaller moisture effect and *Pseudotsuga* establishment displayed very little effect at all. Growth of all species on mineral soil and forest floor seed-plots increased with both moisture content and light levels, while moist decayed wood seed-plots depressed growth at moderate and high light levels.

Differences in moisture content, light levels, and surface temperatures among seed-plots provide potential mechanisms for the substrate and gap size/position effects described above. Soil moisture is a potentially limiting resource for establishing seedlings in the Pacific Northwest due to the characteristic summer droughts which often set in within a few weeks of seedling germination. The ability of establishing seedlings to survive the annual summer drought depends largely on their ability to develop root systems into progressively deeper soil layers as upper layers dry out (Haig *et al.* 1941). The ability to establish root systems may be greatly determined by initial seed size, particularly in low-light environments. *Tsuga heterophylla*, which has the smallest seed of the three species in this study, was the least able to establish on the relatively dry mineral soil and forest floor in control areas, but established quite successfully on moist wood in the same areas.

Soil moisture levels were greater in gaps than in control areas, and seedling establishment of all species was less restricted to wood in gaps than in control areas. Greater light levels in gaps than in controls appeared to aid seedling establishment among plots with similar moisture levels, possibly due to greater photosynthesis allowing seedlings to develop roots into deeper soil layers before upper soil layers dried out. Increased photosynthesis in gaps may also have reduced seedling mortality from light suppression and increased seedling resistance to disease or predation.

Seedling establishment declined at the highest light levels, particularly in north positions of 0.4 gaps and north and center positions of 1.0 gaps where direct radiation made up a large fraction of total radiation. These locations also experienced the highest surface temperatures, with maxima often exceeding 55°C. Seedling establishment was greater on mineral soil, which was the coolest substrate, than on forest floor, which was the hottest, and seedling establishment on forest floor tended to increase with level of shade, which kept surface temperatures lower. Although decayed wood was hotter than mineral soil in 1.0 gaps, it was also much wetter, which apparently led to greater seedling establishment. *Tsuga* seedlings appeared to be the most susceptible to mortality at high temperatures and *Pseudotsuga* the least.

Differences in rooting depth and physiological tolerance of extreme temperatures may explain the patterns associated with temperature. Mortality in this study appeared to be due to desiccation rather than tissue death at the ground line. High temperatures create greater evaporative demand and greater levels of photorespiration in seedlings (Waring and Schlesinger 1985, Larcher 1980). *Abies amabilis* and *Tsuga heterophylla* transpire more under stress than *Pseudotsuga menziesii* (Livingston and Black 1988, Hinckley *et al.* 1982), making them more prone to desiccation, and *Tsuga* also tend to close stomata later in the day than the other species (Livingston and Black 1987). Greater establishment of *Abies* in high light, high temperature environments compared to *Tsuga* may also be due to better moisture status associated with greater rooting depth (Zobel and Antos 1991, Scott *et al.* 1976), and possibly due to the greater height of *Abies* foliage from the hot surface.

## Conclusions

The following conclusions apply to the range of microsites and stand conditions found in this study in the Cascade Range. Some conclusions may apply to other stands and forest types as well.

1. Seedling establishment is greater in canopy gaps than in closed-canopy areas.
2. Seedling establishment is lower in portions of large gaps which receive substantial amounts of direct radiation than in portions which do not, particularly for *Tsuga heterophylla*.
3. Shade from coarse woody debris allows *Tsuga heterophylla* to establish in exposed areas where it otherwise could not.
4. *Tsuga heterophylla* requires class III and IV logs to establish in closed-canopy areas, but establishment is abundant on the forest floor in gaps.
5. *Pseudotsuga menziesii* does not require mineral soil to become established in either shaded or unshaded locations in gaps.
6. Seedling growth increases with gap size, and is greater at centers than edges of gaps.
7. Understory vegetation cover reduces seedling establishment in closed-canopy areas and shaded areas of gaps.
8. Establishment of *Pseudotsuga* in exposed locations tends to increase with understory cover, while establishment of *Tsuga* does not.
9. Low levels of seed rain can limit establishment of *Tsuga heterophylla* in gaps in mature stands.
10. Establishment of *Tsuga heterophylla* is greatly reduced by low moisture content and high surface temperatures, while establishment of *Abies amabilis* is moderately sensitive, and establishment of *Pseudotsuga menziesii* is least sensitive, to moisture and surface temperature.
11. Growth of all three species increases with moisture and light, but growth on decayed wood is lower than growth on forest floor at similar levels of moisture and light.

