SOIL CHARACTERISTICS OF PERSISTENT CANOPY OPENINGS OCCUPIED BY VINE MAPLE IN A COASTAL WESTERN HEMLOCK FOREST

by

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B.Sc.(Agr.), University of Guelph, 1993

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THE REQUIREMENTS FOR THE DEGREE OF
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Abstract

Hardwood species contribute to wildlife habitat, biological diversity, soil ecology and the ecology of riparian areas. In some low-elevation coastal B.C. forests, canopy gaps can be occupied by the hardwood species vine maple. Some gaps occupied by vine maple are not the traditional type of developmental gap created by tree mortality in that these gaps have no evidence of a gapmaker (McGhee 1996). Within some gaps, vine maple has the ability to persist and be self-maintaining over long periods of time.

This study was conducted in a western hemlock forest in the Seymour Demonstration Forest in the North Shore Mountains of the Coast Range, which is within the Coastal Western Hemlock (CWH) biogeoclimatic zone. The study was designed to determine if vine maple gaps are *edaphic gaps* (their location across the landscape is a reflection of a mosaic of inherent soil properties) or *priority gaps* (their location is due to their ability to establish a dense mat of stems early in stand development that is large enough to prevent invasion of the site by conifers). Since no significant differences were found to exist in inherent soil properties between vine maple gaps and the surrounding forest including groundwater table levels, soil moisture below the rooting zone, soil texture and gravel content, the *edaphic gap* hypothesis was not supported. Consequently, the data supported the alternate hypothesis that vine maple gaps represent *priority gaps*.

This study also sought to determine the effect of persistent vine maple gaps on soil properties. Since the vegetation in vine maple gaps has differed from that of the surrounding forest throughout stand development, these gaps were found to cause several alterations to soil properties. Vine maple gaps have significantly thinner forest floor (LFH), less conifer litterfall during the fall, higher pH in the LFH, higher Ca, Mg, K and Al concentrations in the LFH and a lower (not significant) C/N ratio in the upper mineral soil. Vine maple litter was found to decompose significantly faster than conifer litter and to have higher concentrations of N, P, Ca, Mg, K, Fe and Zn. Unlike developmental gaps, vine maple gaps have similar temperature and moisture regimes and rates of total annual litterfall and litter decomposition as compared to the surrounding closed canopy forest. However, larger gaps have a significantly greater influence on nutrient dynamics, temperature regimes and moisture regimes than smaller gaps.

Quotations

"Sunlit gaps in dark coastal forests are often brightened
by the beautiful vine maple; its pale green leaves providing a delicate
contrast to the surrounding shadows. In larger openings, October frosts
turn the leaves flaming orange and scarlet, a small but spectacular show of
fall colour in the evergreen forests."

Richard and Sydney Cannings

"To ask of any living thing what
good it is represents the last word in
ignorance about the workings of nature."

Aldo Leopold

"Wise tinkering includes saving all the parts."

Aldo Leopold

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Very special appreciation is extended to my parents and to my sister Catherine, and especially to my Dad for his meticulous grammatical edit of the final draft. Without the support and encouragement of my family, this thesis would never have been completed ($p=0.001$). Special thanks also to Alan Paige for his support and encouragement over the past few years.

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Chapter 1

Introduction

1.1 Introduction

In low-elevation forests of coastal British Columbia, Washington and Oregon, canopy gaps can be occupied by the hardwood species *Acer circinatum* Pursh., or vine maple, a clonal shrub or small tree with a short twisted trunk that often forms dense thickets of uneven-aged stems (Haeussler et al. 1990). Vine maple has the ability to persist and be self-maintaining over long periods of time within canopy gaps (Spies et al. 1990; O'Dea et al. 1995; McGhee 1996). Some gaps occupied by vine maple are not the traditional type of developmental gap created by tree mortality, for in these gaps there is no evidence of a gapmaker.

McGhee (1996) outlined two alternative hypotheses to explain the origin of vine maple gaps in conifer forests (Figure 1.1), *edaphic gaps* and *priority gaps*. Under the edaphic gap hypothesis, the location of vine maple gaps across the landscape is a reflection of unique inherent soil or site characteristics that give vine maple a competitive advantage over the regeneration of conifers (Table 1.1). Previous studies have shown that small-scale edaphic differences can strongly influence species composition, forest structure, and ecosystem function (Binkley 1995; Lertzman et al. 1996; Whitney 1986; Pritchett and Fisher 1987); and, that species with a competitive advantage on specific inherent conditions can exclude other species from growing on these sites (Kimmins 1987). Since inherent soil properties are relatively stable over the successional time frame, they can be used to provide an indication of the edaphic characteristics of a site throughout the history of a stand. In addition, inherent soil properties can be used to

compare the edaphic characteristics of sites supporting the growth of different species since these properties are not influenced by the type of vegetation growing on the site.

Priority gaps, unlike edaphic gaps, do not have soil and site characteristics that differ from the surrounding forest matrix. *Priority gaps* are the result of small stature vegetation which has been able to maintain a competitive advantage since stand establishment, resisting the regeneration of taller canopy dominants and subsequent canopy closure (McGhee 1996). Using indirect evidence, McGhee (1996) concluded that individual vine maple clones persist in priority gaps by establishing a dense mat of stems early in stand development that is large enough to prevent invasion of the site by conifers and the subsequent overtopping of the site as the stand grows up around them. Priority gaps are distinguished from developmental gaps by the absence of a gapmaker and are distinguished from edaphic gaps by having no identifiable difference in inherent edaphic conditions. McGhee (1996) further categorized vine maple gaps as being 'temporary' or 'persistent' depending on the extent to which conifer saplings growing within vine maple gaps affect future persistence of these gaps.

A number of researchers have studied the influence of tree species on soil properties (Alban 1969; Challinor 1968; Fried et al. 1990; Tappeiner and Alm 1975; Tarrant and Miller 1963). According to Binkley (1995), different species have different influences on soils due to variations in nutrient uptake, litter quality, and growth. Schmidt (1994) identified soil and site characteristics which are influenced by the forest canopy (Table 1.1). Vine maple is known to be efficient at nutrient cycling and is generally

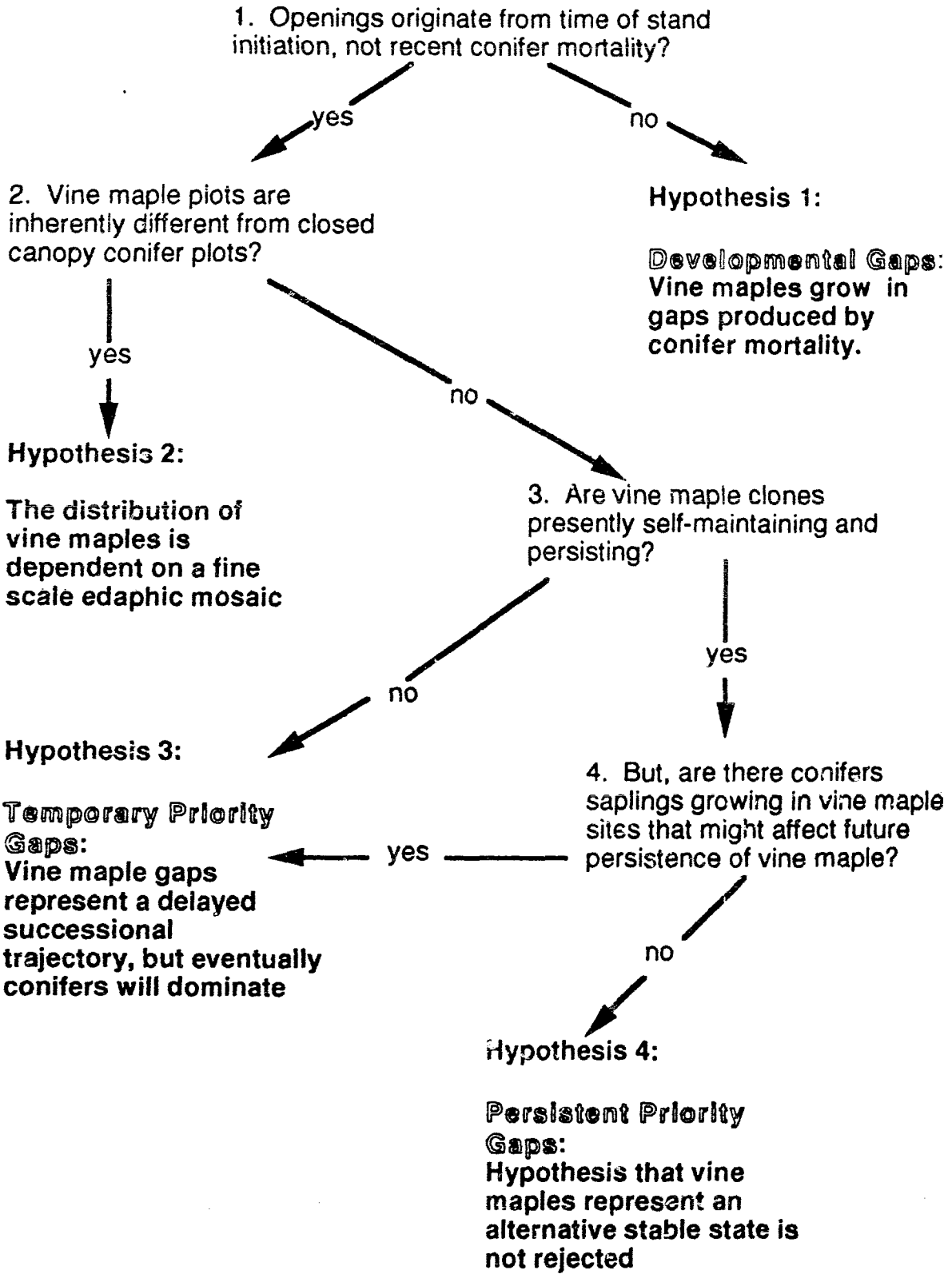

Figure 1.1 Inferential tree of vine maple gap hypotheses showing questions asked to test the hypotheses (McGhee 1996).

Table 1.1 Factors which are inherent to a site and those which are influenced by the type of vegetation growing on a site (Schmidt personal communication 1994). A "*" indicates properties which were measured either in this study or by McGhee (1996).

Inherent Soil or Site Properties:

- elevation*
- aspect*
- slope*
- site position on slope*
- depth to groundwater table*
- soil moisture regime
- drainage class
- moisture content below rooting zone*
- mottles
- parent material type
- gravel content*
- stoniness
- bulk density of C horizon
- particle size*
- pH of C horizon*
- depth to bedrock
- microtopography

Soil and Site Properties Influenced by the Forest Canopy:

- litterfall weight*
- litterfall nutrient content*
- litter decomposition*
- humus type
- weight per unit area forest floor*
- nutrient content of LFH, A and B horizons*
- organic matter content of A and B horizons*
- bulk density of A horizon*
- pH of LFH, A and B horizons*
- horizon depth
- soil colour
- soil structure
- root abundance
- rooting depth
- air temperature*
- surface soil temperature*
- throughfall*
- soil moisture-rooting zone*
- light regime*

associated with the development of Moder humus forms (Haeussler et al. 1990). The persistence of vine maple in canopy gaps may result in significant alterations to soil properties since the vegetation and micro-climate of vine maple gaps have differed from the surrounding forest for a considerable period of time. Vine maple gaps may have a significant influence on soil fertility and long-term site productivity.

The goal of this study is to determine if there are significant differences in soil properties in persistent vine maple gaps compared to those in the surrounding closed canopy western hemlock forest. The research goal is to be achieved by meeting the following primary objectives:

1. To examine selected inherent soil properties within persistent vine maple gaps in a coastal western hemlock forest to determine if the gaps are edaphic or priority in origin.

2. To examine soil properties influenced by the forest canopy to determine the effects of persistent vine maple gaps on forest soils.

The results of the research are presented in five chapters. The first chapter includes a literature review and a description of the study area. Chapter 2 presents the results from the microclimate component of this study in which the temperature and moisture regimes of vine maple gaps are described. A comparison of soil physical and chemical properties between vine maple gaps and the surrounding forest is presented in the third chapter. The fourth chapter presents the results from the comparison of litterfall and litter decomposition between gap plots and closed canopy plots. Chapter 5 presents the conclusions of this study.

1.2 Background

In this section, relevant background information is presented on the ecology and characteristics of coastal B.C. forests, the dynamics of canopy gaps, the role of hardwood species in forest ecosystems, and the characteristics of vine maple.

1.2.1 *Coastal B.C. Forests*

Temperate rainforests of coastal B.C. and the American Pacific Northwest are characterized by high accumulations of biomass, large leaf areas, coarse woody debris, species longevity, slow vegetative growth, infrequent large-scale disturbances, and slow recovery after disturbance (Franklin and Hemstrom 1981). These forests are unique both in the size and longevity of individual trees, and the accumulations of biomass in individual stands (Waring and Franklin 1979). The predominant climatic regime of mild winters with heavy precipitation, and warm and relatively dry summers, plays a major role in the dominance of conifers over deciduous hardwoods in these forests (Franklin and Hemstrom 1981 and Waring and Franklin 1979). Hardwoods often play pioneer roles or occupy habitats which have significantly different environmental features from the regional norm (Waring and Franklin 1979).

Due to the infrequency of large scale disturbances, small scale disturbances such as treefall are an important source of heterogeneity in forest structure and composition in coastal B.C. forests (Lertzman and Krebs 1991; Lertzman et al 1996). Canopy gaps, snags, and logs, (all resulting from small-scale mortality events) influence patterns of tree recruitment, understory vegetation dynamics, wildlife habitat, biomass dynamics, stand

structure, and carbon budgets (Harmon et al. 1986; Maser et al. 1988; Spies et al. 1990). Openings created by tree mortality also result in increased light availability (Canham et al. 1990 and Poulson and Platt 1989) and moisture availability (Denslow 1987) at the forest floor due to decreased interception by vegetation.

1.2.2 *Gap Dynamics*

Openings in the forest canopy associated with tree mortality, the traditional type of canopy gap described in the literature, are called developmental gaps (Lertzman et al. 1996). Topographic and edaphic variation may produce local variation in gap sizes and formation rates (Denslow 1987 and Lertzman et al. 1996); however, these gaps will, in time, fill in to form a closed canopy by the release of previously suppressed saplings, germination of dormant seeds in the soil seed bank, layering or sprouting of pre-disturbance plants, and germination of seeds brought into the gap by wind or animal transport (Feinsinger 1989). In forests dominated by small scale disturbances, some species rely on openings in the forest canopy for regeneration, either for the release of shade tolerant saplings, or to supply the high light levels required for the germination of shade intolerant species (Brokaw 1985 and Denslow 1987). Numerous possibilities exist concerning tree-by tree replacement in gap regenerating forests which relates the species of gapmaker and gapfiller to environmental characteristics within the gap (Lertzman 1992). The species which replaces the gapmaker determines if there will be a change over time in species composition within the forest.