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# APPENDIX

**Table A.1:** Mean cover of plant species by stand in the summer of 1990, prior to gap formation. Tree foliage below 1 m in height was sampled over 0.25 $m^2$, and mid-story tree foliage above 1 m in height was sampled over 1 $m^2$ (foliage of conifers > 5 cm DBH not included). Species names conform to Hitchcock and Cronquist (1973).

| | Stand | | | |
|---|---|---|---|---|
| | HJA | MCY | PCM | TCO |
| Number of plots | 989 | 719 | 991 | 1028 |
| 0.25 $m^2$ plot size | | | | |
| *Abies amabilis* | 0.05 | . | . | 6.11 |
| *Abies grandis* | . | . | 0.01 | . |
| *Acer circinatum* | 0.54 | 6.10 | 4.75 | 0.72 |
| *Acer glabrum* | . | . | 0.04 | . |
| *Acer macrophyllum* | . | 0.02 | 0.00 | . |
| *Achlys triphylla* | 0.05 | 0.12 | 15.40 | 4.03 |
| *Adenocaulon bicolor* | . | 0.00 | 1.45 | 0.00 |
| *Amelanchier alnifolia* | . | 0.00 | 0.04 | 0.01 |
| *Anemone deltoidea* | 0.01 | 0.02 | 1.40 | 0.02 |
| *Anemone lyalii* | 0.00 | . | 0.02 | . |
| *Asarum caudatum* | 0.00 | . | . | . |
| *Berberis nervosa* | 3.70 | 29.59 | 13.69 | 6.69 |
| *Bryophyta* | 7.28 | 9.63 | 4.98 | 8.13 |
| *Castanopsis chrysophylla* | 0.02 | . | . | . |
| *Campanula scouleri* | . | 0.00 | 0.04 | 0.00 |
| *Chimaphila menziesii* | 0.01 | 0.04 | 0.02 | 0.01 |
| *Chimaphila umbellata* | 0.31 | 0.03 | 0.32 | 0.64 |
| *Clintonia uniflora* | . | 0.01 | 0.04 | 1.17 |
| *Cornus canadensis* | 0.47 | . | 0.04 | 2.20 |
| *Corylus cornuta* | 0.00 | 0.06 | 0.39 | 0.00 |
| *Collomia heterophylla* | . | . | 0.00 | . |
| *Coptis laciniata* | 1.78 | . | 0.01 | . |
| *Corallorhiza maculata* | 0.00 | 0.00 | 0.00 | . |
| *Cornus nuttallii* | . | 0.02 | 0.12 | . |
| *Disporum hookeri* | 0.00 | 0.01 | 0.02 | . |
| *Gallium aparine* | 0.00 | . | . | . |
| *Galium oreganum* | 0.00 | . | 0.01 | . |
| *Gaultheria shallon* | 0.01 | 9.95 | 9.41 | 2.40 |
| *Galium triflorum* | 0.00 | 0.02 | 0.04 | . |
| *Goodyera oblongifolia* | 0.17 | 0.01 | 0.08 | 0.00 |
| *Gramineae* | 0.00 | . | 0.04 | 0.00 |
| *Hemitomes congestum* | . | . | 0.00 | . |
| *Hieracium albiflorum* | 0.00 | 0.00 | 0.06 | . |
| *Holodiscus discolor* | . | . | 0.21 | . |
| *Lactuca muralis* | . | 0.04 | 0.00 | . |
| *Lathyrus polyphyllus* | . | . | 0.23 | . |
| *Linnaea borealis* | 0.63 | 0.00 | 0.31 | 0.52 |
| *Listera caurina* | 0.00 | . | 0.01 | 0.00 |

(continued..)