Canopy openings created by tree mortality events have been the focus of most canopy gap research. However, some canopy openings that are not the result of tree mortality have been observed in Appalachian deciduous forests (Barden 1989), coastal forests in British Columbia, Washington and Oregon (Spies et al. 1990; Lertzman et al. 1996; McGhee 1996), boreal forests (Kuukavainen 1994; Hytteborn et al. 1991), and in the New Jersey pinelands (Ehrenfeld et al. 1995; Whitney 1986). Some of these gaps, termed edaphic gaps, are associated with an identifiable edaphic condition, such as a stream course or rock outcrop (Lertzman et al. 1996). Other non-developmental gaps owe their origin to intense patchy burns where the litter and humus layers were completely consumed by fire resulting in openings which fill in very slowly (Ehrenfeld et al 1995; Whitney 1986).

In a recent study in a watershed on the west coast of Vancouver Island in the wetter subzones of the Coastal Western Hemlock biogeoclimatic zone, Lertzman et al.. (1996) characterized gaps as being either developmental or edaphic. Edaphic gaps exist where adverse soil conditions, such as rock outcrops, wet spots, or frost pockets, do not support the growth of trees (Lertzman et al. 1996). They found that roughly 56% of the forest was influenced to some degree by canopy openings; and that 30% of the forested area was occupied by canopy gaps, of which 14% were developmental canopy gaps and 16% were edaphic canopy gaps (Lertzman et al. 1996). Edaphic gaps and developmental gaps play similar yet distinct roles in forest ecosystems (Lertzman 1996). There is little difference in the open space provided by each of these gaps, which is in itself an important resource for some species. However, structural features such as snags and downed wood

found in developmental gaps provide distinct habitat niches that are not associated with edaphic gaps. While the relationship of edaphic gaps to forest structure and forest dynamics has received little attention, Lertzman et al. (1996) found edaphic gaps to be important elements of forest structure that significantly contribute to the overall openness in the forest.

Another type of non-developmental gap, the priority gap, has been recognized recently as a component of coastal British Columbia forest ecosystems (McGhee 1996). Priority effects that occur early in stand development can result in patches of short stature vegetation which resist the subsequent establishment of conifers (McGhee 1996) (for other examples of priority effects see Shulman et al. 1983; Robinson and Dickerson 1987; Robinson and Edgemon 1988). In later successional stages, these patches appear as canopy gaps. Since inherent soil properties in priority gaps are no different from those of the surrounding forest matrix, these sites are no more suitable to the species occupying these gaps than to conifers. In addition, priority gaps have a random distribution across the landscape. Ecosystem processes in priority gaps may be different from those in developmental gaps; however, little research has been carried out to identify these differences. Whereas developmental gaps are characterized by a flush of resources, especially light and moisture, at the forest floor, McGhee (1996) found that the light regime at the forest floor beneath priority gaps was similar to the light regime beneath the adjacent forest. Because priority gaps are present for longer periods of time, their effects on soil characteristics, wildlife habitat and ecosystem processes may be greater than those of developmental gaps. This study on persistent vine maple gaps examines ecosystem

processes within these gaps, determines if vine maple gaps are priority in origin, and compares the ecological roles of vine maple gaps to developmental gaps.

1.2.3 *Role of Hardwoods in Coastal Pacific Northwest Forests*

Until recently, the ecological role of hardwoods in coniferous forests of the Pacific Northwest has attracted little attention from researchers and forest managers (Massie et al. 1994). Most research has concentrated on the removal of broad-leafed species from areas managed for timber production since broad-leaved species are viewed as competitors to merchantable coniferous species (Smith 1986; Daniel et al. 1979). For example, overtopping vegetation is considered to be a severe obstacle to the regeneration of Douglas-fir in the Coast Mountain range (Chan and Walstad 1987). The long-term effects of silvicultural practices which remove hardwoods from conifer-dominated ecosystems in terms of long-term soil productivity, ecosystem resilience, and site sustainability are poorly understood (Massie et al. 1994).

Hardwood species contribute to wildlife habitat, biological diversity, soil ecology, and the ecology of riparian areas (Haeussler et al. 1990; Massie et al. 1994; McGhee 1996). After disturbances, hardwoods maintain ecosystem resilience by establishing quickly, retaining soil nutrients, and reducing soil erosion (Perry and Maghembe 1989). Hardwoods also increase the productivity of forested areas by protecting crop species from browsing animals, moderating temperatures, and by providing a source of food and habitat for wildlife (Lavender et al. 1990).

In coastal British Columbia ecosystems, hardwoods are generally associated with early successional stages in stand development, persisting into later successional stages only in disturbed areas such as canopy openings, and riparian zones (Haeussler et al. 1990). In these forests, the biomass of conifers can be 1000 times greater than that of hardwoods (Waring and Franklin 1979). Despite the overwhelming dominance of coniferous vegetation, several hardwood species are nevertheless indigenous to these ecosystems. These species include bigleaf maple (*Acer macrophyllum*), black cottonwood (*Populus trichocarpa*), red alder (*Alnus rubra*), white birch (*Betula papyrifera*), bitter cherry (*Prunus emarginata*), pacific crab apple (*Malus fusca*), arbutus (*Arbutus menziesii*), western flowering dogwood (*Cornus nuttallii*), Douglas maple (*Acer glabrum*), and vine maple (*Acer circinatum* Pursh.).

Litterfall from bigleaf maple, Douglas maple, and vine maple is thought to decompose rapidly and provide a rich source of nutrients to the humus layers (Krajina et al. 1982). Benefits of red alder include its association with N-fixing bacteria in root nodules, its potential ability to increase the resistance of Douglas-fir to laminated root rot, and its ability to reduce attacks on Sitka spruce from spruce weevils (Chester 1988). The level of nutrients and beneficial fungi under white birch may be higher than under purely coniferous stands (Haeussler et al. 1990); while the growth of black cottonwood moderates forest temperatures, stabilizes stream banks, and may be associated with N-fixing bacteria (Haeussler et al. 1990).

A recent review by Binkley (1995) found that soils can dramatically differ under different species of trees, and suggests that many of the traditional beliefs that conifers

degrade soils and hardwoods improve soils are based on weak evidence. While the effects of species on soils includes nutrient pool sizes, acidity and nutrient supply rates, Binkley (1995) observed that no study has shown that any species uniformly pushes all soil variables in unfavourable (or favourable) directions.

A study by Fried et al. (1990) -- designed to determine if the absence of bigleaf maple from a Douglas-fir forest in the Oregon Coast Range would adversely influence soil properties -- used a paired-plot methodology to compare mineral soil properties, litter and forest floor biomass and chemical composition, and nutrient turnover rates, between soils beneath bigleaf maple trees and soils beneath the adjacent Douglas-fir forest. Fried concluded that bigleaf maple trees, compared to adjacent Douglas-fir trees, increased soil N, organic C content, and annual inputs and cycling of all macronutrients; however, he found few differences in the concentration levels of cations or P in the top 10 cm of mineral soils. Since the current productive capacities of the forest soils of British Columbia and the American Pacific Northwest result from thousands of years of shifting mosaics of coniferous and hardwood vegetation on the land, Fried expressed concern that, although his study could not provide conclusive evidence that removal of bigleaf maples would significantly affect site productivity, the maintenance of long-term forest site productivity warrants the development of a better understanding of the influence of maples and other hardwoods on forest soils before these species are completely eliminated from commercial conifer forests.

Due to the distinct characteristics of hardwood species, B.C. forest management guidelines recommend hardwood retention in timber management areas to maintain and

enhance biodiversity (B.C. M.O.F. 1995). In addition, the Forest Renewal Plan (1994) has a mandate to invest and promote non-timber forest values, including an allocation of funding towards hardwood research. The B.C. Forest Practices Code (1994) also addresses the need for retaining hardwoods in pure and mixed stands and has legislative authority to enforce regulations that promote soil conservation and the maintenance of biodiversity. With further research into hardwood ecology and hardwood-soil interactions, it should become increasingly evident that broad-leafed species are crucial to the future health of forests. Forest management strategies will be improved when the role of hardwood species in conifer-dominated ecosystems is better understood.

1.2.4 *Vine Maple*

Vine maple is a hardwood shrub or small tree with a short twisted trunk that often forms dense thickets (Coward 1977; UBC Bot. Garden 1976) with several branches sprouting out from the base in a leaning or sprawling fashion (Whitney 1985). Reaching heights of 10-20 meters and reproducing largely by layering or sprouting, vine maple clones are often comprised of uneven-aged stems (Haeussler et al. 1990 and McGhee 1996). While vine maple stems typically reach 80 years of age, ages up to 142 years have been documented (Anderson 1967). Vine maple has a shallow extensive rooting system and high nutritional requirements (Haeussler et al. 1990). In Coastal Western Hemlock biogeoclimatic zone, vine maple litter fall begins in the last week of September to the first week of October, and ends in the first and second weeks of November. Vine maple foliage reappears in the first week of May.

In a recent study in the Oregon Coast Range, vine maple clones were found to be adapted to layering and survival in the understory, and vegetative expansion was found to be more important than seedling establishment in the expansion and establishment of vine maple clones (O'Dea et al. 1995). Shade-tolerant vine maple clones have been found to be able to survive the stem exclusion phase in young Douglas-fir stands, and patches have been found in old-growth Douglas-fir forests (O'Dea et al. 1995; Spies et al. 1990). O'Dea et al. (1995) also observed that dense vine maple cover may prevent the establishment of herbs, conifers and other shrubs in openings.

While vine maple is an early seral to late climax species (Haeussler et al. 1990), a study conducted in the Oregon Coast Range by Russell (1973) found that its abundance followed a bi-modal distribution through succession. Russell suggested that in his study area, vine maple became abundant following clearcutting, almost disappeared under dense coniferous canopy 40 years after disturbance, and then increased in abundance as openings in the forest canopy occurred. Other studies have observed that vine maple is able to persist through the stem exclusion phase of stand development, and well-established patches have been found in old growth Douglas-fir forests (O'Dea et al. 1995; Spies et al. 1990). While vine maple is very shade tolerant, it prefers growing in higher light conditions (Haeussler et al. 1990) and its growth has been observed to be greatest in canopy openings (UBC. Bot. Garden 1976). Russell (1973) found that vine maple biomass and stem frequency increases as canopy openness and light intensity increases.

In coastal forests, vine maple grows from sea level to an elevation of approximately 1000m (Anderson 1969 and UBC Bot. Garden 1976). Vine maple is a

significant competitor to crop species in Washington and Oregon (Haeussler et al. 1990); however, in B.C. the range of vine maple is not extensive and it creates competition problems only in localized areas. The seeds of vine maple are an important food source of many songbirds, game birds and mammals (Haeussler et al. 1990 and Whitney 1985); and by providing a distinct habitat niche, vine maple gaps may support different bird populations than the forest matrix (Saunders et al. unpublished data).

1.3 Study Design

1.3.1 *Study Area*

The study area is in the Seymour Demonstration Forest (on the west side of the access road approximately 2 km north of the gatehouse) in the North Shore Mountains of the Coast Range. The stand is a mature, second-growth forest dominated by western hemlock that was logged approximately 80 years ago. The forest cover map of the area indicates that the site class is 'good', average tree height of canopy dominants is 37.5-46.4 m, and canopy closure ranges from 56-65% (GVRD 1988). The dominant tree species in the study area are western hemlock (53.4%), Douglas-fir (27.6%) and western redcedar (18.9%) (McGhee 1996).

The study area is transitional between the moist maritime (CWHmm) and dry maritime (CWHdm) subzones of the Coastal Western Hemlock biogeoclimatic zone. In the southern range of this zone where the study area is located, less than 15% of total precipitation occurs as snowfall. Mean annual precipitation is approximately 2088 mm (Meidinger and Pojar 1991), most falling between the months of October and March with

a pronounced dry period occurring in late summer. Mean annual temperature is 7.8 °C, with mean monthly temperatures remaining above 0°C (Meidinger and Pojar 1991).

Generalized soil descriptions of the study area were obtained from the biogeoclimatic ecosystem classification system (Meidinger and Pojar 1991). The soils in the Coastal Western Hemlock zone are dominantly Orthic Humo-Ferric Podzols, grading into Ferro-Humic Podzols with increasing precipitation. Many podzols in the CWH lack an eluvial (Ae) horizon because in this part of the soil profile the heavy leaching is offset by the rapid addition of organic colloids and the weathering of iron and aluminum (Watts 1983). Throughout the study area, Mor is the dominant humus form, and the parent material consists of compact basal till. Leaching of nutrients from the mineral soil is rapid in this wet climate. Since these soils are acidic, coarse-textured, low in clay minerals, and poor in nutrients (Watts 1983), the storage of nutrients in vegetation and surface organic layers in these stands is extremely important in the maintenance of ecosystem productivity.

Since the study area has a variable microtopography, this factor was included in the soil sampling procedure. Treefall creates a variety of soil microsites; the roots of uprooted trees and the attached soil creates a mound, while the depression remaining where the tree once stood forms a pit. In temperate forests, 10-40% of the soil surface may be occupied by these pits and mounds of various ages (Peterson et al. 1990). Pits and mounds have different physical and chemical characteristics, with organic matter and moisture content being higher in pits, while soil temperatures fluctuate more in mounds (Beatty and Stone 1986; Schaetzl et al. 1988; Peterson et al. 1990). Although the vine maple gaps in the study area were not created by treefall, the pit and mound

microtopography may be the result of windthrow events prior to stand establishment, or may be the result of undulations in the basal till underlying the area creating low microsites and high microsites (will be referred to as pits and mounds).

1.3.2 *Site Selection*

In the summer of 1993, ten parallel transects ranging from 50 m to 250 m in length were established by McGhee (1996) for a study of the demography of vine maple. The transects were at least one tree length from the road or stand edge and were terminated at changes in terrain or forest structure, such as increased slope, boulders or large blowdowns. McGhee (1996) located 31 vine maple clones (26 were in gaps) along the transects and paired each with a closed canopy plot in the surrounding forest. Each closed canopy plot was established at a distance of 25 m from the vine maple plot and located perpendicular to the transect line. The closed canopy plots contained no evidence of vine maple (dead or alive) within 20m of their centers and were dominated by conifers that made up the relatively closed canopy. The structural characteristics of canopy gaps, the morphological characteristics of vine maple, and the characteristics of the surrounding forest, as measured by McGhee (1996), are presented in Table 1.2. Paired plot comparisons are a commonly used method of evaluating differences in resources between canopy gaps and surrounding closed canopies (Crome and Richards 1988; Mladenoff 1987; Schemske and Brokaw 1981; Shelly 1988; Vitousek and Denslow 1986).

For this research study, six representative vine maple gaps and their associated closed canopy plots were selected for further study of soil properties from the paired

plots in the McGhee (1996) study. Each gap was chosen using three criteria: a canopy gap area between $15m^2$ and $180m^2$; a vine maple clone that was healthy; and a paired closed canopy plot with similar slope angle, slope position, aspect and elevation.

1.3.3 *Description of Study Plots*

Since soil development is a function of the interaction of climate, parent materials, topography and organisms over time (Jenny 1941), the effects of species on soils can be determined by comparing soils that formed, with and without an organism present, when the other four factors of soil formation are held constant (Fried et al. 1990). As the predominant climate of the study area is constant, the observed differences in microclimate within the paired plots is assumed to be attributable to the presence of an opening in the forest canopy. The topographic characteristics of the gap and closed canopy plot within each paired plot are also similar; therefore, differences in moisture regime are likewise assumed to be attributable only to the presence of the vine maple gap and not to differences in slope position or slope angle. As there is no evidence of large-scale soil disturbance, such as landslides, the soils within the study area appear to have developed over the same period of time. The stand within the study area has not been treated with herbicides, pesticides, prescribed burns, or other management activities such as spacing or thinning since the stand was harvested approximately 80 years ago (McGhee 1996).

The characteristics of the paired plots measured by McGhee (1996), relevant to this study, are presented in Table 1.2. Plots were selected to have a similar elevation, aspect and slope. Since elevation can influence climatic regimes and ecosystem types,

the paired plots were selected within the same biogeoclimatic subzone, and were located within 200 and 250 m a.s.l, and each pair did not differ by more than 30 m a.s.l. Since, in mountainous areas, aspect can strongly influence temperature, hours of daylight and intensity of radiation reaching the ground surface, the paired plots were selected to have similar aspects (north-east to south-east), and the difference within each paired plot was no greater than 47°. Since slope angle can give an indication of drainage regimes, the suitability of the site for plant growth, and depth to bedrock, the paired plots were selected to have similar slopes (4 to 20%), and the difference in slope of the gap and closed canopy plots within each paired plot did not differ by more than 6%.

The amount of total direct and diffuse light reaching the forest floor and the percentage of open sky influences various soil processes such as leaching and decomposition, and soil properties such as soil moisture and temperature. McGhee (1996) used hemispherical canopy photographs to estimate light regimes in each of the vine maple gap and closed canopy plots during the summer of 1993. For each paired plot, photographs were taken beneath the foliage of the vine maple clone in the gap plot and beneath the forest canopy in the closed canopy plot. The resulting images were analyzed to calculate the penetration of both diffuse and direct-beam radiation below the closed canopy plot and below the small but discrete openings visible between the leaves in the gap plot. In her analysis, McGhee (1996) found that at ground level, the light regime beneath vine maple gaps is similar to that beneath the adjacent closed canopy forest.

Canopy gap area is defined as the vertical projection onto the ground of the opening in the forest canopy (Lertzman and Krebs 1991), while expanded gap area is

defined by the boles of the trees whose canopies define the canopy gap (Runkle 1982; Veblen 1985). These values, measured by McGhee (1996), are useful to this study as they give an indication of the relative impact of the gaps on the microclimate within the plots. Opening size is frequently expressed using the D/H ratio since the ratio of the diameter of the gap to the height of the trees surrounding a gap can provide an indication of the influence of the gap on the microclimate of the understory (Geiger 1965); as the size of an opening decreases, humidity increases and temperatures remain more constant. Light increases with increased opening size, reaching a maximum when D/H=2 (Pickett and White 1985). In this study, gap diameter was estimated from gap area measurements of McGhee (1996) and tree height estimates were obtained from the forest cover map of the Seymour Demonstration Forest (GVRD 1988).

The number of live and dead vine maple stems in each gap provides an indication of the relative past and present impact of vine maple on the gap sites, with clone size being defined as the total number of vine maple stems within a gap. Each vine maple clone was assigned a gap size class and clone size class, (either small, intermediate or large), based on their relative size compared to other clones in the study area. Clone size was found to be significantly related to gap size (McGhee 1996), the larger the canopy gap in terms of both canopy gap area and expanded gap area, the larger the vine maple clone. Since vine maple gaps have resisted the regeneration of coniferous tree species since the time of stand establishment, the size of clone appears to dictate the size of the gap in which it is located.

Within the study area, the dominant tree species are western hemlock (53.4%), Douglas-fir (27.6%) and western redcedar (18.9%) (McGhee 1996). Because Douglas-fir needles have been observed to decompose faster than western hemlock needles (Edmonds 1980), and western redcedar foliage has higher concentrations of Ca than both western hemlock and Douglas-fir foliage (Beaton 1965), the species mix, (or relative proportions) of western hemlock, Douglas-fir and western redcedar surrounding the plots may have an influence on soil properties (such as pH) and nutrient concentrations. In a study conducted in very old forests in Washington and Idaho, Alban (1969) found that pH, Ca, base saturation and the total weight of the forest floor were greater under western redcedar than under western hemlock; and, N, C, Mg, and K were generally higher under cedar than under hemlock but the differences were not large. However, in this study area, McGhee (1996) found no significant difference in the average species composition of conifers surrounding vine maple gaps and closed canopy plots.

Table 1.2 Characteristics of the paired plots measured in the McGhee (1996) study.

Plot	Elevation (m a.s.l.)	Slope (%)	Slope Position	Aspect (degrees)	Total Direct and Diffuse Light - Summer (mol/m^2*day)	% Open Sky - Summer	Expanded Gap Area (m^2)	Canopy Gap Area (m^2)	Gap Size Class [a]	Ratio of Canopy Gap Diameter to Tree Height	Live Stems (#)	Dead Stems (#)	Clone Size Class [b]	Species Mix Surrounding Plot (%)[c]		
														Hw	Fd	Cw
1g	200	14	Mid-slope	97	6.91	19.9	87.4	26.1	S	0.13	3	11	S	67	17	17
1c	210	12	Mid-slope	98	9.83	33.7	5.9							33	66	0
2g	240	15	Mid-slope	140	3.40	11.4	198.1	72.4	I	0.23	17	12	I	67	0	33
2c	210	20	Mid-slope	93	6.36	25.2	15.1							66	33	0
3g	240	9	Mid-slope	116	4.17	18.3	62.6	15.4	S	0.10	14	19	I	29	71	0
3c	240	15	Mid-slope	122	9.21	33.8	17.9							0	33	67
4g	200	9	Toe slope	154	4.14	14.4	221.7	52.6	I	0.20	15	24	I	57	14	29
4c	210	4	Toe slope	110	8.32	28.1	25.3							100	0	0
5g	250	19	Mid-slope	70	11.69	39.2	187.0	45.1	I	0.18	32	33	I	67	0	33
5c	250	15	Mid-slope	95	11.26	41.5	14.5							0	100	0
6g	200	7	Lower slope	80	6.59	24.0	355.1	177.6	L	0.35	64	52	L	45	0	55
6c	200	11	Lower slope	120	7.52	27.8	10.0							33	33	33

a Gap Size Class
Small (S) = 1.0 m^2 to 30.0 m^2
Intermediate (I) = 30.0 m^2 to 100.0 m^2
Large (L) = 100.0 m^2 or larger

b Clone Size Class
Small (S) = 1 to 10 stems
Intermediate (I) = 11 to 40 stems
Large (L) = 41 stems or larger

c Species Abbreviations
Hw = Western hemlock
Cw = Western redcedar
Fd = Douglas-fir

Chapter 2

Temperature and moisture regimes of persistent canopy openings occupied by vine maple in a coastal western hemlock forest

Chapter 2
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2.1 Introduction

Due to the infrequency of large scale natural disturbances in coastal temperate rainforests, canopy openings are an important source of heterogeneity in forest structure and composition (Lertzman and Krebs 1991; Spies and Franklin 1989; Spies et al. 1990; Stewart 1986; Lertzman et al. 1996). In coastal temperate forests, canopy gap dynamics may operate for many centuries due to the long return interval between stand-destroying fires (Spies et al. 1990). Developmental gaps, created by tree mortality, greatly influence regeneration in these forests and are considered necessary even for shade tolerant species such as western hemlock to reach the main canopy (Stewart 1986). Research has been conducted in a variety of forest types concerning the increase in energy and moisture reaching the ground surface due to the loss of biomass following the creation of a canopy gap (Chazdon and Field 1987; Denslow 1987; Poulson and Platt 1989; Lieberman et al. 1989; Canham et al. 1990; March and Skeen 1976, Chazdon and Fetcher 1984; Pickett and White 1985); however very little research exists concerning how gaps influence patterns in below ground resources (Publicover and Vogt 1991), and little research on these patterns has been conducted in coastal temperate rainforests. Much of the literature on canopy openings concerns the role of light gaps in tree regeneration and maintenance of tree species diversity (Beatty and Stone 1986).

The most conspicuous environmental change in canopy gaps is a localized increase in light levels (Pickett and White 1985). However, the actual light regime in and around

any individual gap can be modified strongly by understory vegetation, and differences in the light regime between gaps are a function of canopy height and latitude (Canham et al. 1990). A study of light regimes in developmental gaps (created by single treefall) in old growth Douglas-fir - hemlock forests in Oregon indicated that these small gaps have little effect on understory light regimes due to the low ratio of gap diameter to canopy height; however, as gap size increased, both the mean and range of light levels within the gap increased (Canham et al. 1990). In tropical forests, differences between gap and understory light levels have been observed to be lower in small gaps than in large gaps, and lower on cloudy days than on sunny days (Denslow 1987).

Since the forest canopy moderates temperature extremes by intercepting solar radiation, air and soil temperatures in canopy gaps differ from those in the closed forest. The forest canopy prevents the soil from reaching excessively high temperatures in the summer, and reduces the rate of heat loss from the soil during winter months (Lavender 1990; Pritchett and Fisher 1990). Large openings (such as large clearcuts) have higher maximum and lower minimum soil temperatures than closed forest (McGhee 1976; Ash and Barkham 1976; Pontailler 1979), and air temperatures are higher and fluctuate more in gaps than beneath the intact canopy (Pontailler 1979). Day-to day variations in soil temperatures strongly influence root growth rates; root growth slows during cooler months and during hot and dry midsummer conditions (Lyford and Wilson 1966).

Canopy gaps also influence soil moisture and groundwater table levels since rates of throughfall, evaporation, and transpiration differ in and around gaps as compared to those in a closed canopy forest (Pickett and White 1985; Pritchett and Fisher 1987). A

reduction in the amount of vegetation present on a site to intercept and transpire water following removal of the forest canopy can result in an increase in soil moisture and water table levels (Pritchett and Fisher 1990). However, open areas which receive similar amounts of precipitation as forested areas may have lower soil moisture and water table levels due to greater evaporation during hot periods. In tropical forests, moisture levels in the upper 10 cm of soil have been observed to be consistently and significantly higher in gaps than beneath intact canopies (Lee 1978; Denslow 1987). When soil in the rooting zone is moist, a vegetated surface can be cooler than when the soil is dry because of greater evapotranspirational cooling.

Gap size determines whether a gap will have an environment much different from that of the closed canopy forest; small gaps in either tall or open canopies have little effect (Pickett and White 1985). As opening size decreases, humidity increases and temperatures remain more constant (Geiger 1965). An opening in the canopy less than 5 m across is generally not considered a gap (Brokaw 1982). In very small canopy openings, the development of extremes in surface temperatures is hindered by shade from surrounding trees; whereas, in somewhat larger openings, the wind causes enough turbulent transfer of heat to restrict the diurnal range of surface temperatures (Smith 1986). The greatest extremes in surface temperatures occur where the combined effect of shade and ventilation is the least. This occurs when the diameter of an opening in the forest canopy is one and one-half times the height of surrounding trees (Geiger 1965).

Some canopy openings in coastal temperate forests contain the hardwood species vine maple, and some vine maple gaps have a notable absence of a gapmaker (McGhee

1996; Spies et al. 1990). In some of these gaps, vine maple has been persistent since the time of stand establishment, resisting the regeneration of taller canopy dominants and subsequent canopy closure (McGhee 1996). Accordingly, the effect on temperature and moisture regimes of vine maples occupying persistent gaps is likely to be significant because the influence of both vine maple and the gap environment is prolonged throughout stand development.

Vine maple is very resistant to flooding and most commonly grows on moist, well-drained sites (Krajina et al. 1982). Vine maple also has a shallow extensive rooting system, a high transpiration rate, and is capable of rapidly depleting soil moisture to a depth of 60 cm in late summer (Drew 1968; Haeussler et al. 1990). Vine maple is very shade tolerant but prefers growing beneath canopies with greater light penetration (Krajina et al. 1982). Vine maple growth is greatest in canopy gaps (UBC Bot. Garden 1976); and vine maple biomass and stem frequency increase as light intensity increases (Russell 1973). In a recent study of light regimes within canopy openings occupied by the understory species vine maple, conducted in the North Shore Mountains of the Coast Mountain Range, McGhee (1996) observed that in the summer, the light environment at the ground surface in vine maple gaps is no more favourable than on the ground surface beneath the adjacent forest. McGhee (1996) did not measure light levels above the vine maple in gaps in the summer or light levels in the gaps in the winter. McGhee (1996) also found that the size of vine maple gaps is significantly related to the size of the vine maple clone occupying these gaps: the larger the clone, the larger the gap.

The purpose of this component of the study is to compare air temperature, soil temperature, precipitation, soil moisture, and groundwater levels in canopy openings supporting the growth of vine maple to those in the surrounding closed canopy western hemlock forest, over a one year period. Since developmental gaps typically have different microclimatic conditions than the surrounding forest, a goal of this study is to determine whether or not vine maple gaps show similar microclimatic differences. This study also seeks to determine if vine maple gaps are edaphic gaps or priority gaps, and helps to explain the influence of vine maple gaps on forest soil properties. The following hypotheses were tested concerning temperature and moisture regimes in vine maple gaps:

1. Compared to the closed canopy, surface air and soil temperatures are lower in gaps in the summer months because of the high rates of evapotranspirational cooling associated with the growth of vine maple. Surface air and soil temperatures in gaps are lower in the winter months because of the absence of the canopy which can moderate extremes in temperatures.

2. Throughout the year, the amount of precipitation reaching the surface is greater in vine maple gaps than in the closed canopy due to less interception by vegetation.

3. Throughout the year, surface soil moisture levels are higher in gaps than in the closed canopy due to greater amounts of precipitation reaching the forest floor, except in late summer when the high transpirational requirements of vine maple depletes soil moisture in the rooting zone.

4. Throughout the year, groundwater table levels are higher in the gaps due to higher levels of precipitation reaching the ground surface, except in late summer when the high transpirational requirements of vine maple lowers water table levels.

An additional aspect of this study is to test whether or not microclimatic conditions differ for pits and mounds within this ecosystem. The microtopography of the hemlock forest in the study area is dominated by the presence of pits and mounds. Pit and mound microtopography can persist for several centuries (Beatty and Stone 1985) and can influence soil temperature and moisture regimes. Pits and mounds can differ in their soil characteristics; mounds are accumulations of mineral soil brought up by the roots of trees when they fell; and, pits are small depressions found where trees once stood (which tend to accumulate litterfall and moisture). Peterson et al. (1990) observed that soil temperature and light levels are significantly higher in mound microsites than in pit microsites in the summer. Since the vine maple gaps in this study area have existed since the time of stand establishment (McGhee 1996), it appears that the pits and mounds found in these plots are older than the stand. Pit and mound microsites are hypothesized to demonstrate the extreme temperature and moisture conditions within each of the individual plots. Throughout the year, pits are expected to be wetter than mounds; and pits are expected to be warmer than mounds in the winter and cooler than mounds in the summer.

2.2 Methodology

2.2.1 *Mid-Day Air and Soil Temperature*

Bi-weekly mid-day soil temperature measurements were made at four locations on each plot over the course of one year. For each of the twelve plots, two measurements were made in a pit and two measurements on a mound, approximately 50 cm from each

hydroprobe access tube and groundwater well (see 2.2.3 and 2.2.4). Copper-constantan thermocouple wire was installed to a depth of 10 cm from the surface of the forest floor, and temperature readings were made using a digital voltmeter. Mid-day air temperature readings were taken at approximately 20 cm above the soil surface at each thermocouple location.