**Table A.1** (continued)

| | | | | |
|---|---|---|---|---|
| *Listera cordata* | . | . | 0.01 | 0.00 |
| *Lonicera* | . | . | 0.01 | 0.01 |
| *Monotropa uniflora* | . | . | 0.00 | . |
| *Osmorhiza chilensis* | 0.05 | . | 0.15 | . |
| *Pachistima myrsinites* | 0.02 | . | 0.00 | . |
| *Pedicularis racemosa* | . | . | 0.06 | . |
| *Pinus monticola* | . | . | 0.00 | . |
| *Polystichum munitum* | 0.75 | 0.13 | 0.35 | 0.00 |
| *Pseudotsuga menziesii* | 0.01 | 0.00 | 0.00 | 0.01 |
| *Pteridium aquilinum* | . | 0.22 | 1.51 | 0.05 |
| *Pyrola asarifolia* | 0.00 | . | 0.01 | 0.00 |
| *Pyrola picta* | 0.01 | 0.01 | 0.02 | 0.00 |
| *Pyrola secunda* | 0.02 | . | 0.04 | 0.00 |
| *Rhododendron macrophyllum* | 1.04 | . | . | . |
| *Rosa gymnocarpa* | 0.01 | 0.16 | 2.02 | 0.24 |
| *Rubus lasiococcus* | 0.01 | . | . | 0.02 |
| *Rubus nivalis* | 0.28 | . | . | . |
| *Rubus parviflorus* | . | . | 0.24 | . |
| *Rubus pedatus* | . | . | 0.00 | . |
| *Rubus ursinus* | 0.39 | 0.15 | 0.64 | 0.10 |
| *Smilacina stellata* | 0.00 | 0.00 | 0.05 | 0.01 |
| *Symphoricarpos albus* | . | 0.02 | 0.78 | 0.06 |
| *Taxus brevifolia* | 0.05 | . | 0.00 | 0.00 |
| *Thelipteris nevadensis* | 0.02 | . | . | . |
| *Thuja plicata* | 0.21 | . | . | . |
| *Tiarella trifoliata* | 0.35 | . | 0.31 | 0.10 |
| *Trientalis latifolia* | 0.02 | 0.03 | 0.32 | 0.01 |
| *Trillium ovatum* | 0.01 | 0.00 | 0.08 | 0.06 |
| *Tsuga heterophylla* | 1.14 | 0.63 | 0.36 | 0.99 |
| *Vaccinium alakense* | . | . | 0.02 | 4.60 |
| *Vancouveria hexandra* | 0.11 | 0.02 | 2.08 | 0.48 |
| *Vaccinium membranaceum* | 0.04 | . | 0.06 | 1.36 |
| *Vaccinium parviflorum* | 0.32 | 0.11 | 2.31 | 2.56 |
| *Viola sempivirens* | 0.41 | 0.18 | 1.41 | 0.10 |
| *Xerophyllum tenax* | 0.01 | 0.00 | 1.16 | 0.52 |
| <u>1.0 $m^2$ plot size</u> | | | | |
| *Abies amabilis* | 0.05 | . | 0.00 | 3.37 |
| *Abies grandis* | . | 0.00 | 0.00 | . |
| *Acer circinatum* | 1.94 | 40.16 | 27.30 | 1.29 |
| *Acer glabrum* | . | . | 0.33 | . |
| *Acer macrophyllum* | . | 0.04 | 0.04 | . |
| *Corylus cornuta* | 0.00 | 0.11 | 0.79 | 0.01 |
| *Cornus nuttallii* | 0.08 | 2.09 | 4.86 | . |
| *Holodiscus discolor* | . | . | 0.98 | 0.02 |
| *Taxus brevifolia* | 0.22 | 0.01 | . | 0.60 |
| *Thuja plicata* | 0.26 | . | . | . |
| *Tsuga heterophylla* | 1.21 | 0.98 | 0.26 | 0.45 |

**Table A.2:** Survival of natural regeneration dataset, with seedling counts (May 1992 and October 1993) by level of gap, within-gap position, and cover for *Pseudotsuga menziesii* (PSME) and *Tsuga heterophylla* (TSHE), by stand and substrate.

| G | P | C | **PSME** | | | | | | | | **TSHE** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A | O | O | | | | | | | | | | | | |
| P | S | V | HJA | | TCO | | MCY | | PCM | | HJA | | TCO | |
| *Forest* | *floor* | | | | | | | | | | | | | |
| 0 | n | l | 8 | 0 | 10 | 0 | 10 | 1 | 17 | 0 | 12 | 0 | 5 | 0 |
| 0 | n | m | 13 | 0 | 18 | 0 | 10 | 0 | 27 | 0 | 15 | 0 | 62 | 1 |
| 0 | n | h | 2 | 0 | 3 | 0 | 6 | 0 | 12 | 0 | . | . | 19 | 0 |
| 0 | c | l | 10 | 0 | 5 | 0 | 16 | 0 | 27 | 1 | 6 | 0 | 19 | 1 |
| 0 | c | m | 9 | 0 | 15 | 0 | 18 | 0 | 22 | 2 | 4 | 0 | 18 | 0 |
| 0 | c | h | . | . | 5 | 0 | 8 | 0 | 14 | 0 | . | . | 8 | 0 |
| 0 | s | l | 10 | 0 | 5 | 1 | 6 | 0 | 14 | 0 | 13 | 0 | 7 | 0 |
| 0 | s | m | 9 | 0 | 7 | 0 | 8 | 0 | 24 | 0 | 6 | 0 | 23 | 0 |
| 0 | s | h | . | . | 6 | 0 | 8 | 0 | 9 | 0 | . | . | 51 | 0 |
| 0.2 | c | l | 16 | 2 | 12 | 0 | 8 | 0 | 14 | 1 | 54 | 10 | 116 | 10 |
| 0.2 | c | m | 10 | 0 | 18 | 2 | 13 | 0 | 19 | 4 | 10 | 0 | 66 | 1 |
| 0.2 | c | h | 2 | 0 | 6 | 0 | 2 | 0 | 19 | 0 | 1 | 0 | 14 | 0 |
| 0.4 | n | l | 13 | 2 | 10 | 1 | 18 | 1 | 3 | 0 | 12 | 0 | . | . |
| 0.4 | n | m | 3 | 1 | 9 | 0 | 10 | 1 | 17 | 4 | 12 | 2 | . | . |
| 0.4 | n | h | . | . | . | . | 6 | 2 | 19 | 3 | . | . | 2 | 0 |
| 0.4 | c | l | 13 | 7 | 10 | 1 | 14 | 6 | 4 | 1 | 61 | 14 | 45 | 0 |
| 0.4 | c | m | 4 | 1 | 8 | 3 | 16 | 5 | 4 | 2 | 22 | 4 | 11 | 1 |
| 0.4 | c | h | . | . | 2 | 0 | 6 | 2 | 15 | 6 | 10 | 1 | 5 | 0 |
| 0.4 | s | l | 8 | 3 | 15 | 10 | 2 | 2 | 24 | 10 | 17 | 3 | 141 | 88 |
| 0.4 | s | m | 4 | 1 | 12 | 7 | 5 | 0 | 15 | 6 | 14 | 1 | 104 | 30 |
| 0.4 | s | h | . | . | 3 | 2 | 14 | 0 | 13 | 2 | 8 | 1 | 30 | 6 |
| 1.0 | n | l | 6 | 0 | 9 | 3 | 7 | 0 | 6 | 1 | 17 | 1 | . | . |
| 1.0 | n | m | 10 | 1 | 8 | 1 | 18 | 0 | 15 | 6 | 7 | 0 | 21 | 0 |
| 1.0 | n | h | 4 | 0 | 8 | 1 | 7 | 4 | 12 | 4 | 4 | 0 | 6 | 0 |
| 1.0 | c | l | 4 | 0 | 7 | 2 | 1 | 0 | 3 | 0 | 21 | 1 | 26 | 3 |
| 1.0 | c | m | 7 | 0 | 11 | 3 | 7 | 1 | 20 | 5 | 9 | 2 | 46 | 0 |
| 1.0 | c | h | . | . | 4 | 1 | 10 | 1 | 12 | 8 | 3 | 0 | 45 | 7 |
| 1.0 | s | l | 11 | 4 | 7 | 5 | 4 | 1 | 13 | 0 | 34 | 16 | 49 | 6 |
| 1.0 | s | m | 10 | 3 | 11 | 5 | 13 | 3 | 17 | 9 | 13 | 4 | 93 | 44 |
| 1.0 | s | h | 1 | 0 | 12 | 1 | 10 | 2 | 13 | 8 | 4 | 1 | 46 | 10 |

(continued..)

**Table A.2** (continued)

| GAP | POS | COV | PSME | | | | | | | | TSHE | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | HJA | | TCO | | MCY | | PCM | | HJA | | TCO | |
| *Log* | | | | | | | | | | | | | | |
| 0 | n | l | 1 | 0 | 1 | 0 | 4 | 0 | . | . | 3 | 0 | 71 | 0 |
| 0 | n | m | 1 | 0 | 3 | 0 | 7 | 0 | . | . | 2 | 0 | 72 | 1 |
| 0 | n | h | . | . | 5 | 0 | . | . | . | . | . | . | 34 | 0 |
| 0 | c | l | 9 | 0 | 3 | 1 | 1 | 0 | . | . | 23 | 0 | 3 | 0 |
| 0 | c | m | . | . | 9 | 0 | 2 | 0 | . | . | 2 | 0 | 64 | 0 |
| 0 | c | h | . | . | . | . | . | . | . | . | . | . | . | . |
| 0 | s | l | 4 | 0 | 2 | 0 | 4 | 0 | . | . | 4 | 0 | 30 | 0 |
| 0 | s | m | 1 | 0 | 12 | 0 | 6 | 0 | . | . | . | . | 53 | 0 |
| 0 | s | h | . | . | 1 | 0 | . | . | . | . | . | . | . | . |
| 0.2 | c | l | 3 | 2 | . | . | . | . | . | . | 36 | 8 | . | . |
| 0.2 | c | m | 2 | 0 | 4 | 1 | 3 | 0 | . | . | 4 | 0 | 5 | 0 |
| 0.2 | c | h | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.4 | n | l | 4 | 1 | . | . | 12 | 2 | 7 | 1 | 10 | 0 | . | . |
| 0.4 | n | m | 5 | 1 | . | . | 7 | 0 | 7 | 2 | 6 | 3 | . | . |
| 0.4 | n | h | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.4 | c | l | 5 | 3 | 1 | 1 | 1 | 0 | 2 | 2 | 27 | 17 | . | . |
| 0.4 | c | m | 4 | 2 | 9 | 4 | 1 | 1 | 2 | 0 | . | . | 12 | 0 |
| 0.4 | c | h | . | . | . | . | . | . | 19 | 0 | . | . | 4 | 0 |
| 0.4 | s | l | 3 | 0 | 2 | 2 | 6 | 1 | 10 | 8 | 26 | 18 | 35 | 23 |
| 0.4 | s | m | . | . | 3 | 3 | 3 | 0 | . | . | . | . | 34 | 17 |
| 0.4 | s | h | . | . | 2 | 1 | . | . | . | . | . | . | . | . |
| 1.0 | n | l | . | . | 3 | 0 | . | . | . | . | 15 | 0 | 2 | 0 |
| 1.0 | n | m | 4 | 1 | 4 | 2 | . | . | . | . | 2 | 0 | 3 | 0 |
| 1.0 | n | h | 1 | 1 | 2 | 0 | . | . | . | . | 2 | 0 | . | . |
| 1.0 | c | l | 4 | 3 | 2 | 1 | 6 | 0 | 2 | 0 | 11 | 0 | 11 | 0 |
| 1.0 | c | m | 11 | 4 | 3 | 2 | 2 | 1 | 2 | 1 | 21 | 3 | 9 | 0 |
| 1.0 | c | h | . | . | 3 | 0 | 4 | 0 | . | . | . | . | 18 | 0 |
| 1.0 | s | l | . | . | 5 | 5 | 9 | 7 | . | . | . | . | 31 | 20 |
| 1.0 | s | m | . | . | 1 | 1 | . | . | 1 | 0 | 8 | 7 | 25 | 16 |
| 1.0 | s | h | . | . | 1 | 0 | . | . | 3 | 0 | 4 | 1 | . | . |