2.2.2 *Precipitation*

Beneath the foliage of vine maple in each gap plot and in the centre of each closed canopy plot, a throughfall gauge was situated 10 cm above the soil surface to monitor inputs of moisture to the soil. Throughfall gauges were constructed using 4 L milk jugs and wooden stakes. These containers were chosen because they contained enough volume to hold the large amounts of precipitation which could accumulate during a two week sampling period. The volume of water collected in each throughfall gauge was measured by transferring the water into a graduated cylinder. The throughfall gauges were calibrated to provide data in standard rain gauge units. Data is missing for February 18, March 4 and November 17, 1994 when the throughfall gauges overflowed, and for December 3 and December 14, 1994 when the gauges were frozen.

2.2.3 *Moisture Content*

A Campbell Pacific Nuclear 503 Depth Moisture Gauge (a hydroprobe) was used to determine soil moisture. This instrument is capable of making repeated measurements of moisture contents at various depths in the soil by measuring hydrogen concentrations in

the soil (Campbell Pacific Nuclear 1978). High speed neutrons emitted from the radioactive source contained within the gauge (Am241/Be) slow down upon meeting hydrogen and are reflected back towards the gauge where they are counted (Campbell Pacific Nuclear 1978). To determine moisture content, the field count is compared to a standard count, given in the CPN user manual.

Using an auger, two 2" diameter aluminum access tubes were installed at each site, one in a pit and one in a mound. Where possible, holes were drilled to a depth of 1m and all access tubes reached at least 80 cm beneath the soil surface. The tubes were cut with a pipe cutter so they all rose to a height of 15 cm above the ground surface. This made measurements with the hydroprobe much easier as the depth from the instrument to the gauge in the soil profile did not need to be re-checked at each site. The access tubes were capped with a rubber stopper to prevent debris from entering. Over a one year period, bi-weekly readings were taken at 30, 50 and 80 cm depths. To ensure that the hydroprobe was reading accurately, hydroprobe readings were taken each field day in the laboratory in a drum of dry sand.

2.2.4 *Groundwater Table Measurements*

Two groundwater wells were installed in each of the twelve plots, one in a pit and one in a mound. Using an auger, the wells were installed where possible to a depth of one meter beneath the soil surface. All wells reached at least 80 cm beneath the soil surface. The maximum depth of the well below the surface was recorded since groundwater table measurements were not possible below this point. Wells were constructed from 2" PVC

tubing with holes drilled at 1" intervals to allow for flow of water into the well. A nylon stocking was placed around the well to prevent debris from entering into the well, and the well was covered with a cap to prevent material from falling in from above.

A hollow 3/4" plastic tube, approximately the same length as the well, was placed inside the well and the location of the soil surface was marked on this tubing. The tubing contained a piece of styrofoam, and water table measurements were recorded on every field day by blowing the styrofoam down to the bottom of the tube and allowing it to rise to the level of the water table. Water table measurements, recorded as depth below the soil surface, were made on a bi-weekly basis over a one-year period.

2.2.5 *Statistical Design*

2.2.5.1 *Analysis*

The underlying statistical principle in the design of this study is the split-plot design, a special kind of incomplete block design. In this design, whole plots, to which levels of one or more factors are applied, are divided into sub-plots to which levels of one or more additional factors are applied (Steele and Torrie 1980). In this study, the whole plots were the six paired plots, which were subdivided into gap and closed canopy sub-plots. The gap and closed canopy sub-plots were further subdivided into pit and mound microsites, giving rise to a split-split plot design (Figure 2.1).

Each sampling date was individually tested using the split-split plot design to determine whether or not significant differences existed between gap and closed canopy

		N
r	1 2 3 4 5 6	6
a	g c g c g c g c g c g c	12
b	p m p m p m p m p m p m p m p m p m p m p m p m	48
subsamples	2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2	96

Factors: r = Site Replicate (Block) = 6
a = Gap or Closed Canopy Plot = 2
b = Pit or Mound Microsite = 2

	Source		DF	SS	MS	F	P
I	Blocks, r	r-1	5	11.58	2.31	6.33	0.032
	Gap/CC, a	a-1	1	0.701	0.365	1.01	0.225
	Error (a) ra	(r-1)(a-1)	5	1.83	0.36		
	subtotal I		11				
II	Pit/Mound, b	b-1	1	0.16	0.16	1.33	0.276
	ab	(a-1)(b-1)	1	0.03	0.03	0.27	0.872
	E(b), rb+rab	(r-1)a(b-1)	10	1.22	0.12		
	subtotal II		12				
Grand Total I+II		rab-1	23				

Figure 2.1 Split - split plot analysis of variance design (Steele and Torrie 1980) used to determine whether or not significant differences existed between gap and closed canopy plots with respect to temperature and moisture regimes.

plots with respect to temperature and moisture regimes. To avoid the conclusion of significant differences when they do not in fact exist (type 1 error), it was critical to apply the appropriate error term to the hypothesis being considered when performing the ANOVA. In the statistical analysis of the datasets in this study, the split-split-plot experimental design used ensured that the appropriate error term was employed.

In addition, an ANOVA was performed on a sequential series of sampling dates to test for significant differences on a seasonal basis. The use of sequential sampling dates as replicates may be pseudoreplication. For field studies in ecology to have either no replication, or to have so few replicates that statistical power is low, is a common occurrence. Hurlbert (1984) found that pseudoreplication occurred in 48% of ecological studies that applied inferential statistics between 1960 and 1984. The individual sampling dates within the time periods represent statistically independent data since they were sampled two weeks apart.

Because of the small sample size and the exploratory nature of the study, a significance level of $p=0.10$ was used in testing for significant differences. Statistical power was not calculated because of the complex experimental design; however, the power of the statistical tests is likely to be low due to small sample size, small effect size, and the high within-plot sample variability (Toft and Shea 1983). In the figures, error bars represent one standard deviation from the mean. Linear regression was performed to determine if gap size, clone size, and other vine maple gap characteristics are related to temperature and moisture regimes in the vine maple gap plots.

2.2.5.2 *Definition of Seasonal Time Periods*

For each parameter measured in this study, seasonal time periods were selected for statistical analysis from trends that were visible in the dataset. Each seasonal time period was defined by the existence of similar conditions over a number of consecutive sampling dates. Since not all of the field measurements commenced at the same time, some parameters in the dataset contain more time periods than others. Table 2.1 outlines the seasonal time periods and number of sampling days within each period (in brackets) used in the statistical analysis of each of the five measured parameters.

Table 2.1
Seasonal time periods used in statistical analysis. The numbers in brackets indicate the number of sampling days within each time period.

Parameter	Fall 1a	Fall 1b	Winter 1	Spring	Summer	Fall 2	Winter 2
Air Temperature			Jan 7, 1994 to Mar 18, 1994 (5)	Apr 1, 1994 to May 31, 1994 (5)	June 21, 1994 to Aug 23, 1994 (6)	Sept 10, 1994 to Oct 20, 1994 (4)	Nov 3, 1994 to Dec 14, 1994 (4)
Soil Temperature			Dec 14, 1993 to Feb 4, 1994 (4)	Mar 4, 1994 to May 31, 1994 (8)	June 21, 1994 to Aug 23, 1994 (6)	Sept 10, 1994 to Oct 20, 1994 (4)	Nov 3, 1994 to Dec 14, 1994 (4)
Precipitation		Sept 26, 1993 to Nov 23, 1993 (9)	Feb 4, 1994 to March 31, 1994 (4)	April 1, 1994 to May 31, 1994 (5)	June 21, 1994 to Aug 23, 1994 (6)	Sept 10, 1994 to Oct 20, 1994 (4)	Nov 3, 1994 to Dec 14, 1994 (4)
Soil Moisture		Oct 26, 1993 to Nov 23, 1993 (4)	Jan 21, 1994 to Feb, 4, 1994 (3)	Mar 4, 1994 to May 31, 1994 (8)	June 21, 1994 to Aug 23, 1994 (6)	Sept 10, 1994 to Oct 20, 1994 (3)	Nov 3, 1994 to Dec 14, 1994 (3)
Depth to Groundwater	Sept 26, 1993 to Oct 19, 1993 (4)	Oct 26, 1993 to Dec 14, 1993 (6)	Jan 7, 1993 to Feb 18, 1993 (4)	March 4, 1994 to June 21, 1994 (8)	June 28, 1994 to Sept 19, 1994 (6)	Sept 22, 1994 to Nov 3, 1994 (4)	Nov 17, 1994 to Dec 14, 1994 (3)

2.3 Results

2.3.1 *Mid-Day Air Temperature*

The gap and closed canopy plots demonstrated a remarkably similar air temperature trend throughout the year (Table 2.2 and Figure 2.2). However, in the spring and summer, gap plots appear to be slightly cooler (not significantly) than the closed canopy plots; and, in the winter, gaps are slightly warmer (not significantly) than closed canopy plots. On five of the 24 sampling days, significant differences were found to exist in air temperatures between gap and closed canopy plots. On one sampling date in the summer ($p=0.01$, $F=14.10$, $df=1$) and one in the fall ($p=0.01$, $F=19.53$, $df=1$), gaps were significantly cooler than the closed canopy; and, on three of seven sampling dates in the winter ($p=0.04$, $F=7.52$, $df=1$; $p=0.05$, $F=6.37$, $df=1$; $p=0.07$, $F=5.57$, $df=1$), gaps were significantly warmer than the closed canopy. Throughout the rest of the year, vine maple gaps were not found to significantly influence air temperatures.

Air temperatures were compared between the gap and closed canopy plots above similar microsites(Figure 2.3). The pit microsites in the gap plots were compared to pit microsites in the closed canopy plots, and mound microsites in the gap plots were compared to mound microsites in the closed canopy. On most sampling dates, vine maple gaps were not found to have a significant effect on air temperatures. Temperature trends of similar microsites in gaps compared to similar microsites in closed canopy plots were similar to the overall comparisons: air temperature was cooler on some sampling dates in the spring and summer, and warmer on some sampling dates in the winter.

Table 2.2

Mean mid-day air temperatures and standard deviations for the five time periods outlined in Table 2.1, measured in °C from January 1994 to December 1994. For each individual plot, the mean and standard deviation are from two measurements above pit microsites and two measurements above mound microsites for each sampling date within the time period. The overall means and standard deviations for each time period were calculated from the plot means for each sampling date within the time period.

Plot	Winter 1	Spring	Summer	Fall 2	Winter 2
1g	4.99 ± 1.19	9.88 ± 1.77	16.60 ± 1.81	12.20 ± 2.87	1.03 ± 1.51
1c	5.10 ± 1.50	10.12 ± 1.85	17.20 ± 1.83	12.16 ± 3.32	0.66 ± 1.59
2g	5.37 ± 1.49	10.37 ± 1.90	17.26 ± 1.74	12.43 ± 3.22	0.97 ± 1.39
2c	5.13 ± 1.59	10.66 ± 1.89	17.41 ± 1.93	12.72 ± 3.36	0.85 ± 1.38
3g	5.22 ± 1.61	11.03 ± 1.49	17.58 ± 1.62	12.04 ± 2.53	1.03 ± 1.43
3c	5.05 ± 1.59	10.88 ± 1.34	17.88 ± 1.96	12.11 ± 2.89	0.91 ± 1.36
4g	5.34 ± 1.60	11.27 ± 0.99	17.99 ± 1.80	12.79 ± 3.20	0.86 ± 1.14
4c	5.26 ± 1.54	11.48 ± 1.09	18.34 ± 2.01	12.79 ± 3.55	1.04 ± 1.34
5g	5.50 ± 2.16	11.34 ± 1.36	18.02 ± 2.29	11.76 ± 2.42	1.09 ± 1.55
5c	5.53 ± 2.35	11.56 ± 1.44	18.33 ± 1.97	11.97 ± 2.50	0.88 ± 1.84
6g	5.39 ± 1.66	11.46 ± 1.17	18.39 ± 1.89	13.01 ± 3.38	0.78 ± 1.24
6c	5.35 ± 1.60	11.51 ± 1.35	18.11 ± 1.89	12.95 ± 3.48	0.80 ± 1.29
Gap Mean	5.30 ± 1.63	10.89 ± 1.57	17.65 ± 1.94	12.37 ± 2.95	0.96 ± 1.36
Gap Pit	5.31 ± 1.61	10.88 ± 1.56	17.60 ± 1.92	12.33 ± 2.87	0.98 ± 1.34
Gap Mound	5.29 ± 1.66	10.90 ± 1.58	17.70 ± 1.96	12.41 ± 3.04	0.94 ± 1.39
CC Mean	5.24 ± 1.67	11.03 ± 1.59	17.88 ± 1.95	12.49 ± 3.26	0.86 ± 1.46
CC Pit	5.27 ± 1.71	11.04 ± 1.62	17.78 ± 1.90	12.46 ± 3.19	0.87 ± 1.45
CC Mound	5.22 ± 1.69	11.03 ± 1.58	17.98 ± 2.01	12.44 ± 3.20	0.84 ± 1.47

Significant differences in air temperature in pit microsites between gap and closed canopy plots were found for five of twenty-two sampling dates. On three of seven sampling dates in the winter, pit microsites in the gap were significantly warmer than pit microsites in the closed canopy ($p=0.09$, $F=4.42$, $df=1$; $p=0.07$, $F=5.17$, $df=1$; $p=0.07$, $F=5.08$, $df=1$); and on one sampling date in each of the summer ($p=0.01$, $F=13.80$, $df=1$) and fall ($p=0.02$, $F=13.29$, $df=1$), pit microsites were significantly cooler in the gap than in the closed canopy. Significant differences in air temperatures in mound microsites between gap and closed canopy plots were obtained for four of twenty-two sampling

dates. On one sampling date in the winter, mound microsites in the gap were significantly warmer than mound microsites in the closed canopy ($p=0.03$, $F=8.59$, $df=1$); and on one sampling date in each of the winter ($p=0.08$, $F=4.74$, $df=1$), summer ($p=0.02$, $F=11.40$, $df=1$) and fall ($p=0.11$, $F=3.92$, $df=1$), mound microsites were significantly cooler in the gap than in the closed canopy.

To distinguish seasonal trends in the overall mid-day air temperature measurements, mean air temperature was calculated for both the gap and closed canopy plots for the five seasonal time periods outlined in the methodology. In the spring ($p=0.08$, $F=4.85$, $df=1$) and summer ($p=0.10$, $F=3.98$, $df=1$) time periods, mean seasonal air temperatures were significantly cooler in gap plots than in closed canopy plots. In the winter time periods, mean seasonal air temperatures were warmer (not significantly) in the gap plots than in the closed canopy plots. In both winter time periods, air temperatures above pit microsites were warmer than above mound microsites, however, the difference was significant in the first winter time period only ($p=0.00$, $F=34.42$, $df=1$).

Mean air temperatures above pit and mound microsites in both the gap and closed canopy demonstrated an interesting stratification over the seasonal time periods. The order of increasing air temperature in the winter time periods was as follows: the mound microsite in the closed canopy, the mound microsite in the gap, the pit microsite in the closed canopy, and the pit microsite in the gap. In contrast, the order of increasing air temperature in the spring, summer and fall was: the pit microsite in gap, the mound microsite in the gap, the pit microsite in the closed canopy and the mound microsite in the closed canopy.