**Table A.3:** Density of natural regeneration dataset, with seedling counts (1992 cohort) and number of vegetation plots (respectively per stand) by level of gap, within-gap position, and cover for *Pseudotsuga menziesii* (PSME) and *Tsuga heterophylla* (TSHE), by stand and substrate.

| GAP | POS | COV | PSME | | | | | | | | TSHE | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | HJA | | TCO | | MCY | | PCM | | HJA | | TCO | |
| *Forest floor* | | | | | | | | | | | | | | |
| 0 | n | low | 0 | 9 | 0 | 1 | 0 | 1 | . | . | 0 | 9 | 3 | 1 |
| 0 | n | med | 0 | 2 | 0 | 4 | 0 | 4 | 1 | 9 | 0 | 2 | 1 | 4 |
| 0 | n | hi | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 6 | 0 | 1 | 0 | 1 |
| 0 | c | low | 0 | 22 | 0 | 3 | 0 | 1 | 1 | 5 | 0 | 22 | 7 | 3 |
| 0 | c | med | . | . | 0 | 15 | 0 | 11 | 0 | 17 | . | . | 2 | 15 |
| 0 | c | hi | . | . | 0 | 2 | 0 | 11 | 0 | 6 | . | . | 0 | 2 |
| 0 | s | low | 0 | 5 | 0 | 7 | . | . | . | . | 4 | 5 | 10 | 7 |
| 0 | s | med | 0 | 3 | 3 | 6 | 0 | 5 | 0 | 10 | 0 | 3 | 2 | 6 |
| 0 | s | hi | . | . | 0 | 1 | 0 | 4 | 0 | 4 | . | . | 0 | 1 |
| 0.2 | c | low | 0 | 5 | 1 | 1 | 0 | 1 | . | . | 12 | 5 | 0 | 1 |
| 0.2 | c | med | 0 | 3 | 2 | 9 | 0 | 8 | 6 | 9 | 0 | 3 | 38 | 9 |
| 0.2 | c | hi | . | . | 0 | 1 | . | . | 0 | 14 | . | . | 0 | 1 |
| 0.4 | n | low | 0 | 1 | 0 | 3 | . | . | . | . | 0 | 1 | 0 | 3 |
| 0.4 | n | med | . | . | 1 | 1 | 0 | 1 | 4 | 2 | . | . | 0 | 1 |
| 0.4 | n | hi | . | . | . | . | 0 | 1 | 0 | 3 | . | . | . | . |
| 0.4 | c | low | 1 | 11 | 5 | 6 | . | . | . | . | 26 | 11 | 41 | 6 |
| 0.4 | c | med | 0 | 2 | 0 | 3 | 2 | 11 | 0 | 3 | 4 | 2 | 1 | 3 |
| 0.4 | c | hi | 1 | 1 | 2 | 2 | 0 | 9 | 5 | 17 | 0 | 1 | 11 | 2 |
| 0.4 | s | low | 1 | 4 | 1 | 3 | 0 | 1 | . | . | 9 | 4 | 32 | 3 |
| 0.4 | s | med | 0 | 1 | . | . | 0 | 1 | 3 | 1 | 1 | 1 | . | . |
| 0.4 | s | hi | . | . | . | . | . | . | 2 | 4 | . | . | . | . |
| 0.6 | n | low | 0 | 1 | 0 | 4 | . | . | . | . | 0 | 1 | 0 | 4 |
| 0.6 | n | med | . | . | 0 | 1 | 0 | 1 | 0 | 1 | . | . | 0 | 1 |
| 0.6 | n | hi | 0 | 1 | . | . | 0 | 1 | 2 | 4 | 0 | 1 | . | . |
| 0.6 | c | low | 0 | 5 | 2 | 3 | . | . | . | . | 1 | 5 | 2 | 3 |
| 0.6 | c | med | 0 | 3 | 7 | 12 | 2 | 5 | 0 | 1 | 0 | 3 | 63 | 12 |
| 0.6 | c | hi | 0 | 1 | 1 | 4 | 0 | 9 | 1 | 19 | 0 | 1 | 6 | 4 |
| 0.6 | s | low | 0 | 4 | 1 | 4 | . | . | 0 | 1 | 0 | 4 | 86 | 4 |
| 0.6 | s | med | 0 | 1 | 2 | 3 | 4 | 2 | 0 | 4 | 1 | 1 | 94 | 3 |
| 0.6 | s | hi | . | . | 0 | 1 | 0 | 3 | 0 | 4 | . | . | 10 | 1 |
| 1.0 | n | low | 0 | 4 | 0 | 3 | . | . | 1 | 1 | 0 | 4 | 0 | 3 |
| 1.0 | n | med | 0 | 1 | 1 | 1 | 2 | 7 | 5 | 4 | 0 | 1 | 0 | 1 |
| 1.0 | n | hi | . | . | 3 | 2 | 1 | 1 | 3 | 7 | . | . | 0 | 2 |
| 1.0 | c | low | 1 | 12 | 0 | 3 | 1 | 1 | . | . | 8 | 12 | 3 | 3 |
| 1.0 | c | med | . | . | 1 | 7 | 1 | 6 | 3 | 7 | . | . | 9 | 7 |
| 1.0 | c | hi | . | . | 0 | 9 | 1 | 12 | 7 | 24 | . | . | 4 | 9 |
| 1.0 | s | low | 0 | 1 | . | . | 0 | 1 | . | . | 10 | 1 | . | . |
| 1.0 | s | med | . | . | 4 | 3 | 0 | 3 | 0 | 1 | . | . | 98 | 3 |
| 1.0 | s | hi | . | . | 0 | 5 | 0 | 2 | 0 | 8 | . | . | 111 | 5 |
| *Class III log* | | | | | | | | | | | | | | |
| 0 | n | low | . | . | 0 | 1 | 0 | 1 | . | . | . | . | 4 | 1 |
| 0 | n | med | . | . | 0 | 1 | . | . | . | . | . | . | 0 | 1 |
| 0 | n | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0 | c | low | . | . | 0 | 2 | 0 | 1 | 1 | 1 | . | . | 3 | 2 |

**Table A.3** (continued)

| G<br>A<br>P | P<br>O<br>S | C<br>O<br>V | PSME |  |  |  |  |  |  |  | TSHE |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  | HJA |  | TCO |  | MCY |  | PCM |  | HJA |  | TCO |  |
| *Class III log (continued)* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 0 | c | med | . | . | 0 | 2 | . | . | . | . | . | . | 3 | 2 |
| 0 | c | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0 | s | low | . | . | . | . | . | . | . | . | . | . | . | . |
| 0 | s | med | . | . | . | . | 0 | 1 | . | . | . | . | . | . |
| 0 | s | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.2 | c | low | 0 | 1 | . | . | 0 | 2 | . | . | 2 | 1 | . | . |
| 0.2 | c | med | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.2 | c | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.4 | n | low | 0 | 1 | . | . | . | . | . | . | 0 | 1 | . | . |
| 0.4 | n | med | . | . | . | . | 0 | 1 | . | . | . | . | . | . |
| 0.4 | n | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.4 | c | low | 0 | 1 | 4 | 3 | . | . | . | . | 1 | 1 | 141 | 3 |
| 0.4 | c | med | . | . | . | . | . | . | 2 | 1 | . | . | . | . |
| 0.4 | c | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.4 | s | low | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.4 | s | med | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.4 | s | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.6 | n | low | . | . | 0 | 1 | . | . | . | . | . | . | 0 | 1 |
| 0.6 | n | med | . | . | . | . | 0 | 1 | . | . | . | . | . | . |
| 0.6 | n | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.6 | c | low | . | . | 1 | 1 | 2 | 3 | . | . | . | . | 42 | 1 |
| 0.6 | c | med | . | . | . | . | 0 | 2 | . | . | . | . | . | . |
| 0.6 | c | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.6 | s | low | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.6 | s | med | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.6 | s | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 1.0 | n | low | 0 | 1 | . | . | 0 | 1 | . | . | 0 | 1 | . | . |
| 1.0 | n | med | . | . | . | . | 0 | 1 | . | . | . | . | . | . |
| 1.0 | n | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 1.0 | c | low | 0 | 1 | . | . | 1 | 2 | . | . | 0 | 1 | . | . |
| 1.0 | c | med | . | . | . | . | 2 | 2 | . | . | . | . | . | . |
| 1.0 | c | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 1.0 | s | low | . | . | . | . | . | . | . | . | . | . | . | . |
| 1.0 | s | med | . | . | . | . | 1 | 1 | 0 | 1 | . | . | . | . |
| 1.0 | s | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| *Class V log* |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 0 | n | low | 0 | 4 | 1 | 2 | . | . | . | . | 0 | 4 | 9 | 2 |
| 0 | n | med | . | . | 0 | 5 | 0 | 1 | 0 | 1 | . | . | 0 | 5 |
| 0 | n | hi | . | . | . | . | 0 | 1 | . | . | . | . | . | . |
| 0 | c | low | 0 | 10 | 1 | 2 | 0 | 1 | . | . | 1 | 10 | 1 | 2 |
| 0 | c | med | . | . | 1 | 6 | 0 | 2 | . | . | . | . | 2 | 6 |
| 0 | c | hi | . | . | . | . | 0 | 2 | . | . | . | . | . | . |
| 0 | s | low | 0 | 6 | 0 | 1 | . | . | . | . | 1 | 6 | 0 | 1 |
| 0 | s | med | . | . | . | . | . | . | . | . | . | . | . | . |
| 0 | s | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.2 | c | low | 0 | 3 | 3 | 8 | . | . | . | . | 3 | 3 | 261 | 8 |
| 0.2 | c | med | . | . | 0 | 2 | 0 | 2 | 0 | 1 | . | . | 16 | 2 |
| 0.2 | c | hi | . | . | . | . | 0 | 3 | . | . | . | . | . | . |