The distinct characteristics of topography, gap size, and clone size, of each of the vine maple gap plots may influence air temperature, but would not be detected by the overall ANOVA described previously. Therefore, for each time period, linear regression was used to determine if mean mid-day air temperature was significantly related to characteristics of the vine maple gaps. In the summer ($p=0.10$, $r^2=0.52$, $n=6$) and fall ($p=0.10$, $r^2=0.54$, $n=6$) time periods, air temperatures were significantly warmer under larger gaps than smaller gaps (Figures 2.4a and 2.4b). In the summer, air temperatures were significantly warmer under larger clones than smaller clones ($p=0.06$, $r^2=0.63$, $n=6$) (Figure 2.4c). However, mid-day air temperature measurements in the gap plots in the study area were not significantly influenced by soil moisture, light regime and the topographic characteristics of the gaps, including slope angle, aspect and elevation.

2.3.2 *Mid-Day Soil Temperature*

The gap and closed canopy plots demonstrated similar soil temperature trends throughout the year (Table 2.3 and Figure 2.5). No significant differences were found to exist between gap and closed canopy plots for any of the 26 sampling dates; however, mean soil temperatures were lower (not significant) in the gap plots in all of the six dates sampled in the summer, and in three of the four dates sampled in the fall. While for 16 of the 26 weeks sampled, significant differences were found to exist in soil temperatures between pit and mound microsites ($p=0.10$), pit microsites in the summer months were

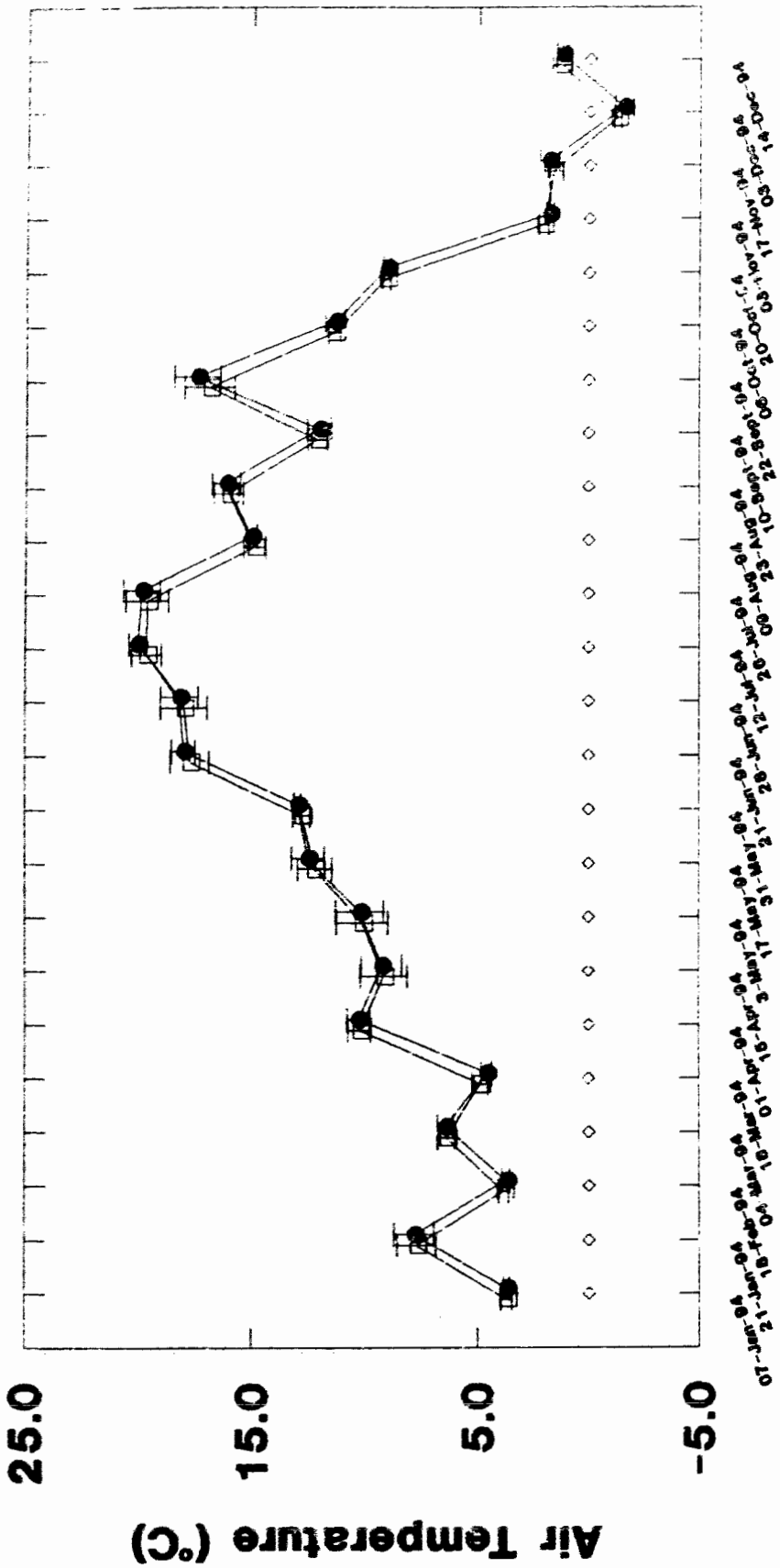

Figure 2.2 Mean mid-day air temperatures, measured in °C on 24 sampling dates from January 1994 to December 1994. The mean for each sampling date was calculated from two measurements above pit microsites and two measurements above mound microsites in six plots. Gap plots are designated by the symbol "□" and closed canopy plots are designated by the symbol "●".

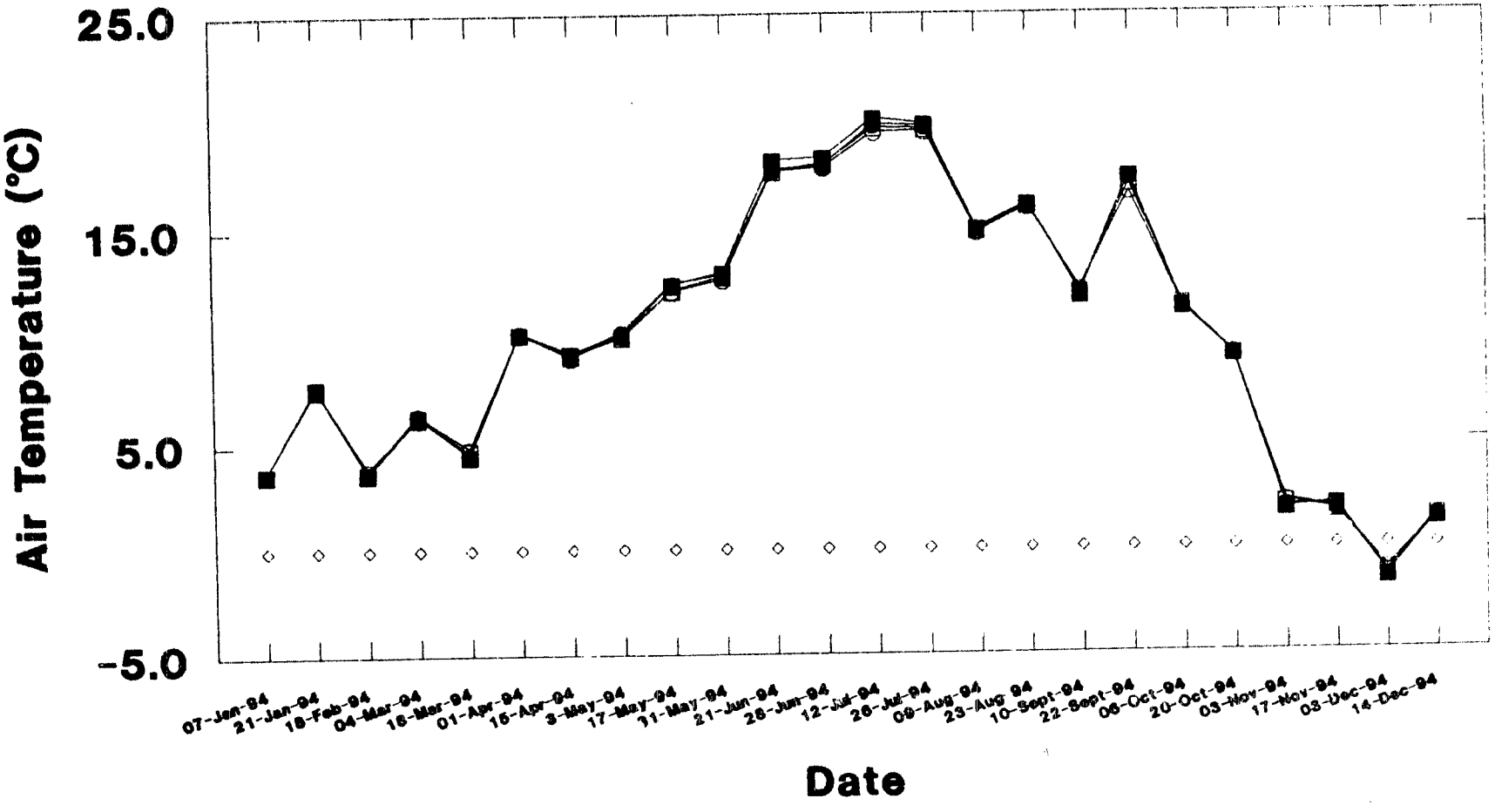

Figure 2.3 Mean mid-day air temperatures, measured in °C on 24 sampling dates from January 1994 to December 1994. The mean for each sampling date was calculated from two measurements above each microsite in six plots. Pit microsites in gap plots are designated by the symbol "o" and pit microsites in closed canopy plots are designated by the symbol "• ". Mound microsites in gap plots are designated by the symbol "□" and mound microsites in closed canopy plots are designated by the symbol "■".

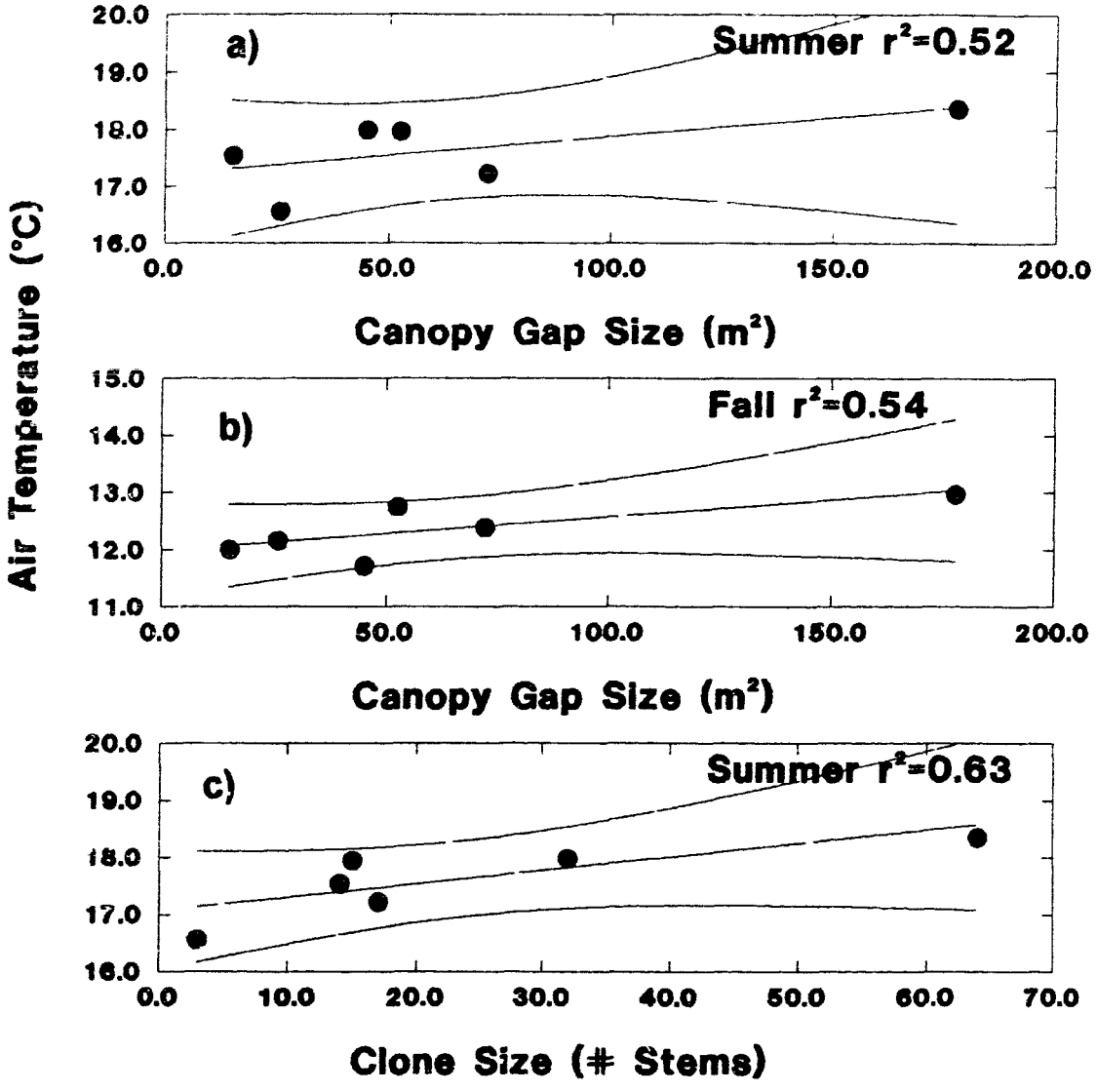

Figure 2.4 a) A regression of mean mid-day air temperatures in gap plots to canopy gap size for the summer time period and b) fall2 time period. c) A regression of mean mid-day air temperatures in gap plots to the number of stems on the vine maple clone for the summer time period.

cooler than mound microsites, and pit microsites in the winter months were warmer than mound microsites, on all of the sampling dates. Weekly variability in mid-day soil temperatures, therefore, appeared to be due more to the presence of pit-mound microtopography in the study area than to the presence of a vine maple gap.

Soil temperature regimes in gap and closed canopy plots were also compared by testing for significant differences in similar microsites (Figure 2.6). While in pit microsites, mean soil temperatures were cooler in the gap plots than pit microsites in closed canopy plots on all of the sampling days in the winter, the first three sampling days in the spring, and the last few sampling days in the fall, none of the differences were significant. Similarly, although pit microsites were warmer in the gap plots than in the closed canopy plots in all weeks sampled in the summer, and in the first few weeks of the fall, none of the differences were significant. Temperatures in mound microsites in the gaps were warmer than mound microsites in the closed canopy on all sampling dates in both winter periods, and cooler in the gaps on all sampling dates in the summer; however, significant differences were detected in only 4 of the 26 sampling days in the mound microsites between gap and closed canopy plots. Two of these sampling dates were in the winter ($p=0.10$, $F=4.00$, $df=1$ and $p=0.01$, $F=14.76$, $df=1$) when mound microsites were significantly warmer in the gap than in the closed canopy plots, and two sampling dates were in the late summer ($p=0.04$, $F=7.56$, $df=1$ and $p=0.04$, $F=7.95$, $df=1$) when mound microsites in the gap were significantly cooler than mound microsites in the closed canopy.