**Table A.3** (continued)

| GAP | POS | COV | PSME | | | | | | | | TSHE | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | HJA | | TCO | | MCY | | PCM | | HJA | | TCO | |
| *Class V log (continued)* | | | | | | | | | | | | | | |
| 0.4 | n | low | 0 | 2 | 0 | 1 | . | . | . | . | 1 | 2 | 0 | 1 |
| 0.4 | n | med | . | . | . | . | . | . | 3 | 1 | . | . | . | . |
| 0.4 | n | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.4 | c | low | 1 | 7 | 5 | 6 | 5 | 2 | . | . | 45 | 7 | 128 | 6 |
| 0.4 | c | med | 1 | 2 | 2 | 1 | 1 | 1 | . | . | 2 | 2 | 2 | 1 |
| 0.4 | c | hi | . | . | . | . | 0 | 1 | 4 | 3 | . | . | . | . |
| 0.4 | s | low | . | . | . | . | 0 | 1 | . | . | . | . | . | . |
| 0.4 | s | med | . | . | 5 | 1 | 0 | 1 | . | . | . | . | 54 | 1 |
| 0.4 | s | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.6 | n | low | . | . | 1 | 4 | 0 | 2 | 0 | 1 | . | . | 5 | 4 |
| 0.6 | n | med | . | . | . | . | 1 | 1 | 0 | 1 | . | . | . | . |
| 0.6 | n | hi | . | . | . | . | . | . | 0 | 2 | . | . | . | . |
| 0.6 | c | low | 0 | 1 | 3 | 4 | . | . | . | . | 0 | 1 | 54 | 4 |
| 0.6 | c | med | . | . | 0 | 2 | . | . | . | . | . | . | 15 | 2 |
| 0.6 | c | hi | . | . | 1 | 1 | 0 | 5 | 0 | 8 | . | . | 0 | 1 |
| 0.6 | s | low | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.6 | s | med | . | . | . | . | 0 | 1 | 0 | 1 | . | . | . | . |
| 0.6 | s | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 1.0 | n | low | . | . | 0 | 5 | . | . | . | . | . | . | 5 | 5 |
| 1.0 | n | med | . | . | 0 | 1 | . | . | . | . | . | . | 0 | 1 |
| 1.0 | n | hi | 0 | 1 | 0 | 1 | . | . | 0 | 1 | 0 | 1 | 1 | 1 |
| 1.0 | c | low | 0 | 2 | 0 | 6 | 0 | 1 | . | . | 0 | 2 | 8 | 6 |
| 1.0 | c | med | . | . | 1 | 6 | 3 | 3 | . | . | . | . | 20 | 6 |
| 1.0 | c | hi | . | . | 0 | 2 | 2 | 3 | 0 | 1 | . | . | 0 | 2 |
| 1.0 | s | low | 1 | 4 | 6 | 3 | . | . | . | . | 9 | 4 | 242 | 3 |
| 1.0 | s | med | 1 | 1 | 11 | 4 | . | . | . | . | 0 | 1 | 93 | 4 |
| 1.0 | s | hi | 1 | 1 | 2 | 1 | 0 | 2 | 0 | 1 | 3 | 1 | 5 | 1 |
| *Skirt* | | | | | | | | | | | | | | |
| 0 | n | low | . | . | 0 | 1 | . | . | . | . | . | . | 0 | 1 |
| 0 | n | med | . | . | . | . | . | . | . | . | . | . | . | . |
| 0 | n | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0 | c | low | 0 | 1 | 0 | 2 | . | . | 0 | 3 | 0 | 1 | 0 | 2 |
| 0 | c | med | . | . | . | . | . | . | 0 | 1 | . | . | . | . |
| 0 | c | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0 | s | low | 0 | 2 | 0 | 1 | . | . | . | . | 0 | 2 | 0 | 1 |
| 0 | s | med | . | . | . | . | . | . | 0 | 2 | . | . | . | . |
| 0 | s | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.2 | c | low | . | . | 2 | 3 | . | . | . | . | . | . | 35 | 3 |
| 0.2 | c | med | . | . | 1 | 1 | 0 | 1 | 0 | 1 | . | . | 1 | 1 |
| 0.2 | c | hi | . | . | . | . | 0 | 1 | . | . | . | . | . | . |
| 0.4 | n | low | 0 | 2 | . | . | . | . | . | . | 0 | 2 | . | . |
| 0.4 | n | med | . | . | . | . | 0 | 1 | . | . | . | . | . | . |
| 0.4 | n | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.4 | c | low | . | . | 2 | 3 | . | . | . | . | . | . | 15 | 3 |
| 0.4 | c | med | . | . | . | . | 4 | 1 | . | . | . | . | . | . |
| 0.4 | c | hi | . | . | . | . | . | . | 1 | 2 | . | . | . | . |
| 0.4 | s | low | . | . | 5 | 2 | . | . | . | . | . | . | 92 | 2 |
| 0.4 | s | med | . | . | . | . | . | . | 1 | 1 | . | . | . | . |