To distinguish seasonal trends in the overall mid-day soil temperature measurements, mean soil temperature was calculated for the gap and closed canopy plots

for the five seasonal time periods outlined in the methodology (Table 2.3). The results indicated that the presence of a vine maple gap in the hemlock-fir forest did not significantly affect soil temperatures in any of the time periods. However, mid-day soil temperatures were significantly influenced by pit-mound microtopography in both winter time periods ($p=0.01$, $F=10.70$, $df=1$; $p=0.00$, $F=28.70$, $df=1$), in the spring time period ($p=0.04$, $F=5.66$, $df=1$), and in the summer time period ($p=0.01$, $F=11.06$, $df=1$). Pit microsites have significantly warmer mid-day soil temperatures than mound microsites in the winter and spring time periods. Conversely, in the summer months, pit microsites have significantly cooler soil temperatures than mound microsites.

Table 2.3

Mean mid-day soil temperatures and standard deviations for the five time periods outlined in Table 2.1, measured in °C from December 1993 to December 1994. The measurements that contributed to these values are the same as in Table 2.2.

Plot	Winter 1	Spring	Summer	Fall 2	Winter 2
1g	4.35 ± 1.59	6.71 ± 1.84	13.00 ± 1.37	11.19 ± 1.75	2.93 ± 1.25
1c	4.19 ± 1.67	6.88 ± 1.87	13.41 ± 1.30	11.14 ± 1.90	2.60 ± 1.53
2g	4.54 ± 1.19	7.03 ± 1.78	13.03 ± 1.42	11.45 ± 1.80	3.78 ± 1.65
2c	4.15 ± 1.46	6.62 ± 1.84	12.94 ± 1.29	11.21 ± 1.83	2.71 ± 1.60
3g	4.10 ± 1.45	6.89 ± 1.97	13.17 ± 1.27	11.19 ± 1.93	2.92 ± 1.50
3c	4.26 ± 1.37	6.91 ± 1.89	13.30 ± 1.42	11.36 ± 1.99	3.21 ± 1.63
4g	4.59 ± 1.33	6.88 ± 1.74	12.89 ± 1.37	11.27 ± 1.77	3.76 ± 1.41
4c	4.59 ± 1.33	7.03 ± 1.78	13.20 ± 1.24	11.49 ± 1.78	3.66 ± 1.51
5g	4.14 ± 1.36	6.84 ± 1.93	13.33 ± 1.29	11.22 ± 2.07	2.65 ± 1.64
5c	4.24 ± 1.39	7.04 ± 2.06	13.84 ± 1.19	11.41 ± 2.20	2.33 ± 1.44
6g	3.94 ± 1.63	7.13 ± 2.12	14.22 ± 1.22	11.46 ± 2.15	2.03 ± 1.28
6c	4.24 ± 1.24	7.01 ± 1.93	13.43 ± 1.59	11.51 ± 2.03	3.25 ± 1.77
Gap Mean	4.28 ± 1.34	6.91 ± 1.89	13.27 ± 1.37	11.29 ± 1.89	3.01 ± 1.50
Gap Pit	4.34 ± 1.37	6.93 ± 1.86	13.25 ± 1.37	11.28 ± 1.87	3.19 ± 1.47
Gap Mound	4.21 ± 1.44	6.90 ± 1.92	13.29 ± 1.38	11.31 ± 1.92	2.83 ± 1.56
CC Mean	4.28 ± 1.34	6.91 ± 1.87	13.35 ± 1.30	11.34 ± 1.93	2.96 ± 1.50
CC Pit	4.53 ± 1.29	6.95 ± 1.78	13.14 ± 1.28	11.30 ± 1.82	3.47 ± 1.50
CC Mound	4.02 ± 1.43	6.88 ± 1.97	13.57 ± 1.36	11.39 ± 2.05	2.45 ± 1.54

Mean soil temperatures in pit and mound microsites in the gap and closed canopy demonstrated an interesting stratification over the seasonal time periods. The order of increasing soil temperature in the winter and spring time periods was as follows: the mound microsite in the closed canopy, the mound microsite in the gap, the pit microsite in the gap and the pit microsite in the closed canopy. In contrast, the order of increasing soil temperature in the summer and fall was: the pit microsite in the closed canopy, the pit microsite in the gap, the mound microsite in the gap, and the mound microsite in the closed canopy.

For each time period, linear regression was used to determine if mean seasonal soil temperatures in vine maple gaps were related to vine maple gap characteristics. In the spring ($p=0.07$, $r^2=0.60$, $n=6$) and fall ($p=0.06$, $r^2=0.62$, $n=6$), smaller gaps have significantly cooler soil temperatures than larger gaps (Figures 2.7a to 2.7b); however, soil temperature was not related to gap size in the winter periods. Aspect was significantly related to soil temperature in vine maple gaps in the winter months; however, no significant relationship existed during any other time period. In the winter, soil temperatures in gaps with a more north-east facing aspect were significantly colder than in gaps with a south-east facing aspect ($p=0.05$, $r^2=0.67$, $n=6$) (Figure 2.7d). In the spring ($p=0.08$, $r^2=0.57$, $n=6$) and summer ($p=0.00$, $r^2=0.91$, $n=6$), soil temperatures were significantly cooler beneath smaller clones than larger clones (Figures 2.8a and 2.8b).

Moisture content in the upper profile had a significant moderating effect on soil temperature values in both the summer and winter time periods. In the summer, the wetter the soil, the cooler the soil temperature $p=0.08$, $r^2=0.59$, $n=6$) and in the winter,

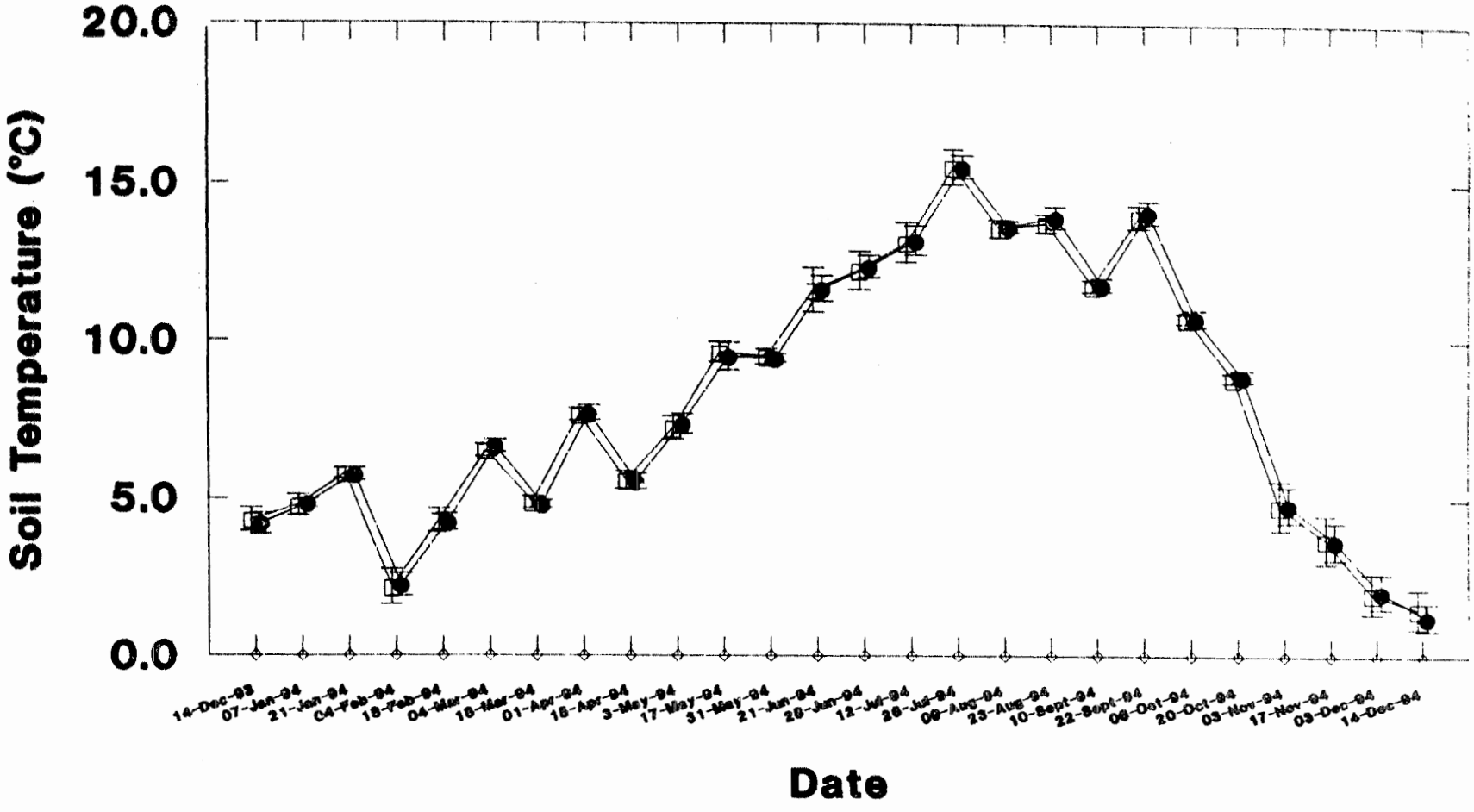

Figure 2.5 Mean mid-day soil temperatures, measured in °C on 26 sampling dates from December 1993 to December 1994. The mean for each sampling date was calculated from two measurements in pit microsites and two measurements in mound microsites at 10 cm depth in the soil profile in six plots. Gap plots are designated by the symbol "□" and closed canopy plots are designated by the symbol "• ".

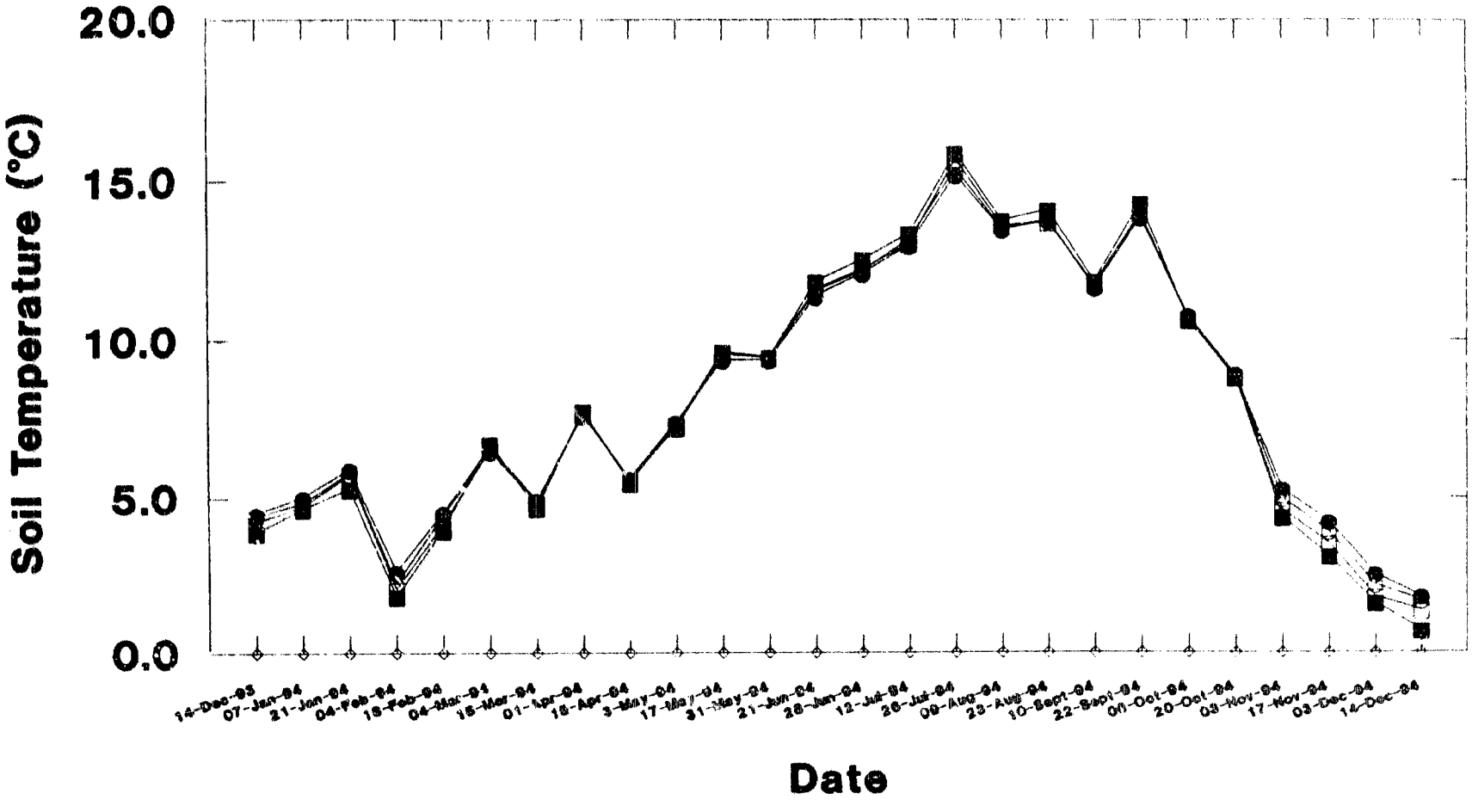

Figure 2.6 Mean mid-day soil temperatures, measured in °C on 26 sampling dates from December 1993 to December 1994. The mean for each sampling date was calculated from two measurements in each microsite at 10 cm depth in the soil profile in six plots. Pit microsites in gap plots are designated by the symbol "o" and pit microsites in closed canopy plots are designated by the symbol "•". Mound microsites in gap plots are designated by the symbol "□" and mound microsites in closed canopy plots are designated by the symbol "■".