**Table A.3** (continued)

| G A P | P O S | C O V | PSME | | | | | | | | TSHE | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | HJA | | TCO | | MCY | | PCM | | HJA | | TCO | |
| *Skirt (continued)* | | | | | | | | | | | | | | |
| 0.6 | n | low | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.6 | n | med | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.6 | n | hi | . | . | . | . | . | . | 0 | 1 | . | . | . | . |
| 0.6 | c | low | . | . | 0 | 1 | 1 | 1 | . | . | . | . | 0 | 1 |
| 0.6 | c | med | . | . | 0 | 1 | 1 | 1 | . | . | . | . | 0 | 1 |
| 0.6 | c | hi | . | . | 1 | 1 | . | . | 2 | 2 | . | . | 0 | 1 |
| 0.6 | s | low | . | . | . | . | . | . | . | . | . | . | . | . |
| 0.6 | s | med | . | . | 2 | 2 | . | . | . | . | . | . | 12 | 2 |
| 0.6 | s | hi | . | . | . | . | . | . | . | . | . | . | . | . |
| 1.0 | n | low | . | . | 0 | 1 | . | . | . | . | . | . | 0 | 1 |
| 1.0 | n | med | . | . | 0 | 2 | . | . | 0 | 2 | . | . | 0 | 2 |
| 1.0 | n | hi | . | . | . | . | . | . | 0 | 1 | . | . | . | . |
| 1.0 | c | low | . | . | . | . | . | . | . | . | . | . | . | . |
| 1.0 | c | med | . | . | 0 | 1 | . | . | 0 | 1 | . | . | 2 | 1 |
| 1.0 | c | hi | . | . | . | . | . | . | 0 | 1 | . | . | . | . |
| 1.0 | s | low | . | . | . | . | . | . | . | . | . | . | . | . |
| 1.0 | s | med | . | . | . | . | 0 | 1 | 1 | 2 | . | . | . | . |
| 1.0 | s | hi | . | . | . | . | . | . | 0 | 1 | . | . | . | . |
| *Substrate data missing* | | | | | | | | | | | | | | |
| 0 | c | low | 0 | 1 | . | . | . | . | . | . | 0 | 1 | . | . |
| 0.2 | c | low | 2 | 14 | 0 | 1 | . | . | 1 | 1 | 32 | 14 | 23 | 1 |
| 0.4 | n | low | . | . | 0 | 1 | . | . | . | . | . | . | 0 | 1 |
| 0.4 | c | low | 0 | 1 | 0 | 1 | . | . | . | . | 0 | 1 | 1 | 1 |
| 0.4 | s | low | 0 | 1 | . | . | . | . | . | . | 0 | 1 | . | . |
| 0.6 | n | low | 1 | 6 | . | . | . | . | . | . | 3 | 6 | . | . |
| 0.6 | n | med | 0 | 2 | . | . | . | . | . | . | 0 | 2 | . | . |
| 0.6 | c | low | 8 | 18 | . | . | . | . | . | . | 44 | 18 | . | . |
| 0.6 | c | med | 0 | 1 | . | . | . | . | . | . | 0 | 1 | . | . |
| 0.6 | c | hi | 0 | 1 | . | . | . | . | . | . | 0 | 1 | . | . |
| 0.6 | s | low | 0 | 4 | . | . | . | . | . | . | 1 | 4 | . | . |
| 0.6 | s | med | 0 | 1 | . | . | . | . | . | . | 1 | 1 | . | . |
| 1.0 | n | low | 1 | 5 | . | . | . | . | . | . | 1 | 5 | . | . |
| 1.0 | n | med | 0 | 2 | . | . | . | . | . | . | 0 | 2 | . | . |
| 1.0 | n | hi | 0 | 2 | . | . | . | . | . | . | 0 | 2 | . | . |
| 1.0 | c | low | 3 | 18 | . | . | . | . | . | . | 6 | 18 | . | . |
| 1.0 | c | med | 0 | 1 | . | . | . | . | . | . | 0 | 1 | . | . |
| 1.0 | s | low | 2 | 8 | . | . | . | . | . | . | 57 | 8 | . | . |
| 1.0 | s | med | 0 | 1 | . | . | . | . | . | . | 4 | 1 | . | . |
| 1.0 | s | hi | . | . | . | . | . | . | 0 | 2 | . | . | . | . |