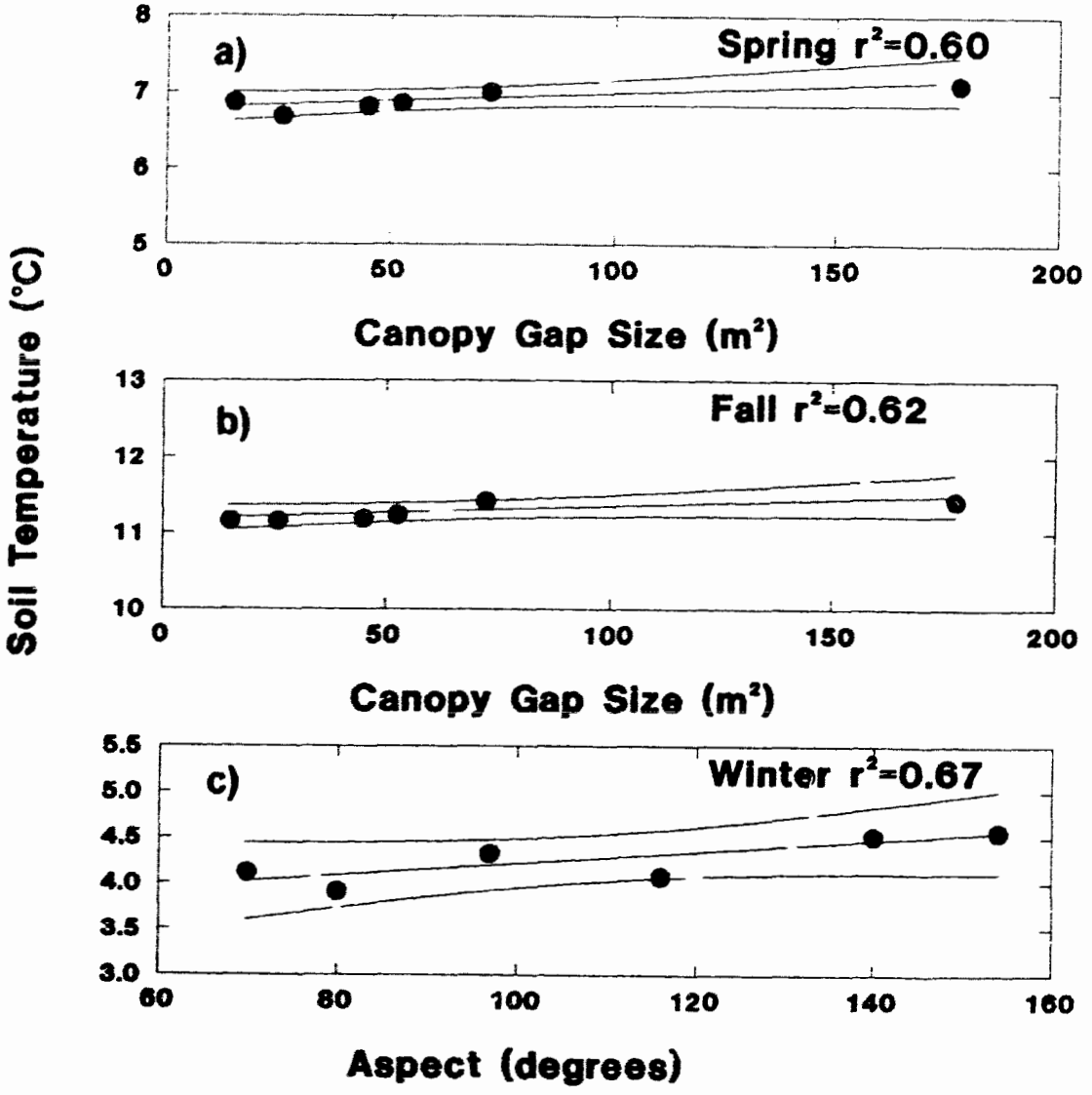

Figure 2.7 a) A regression of mean mid-day soil temperatures in gap plots to canopy gap size for the spring time period and b) fall2 time period. c) A regression of mean mid-day soil temperatures in gap plots to aspect for the winter time period.

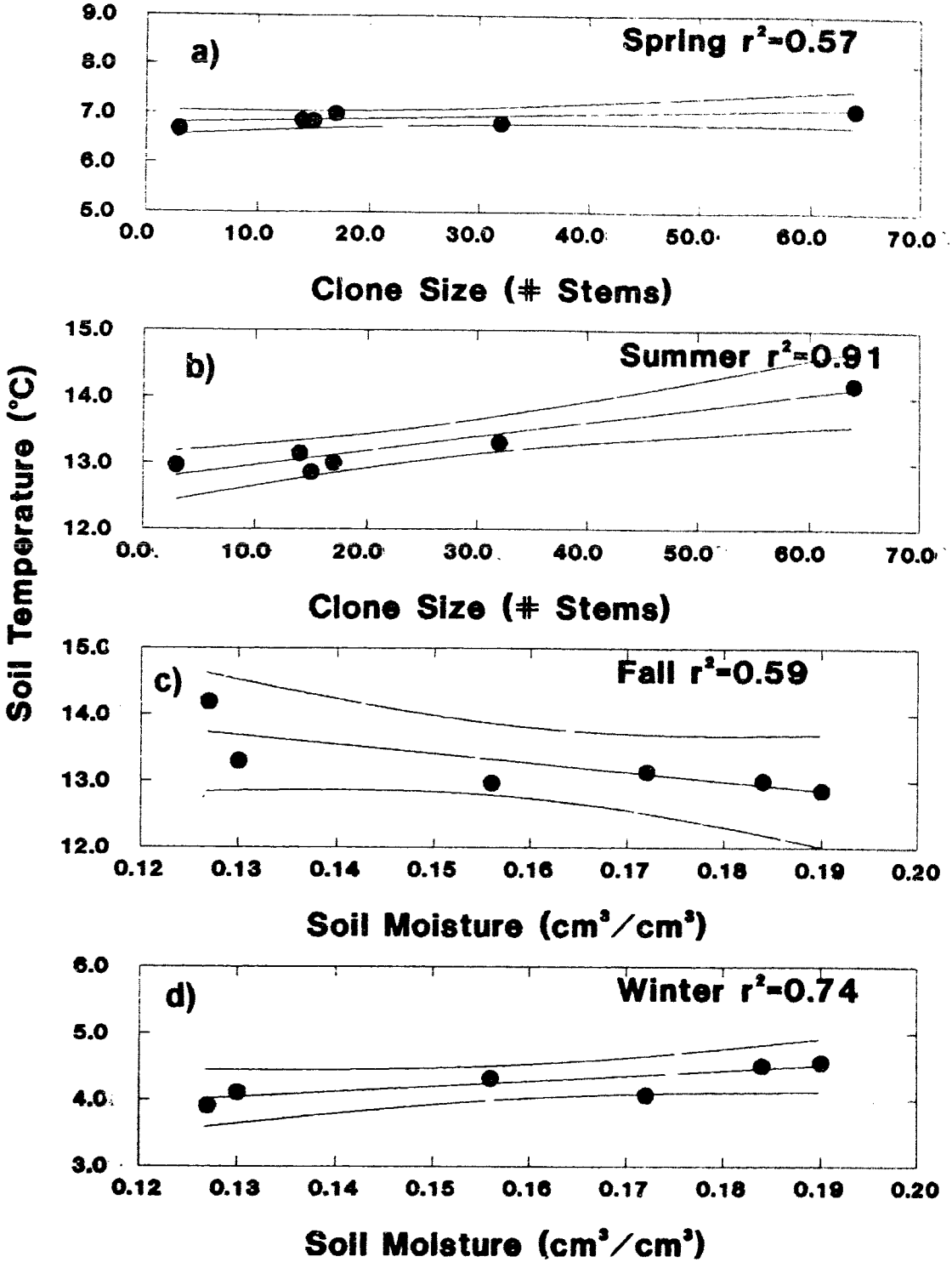

Figure 2.8 a) A regression of mean mid-day soil temperatures in gap plots to the number of stems on the vine maple clone for the spring time period and b) summer time period. c) A regression of mean mid-day soil temperatures in gap plots to soil moisture content in the upper 30 cm of mineral soil for the fall2 time period and d) winter time period.

the wetter the soil the warmer the soil temperature ($p=0.03$, $r^2=0.74$, $n=6$) (Figures 2.8c and 2.8d). Slope, elevation and summer light regime did not significantly influence soil temperature regimes in vine maple gaps in the study area.

2.3.3 *Precipitation*

Although a greater amount of precipitation reached the soil surface in the gaps than beneath the closed canopy on all but two collection dates (Figure 2.9), none of the bi-weekly differences were significant at the $p=0.10$ level. Total precipitation was calculated on a seasonal basis for the gap and closed canopy plots (Table 2.4); and although mean total precipitation was found to be higher in the gaps in all seasonal time periods, these differences were not significant at the $p=0.10$ level. The precipitation measurements made in this study demonstrated a notable absence of a late-summer dry-period which is unusual since a dry-period is typical of the Coastal Western Hemlock Biogeoclimatic zone (Meidinger and Pojar 1991).

For each season, linear regression was used to determine if the amount of precipitation reaching the forest floor in vine maple gap plots was related to gap characteristics. In the spring ($p=0.08$, $r^2=0.57$, $n=6$) and second fall period ($p=0.05$, $r^2=0.65$, $n=6$), larger gaps received significantly more precipitation than smaller gaps (Figures 2.10a and 2.10b). In the second winter period, significantly more precipitation reached the ground in gaps at lower elevations than at higher elevations ($p=0.05$, $r2=0.66$, $n=6$) (Figure 2.10c). The size of vine maple clone and the slope and aspect of the plots

were not significantly related to the amount of precipitation reaching the forest floor in any of the time periods.

Table 2.4
Total precipitation over each of the six seasonal time periods outlined in Table 2.1, measured in cm from September 1993 to December 1994. For each individual plot, the totals are summed from one measurement taken on each sampling date within the time period. The overall means were calculated from the individual plot totals for each time period.

Plot	Fall 1b	Winter 1	Spring	Summer	Fall 2	Winter 2
1g	39.64	5.90	10.55	18.63	13.85	12.25
1c	37.21	9.80	22.85	22.23	18.75	12.25
2g	30.41	9.40	21.65	19.43	20.55	11.55
2c	32.16	8.00	20.15	19.50	16.15	11.55
3g	31.69	6.45	16.50	15.19	11.45	8.50
3c	32.44	7.15	15.50	14.83	12.75	5.82
4g	38.82	13.68	33.45	34.70	26.25	12.00
4c	35.43	8.25	17.80	17.70	14.90	9.55
5g	48.70	18.10	24.80	23.48	20.90	9.50
5c	36.75	9.40	19.90	22.65	17.35	9.50
6g	38.99	9.70	28.10	26.53	22.75	13.00
6c	35.53	9.35	21.95	20.48	17.20	12.25
Gap Mean	38.04	10.54	22.51	23.32	18.65	11.13
CC Mean	34.92	8.66	19.69	19.56	16.18	10.15

2.3.4 *Soil Moisture*

Soil moisture values in gap and closed canopy plots were quite similar throughout the year and no large seasonal variation in soil moisture values was observed. Mean soil moisture values were lower (not significant) on 25 of 28 sampling dates in the gap plots at 30 cm (Figure 2.11), and lower (not significant) on 23 of 28 sampling dates in the gap plots at 50 cm (Figure 2.12) than in the closed canopy plots. The opposite trend existed at the 80 cm depth where soil moisture was higher (not significant) on 25 of 28 sampling dates in the gap plots than in the closed canopy plots (Figure 2.13). Vine maple gaps in

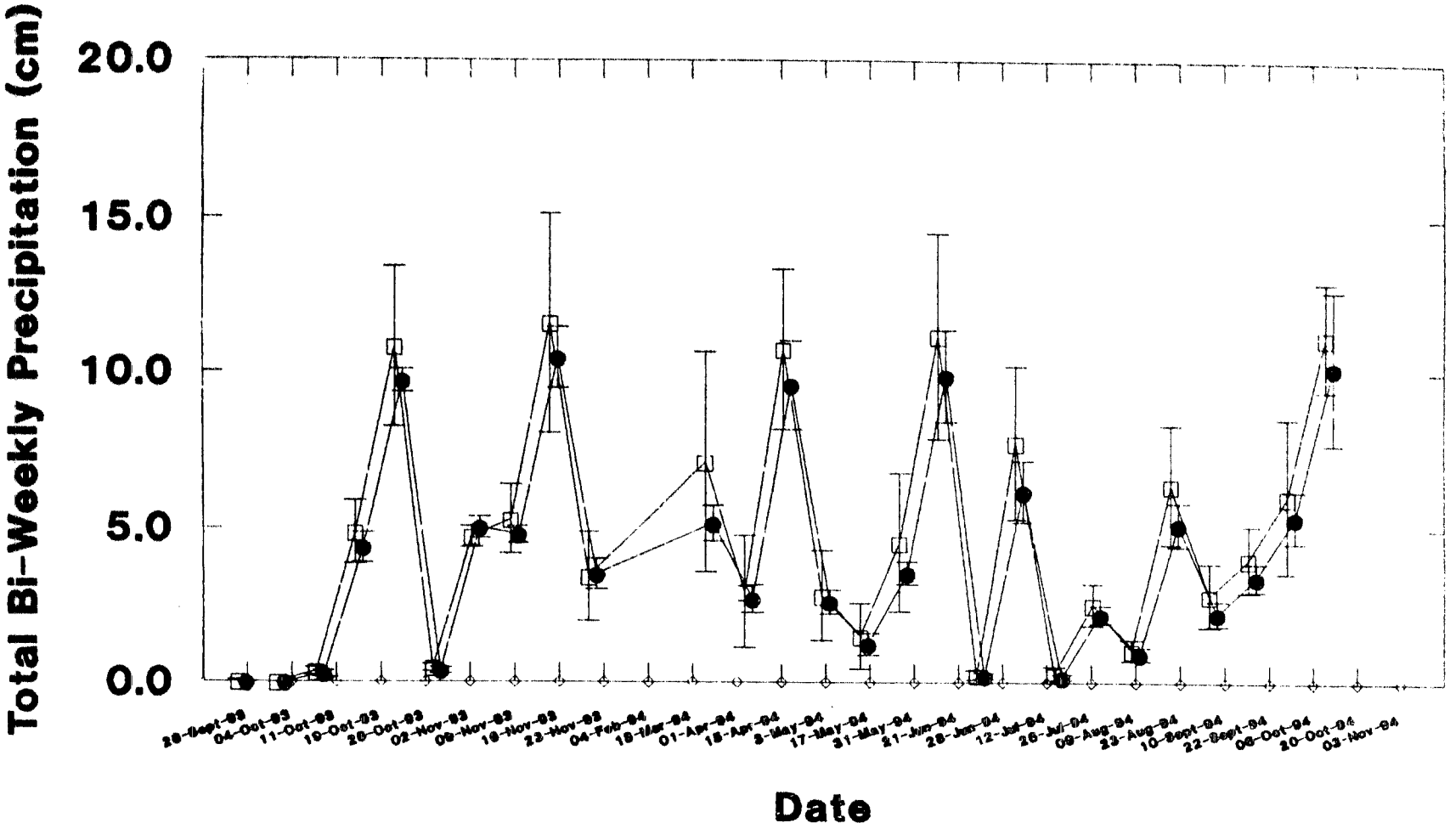

Figure 2.9 Mean bi-weekly precipitation, measured in cm, on 32 sampling dates from September 1993 to December 1994. The mean for each sampling date was calculated from one measurement in six plots. Gap plots are designated by the symbol "[]" and closed canopy plots are designated by the symbol "• ".

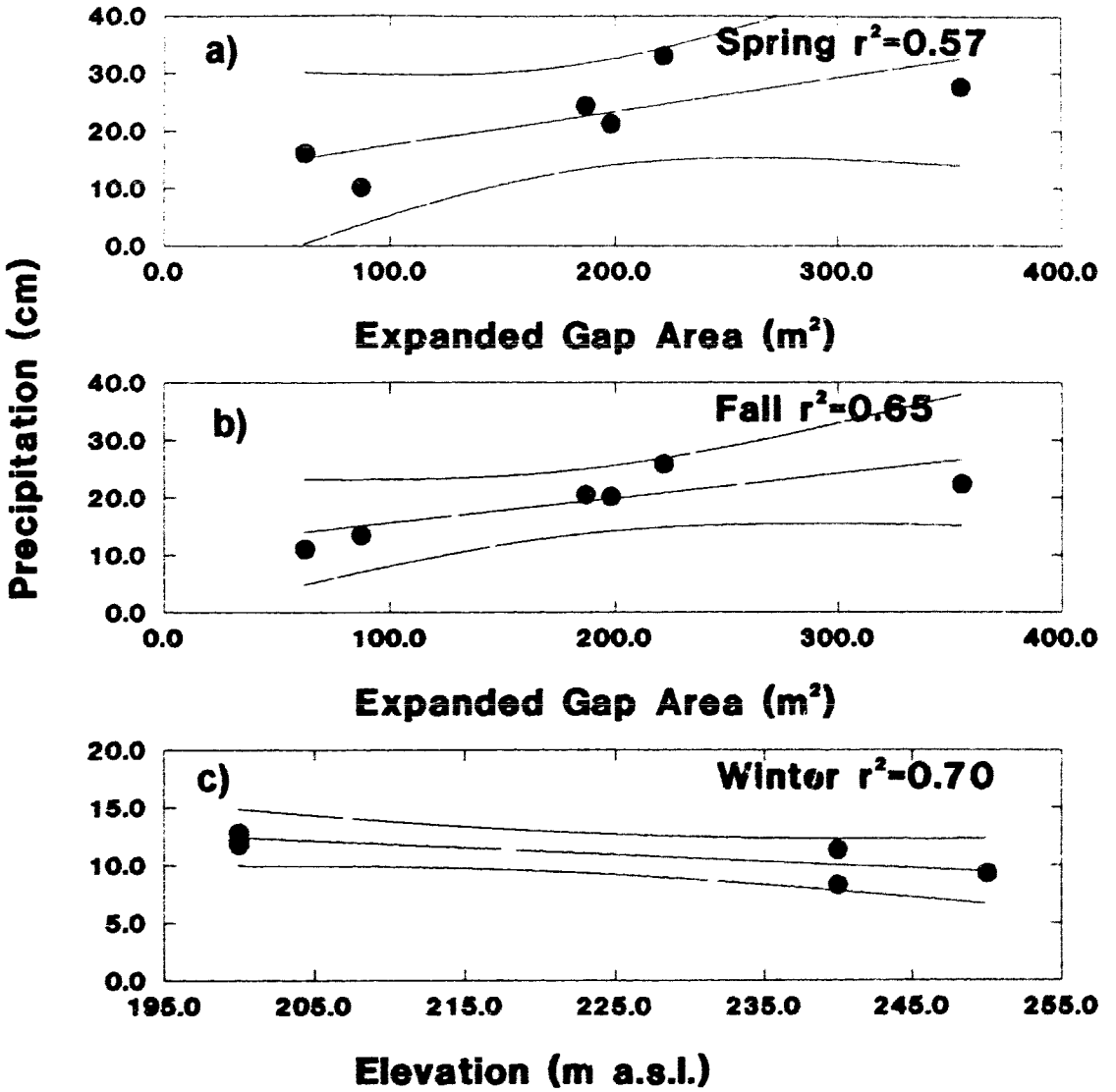

Figure 2.10 a) A regression of total precipitation in gap plots to canopy gap size for the spring time period and b) fall2 time period. c) A regression of total precipitation in gap plots to elevation for the winter2 time period.

two of the six paired plots (plots 4 and 6) were observed to have ephemeral streams that flowed during high precipitation events.

Soil moisture values were compared between pit and mound microsites in both the gap and closed canopy plots to compare moisture regimes in similar microsites. At a depth of 30 cm, pit microsites in the gap had a higher moisture content (not significant) on 27 of 28 sampling dates than pit microsites in the closed canopy. The opposite trend existed for mound microsites at 30 cm where 22 of 28 sampling dates had higher soil moisture values (not significant) under the closed canopy than in the vine maple gap plots (Figure 2.14). At a depth of 50 cm, almost half of the sampling dates demonstrated higher soil moisture values (not significant) in pit microsites in the gap plots compared to closed canopy plots; whereas, 25 of 28 sampling dates had lower soil moisture values (not significant) in mound microsites in the gap plots compared to the closed canopy plots (Figure 2.15). At a depth of 80 cm, pit microsites in the gap had a lower moisture content (not significant) compared to closed canopy plots on 19 of 28 sampling dates; and, in mound microsites, all sampling dates had higher moisture contents (not significant) in the gap plots than in the closed canopy plots. However, in both the gap plots and closed canopy plots, pit microsites were significantly wetter than mound microsites on most sampling dates at the p=0.10 level at all depths in the soil profile (Figure 2.16).

To distinguish seasonal trends in the overall soil moisture dataset, mean soil moisture values were calculated for the gap and closed canopy plots for the six time periods outlined in Section 2.2.5.2 (Tables 2.5 and 2.6). At all depths in the profile during all seasons, mean seasonal soil moisture contents were not significantly different between

Table 2.5

Mean soil moisture measurements and standard deviations for the six time periods outlined in Table 2.1, measured in cm^3/cm^3 from October 1993 to December 1994. For each individual plot, the mean and standard deviation are from one measurement in a pit microsite and one measurement in a mound microsite for each sampling date within the time period.

Plot		Fall 1b	Winter 1	Spring	Summer	Fall 2	Winter 2
1g	30 cm	0.19 ± 0.02	0.20 ± 0.10	0.18 ± 0.06	0.16 ± 0.02	0.17 ± 0.03	0.17 ± 0.02
	50 cm	0.21 ± 0.03	0.24 ± 0.06	0.24 ± 0.05	0.22 ± 0.02	0.23 ± 0.02	0.24 ± 0.02
	80 cm	0.26 ±0.04	0.29 ±0.03	0.29 ± 0.02	0.28 ± 0.02	0.28 ± 0.03	0.31 ± 0.03
1c	30 cm	0.14 ± 0.03	0.18 ± 0.09	0.16 ± 0.06	0.13 ± 0.02	0.14 ± 0.04	0.16 ± 0.03
	50 cm	0.15 ± 0.05	0.18 ± 0.09	0.18 ± 0.07	0.14 ± 0.03	0.14 ± 0.04	0.17 ± 0.04
	80 cm	0.21 ± 0.08	0.24 ± 0.06	0.24 ± 0.05	0.22 ± 0.04	0.22 ± 0.05	0.27 ± 0.04
2g	30 cm	0.19 ± 0.01	0.21 ± 0.04	0.21 ± 0.02	0.18 ± 0.01	0.21 ± 0.02	0.21 ± 0.01
	50 cm	0.22 ± 0.01	0.25 ± 0.05	0.23 ± 0.04	0.20 ± 0.01	0.21 ± 0.01	0.23 ± 0.02
	80 cm	0.26 ± 0.06	0.29 ± 0.06	0.29 ± 0.05	0.27 ± 0.04	0.27 ± 0.02	0.33 ± 0.06
2c	30 cm	0.15 ± 0.01	0.16 ± 0.01	0.17 ± 0.01	0.14 ± 0.02	0.15 ± 0.02	0.17 ± 0.00
	50 cm	0.14 ± 0.01	0.15 ± 0.00	0.15 ± 0.01	0.14 ± 0.01	0.15 ± 0.02	0.15 ± 0.00
	80 cm	0.16 ± 0.01	0.16 ± 0.01	0.17 ± 0.01	0.16 ± 0.01	0.17 ± 0.03	0.18 ± 0.01
3g	30 cm	0.18 ± 0.02	0.18 ± 0.01	0.19 ± 0.01	0.17 ± 0.02	0.19 ± 0.02	0.19 ± 0.01
	50 cm	0.15 ± 0.00	0.15 ± 0.00	0.16 ± 0.01	0.15 ± 0.01	0.15 ± 0.01	0.16 ± 0.00
	80 cm	0.19 ± 0.06	0.21 ± 0.07	0.19 ± 0.04	0.17 ± 0.02	0.17 ± 0.02	0.17 ± 0.02
3c	30 cm	0.18 ± 0.02	0.18 ± 0.04	0.19 ± 0.04	0.18 ± 0.04	0.19 ± 0.05	0.20 ± 0.04
	50 cm	0.21 ± 0.05	0.21 ± 0.05	0.22 ± 0.05	0.20 ± 0.05	0.20 ± 0.05	0.23 ± 0.05
	80 cm	0.28 ± 0.09	0.27 ± 0.09	0.27 ± 0.07	0.24 ± 0.06	0.23 ± 0.07	0.29 ± 0.06
4g	30 cm	0.19 ± 0.01	0.19 ± 0.01	0.20 ± 0.01	0.19 ± 0.02	0.20 ± 0.02	0.21 ± 0.02
	50 cm	0.24 ± 0.03	0.24 ± 0.02	0.26 ± 0.04	0.24 ± 0.03	0.26 ± 0.04	0.29 ± 0.03
	80 cm	0.32 ± 0.03	0.32 ± 0.04	0.32 ± 0.03	0.31 ± 0.03	0.31 ± 0.03	0.32 ± 0.03
4c	30 cm	0.18 ± 0.07	0.19 ± 0.07	0.20 ± 0.06	0.18 ± 0.06	0.20 ± 0.06	0.22 ± 0.06
	50 cm	0.31 ± 0.03	0.27 ± 0.03	0.30 ± 0.05	0.25 ± 0.05	0.32 ± 0.06	0.35 ± 0.01
	80 cm	0.33 ± 0.02	0.33 ± 0.01	0.33 ± 0.01	0.32 ± 0.01	0.33 ± 0.01	0.33 ± 0.01
5g	30 cm	0.14 ± 0.01	0.14 ± 0.01	0.15 ± 0.01	0.13 ± 0.01	0.15 ± 0.02	0.15 ± 0.01
	50 cm	0.17 ± 0.02	0.17 ± 0.01	0.18 ± 0.01	0.17 ± 0.01	0.19 ± 0.02	0.19 ± 0.01
	80 cm	0.21 ± 0.02	0.23 ± 0.01	0.24 ± 0.02	0.24 ± 0.01	0.25 ± 0.02	0.26 ± 0.02
5c	30 cm	0.16 ± 0.01	0.15 ± 0.01	0.17 ± 0.03	0.14 ± 0.02	0.16 ± 0.02	0.17 ± 0.01
	50 cm	0.19 ± 0.02	0.18 ± 0.00	0.21 ± 0.06	0.17 ± 0.01	0.18 ± 0.02	0.20 ± 0.01
	80 cm	0.24 ± 0.07	0.25 ± 0.04	0.27 ± 0.06	0.25 ± 0.04	0.23 ± 0.04	0.30 ± 0.06
6g	30 cm	0.13 ± 0.02	0.13 ± 0.03	0.15 ± 0.04	0.13 ± 0.03	0.13 ± 0.03	0.16 ± 0.06
	50 cm	0.17 ± 0.06	0.18 ± 0.07	0.23 ± 0.08	0.17 ± 0.07	0.17 ± 0.06	0.24 ± 0.10
	80 cm	0.26 ± 0.09	0.26 ± 0.08	0.29 ± 0.05	0.25 ± 0.06	0.23 ± 0.05	0.32 ± 0.03
6c	30 cm	0.23 ± 0.04	0.24 ± 0.05	0.25 ± 0.04	0.24 ± 0.05	0.25 ± 0.05	0.25 ± 0.05
	50 cm	0.23 ± 0.04	0.26 ± 0.03	0.26 ± 0.02	0.25 ± 0.02	0.26 ± 0.02	0.26 ± 0.02
	80 cm	0.23 ± 0.06	0.24 ± 0.03	0.26 ± 0.04	0.26 ± 0.02	0.27 ± 0.03	0.27 ± 0.04

Table 2.6

Mean soil moisture measurements and standard deviations for the six time periods outlined in Table 2.1, measured in cm^3/cm^3 from October 1993 to December 1994. The overall means and standard deviations for each time period were calculated from the plot means for each sampling date within the time period.

Plot		Fall 1b	Winter 1	Spring	Summer	Fall 2	Winter 2
Gap	30 cm	0.18 ± 0.03	0.18 ± 0.05	0.20 ± 0.14	0.16 ± 0.03	0.18 ± 0.03	0.18 ± 0.02
	50 cm	0.19 ± 0.04	0.21 ± 0.05	0.21 ± 0.04	0.19 ± 0.04	0.20 ± 0.04	0.23 ± 0.05
	80 cm	0.25 ± 0.05	0.27 ± 0.05	0.27 ± 0.05	0.25 ± 0.05	0.25 ± 0.05	0.28 ± 0.06
Gap Pit	30 cm	0.18 ± 0.03	0.19 ± 0.07	0.19 ± 0.04	0.17 ± 0.03	0.18 ± 0.03	0.19 ± 0.03
	50 cm	0.21 ± 0.04	0.23 ± 0.06	0.24 ± 0.06	0.21 ± 0.05	0.22 ± 0.05	0.25 ± 0.07
	80 cm	0.27 ± 0.05	0.30 ± 0.04	0.28 ± 0.04	0.26 ± 0.05	0.26 ± 0.04	0.30 ± 0.07
Gap Mound	30 cm	0.17 ± 0.03	0.17 ± 0.04	0.17 ± 0.07	0.15 ± 0.03	0.17 ± 0.04	0.17 ± 0.04
	50 cm	0.18 ± 0.04	0.19 ± 0.05	0.19 ± 0.04	0.18 ± 0.04	0.18 ± 0.04	0.20 ± 0.04
	80 cm	0.23 ± 0.07	0.24 ± 0.07	0.25 ± 0.06	0.24 ± 0.06	0.25 ± 0.06	0.27 ± 0.06
CC	30 cm	0.17 ± 0.03	0.18 ± 0.04	0.19 ± 0.03	0.17 ± 0.04	0.18 ± 0.04	0.19 ± 0.04
	50 cm	0.21 ± 0.06	0.21 ± 0.05	0.22 ± 0.06	0.19 ± 0.05	0.21 ± 0.07	0.23 ± 0.07
	80 cm	0.24 ± 0.06	0.25 ± 0.05	0.26 ± 0.05	0.24 ± 0.05	0.24 ± 0.05	0.27 ± 0.05
CC Pit	30 cm	0.19 ± 0.04	0.20 ± 0.06	0.20 ± 0.05	0.18 ± 0.05	0.20 ± 0.04	0.20 ± 0.04
	50 cm	0.22 ± 0.06	0.22 ± 0.07	0.24 ± 0.07	0.20 ± 0.05	0.23 ± 0.06	0.24 ± 0.06
	80 cm	0.28 ± 0.07	0.28 ± 0.06	0.29 ± 0.06	0.26 ± 0.05	0.27 ± 0.05	0.30 ± 0.06
CC Mound	30 cm	0.15 ± 0.05	0.16 ± 0.06	0.17 ± 0.05	0.16 ± 0.06	0.17 ± 0.06	0.18 ± 0.05
	50 cm	0.19 ± 0.07	0.19 ± 0.06	0.20 ± 0.06	0.18 ± 0.06	0.19 ± 0.08	0.21 ± 0.08
	80 cm	0.20 ± 0.07	0.22 ± 0.06	0.23 ± 0.06	0.24 ± 0.06	0.22 ± 0.07	0.24 ± 0.05

gap and closed canopy plots. At 50 cm and 80 cm depths in the soil profile, mean seasonal soil moisture contents in pits were significantly higher than in mounds at the p=0.10 level in all seasons. In the study area, differences in soil moisture therefore are due more to pit-mound microtopography than to the presence of a vine maple gap.

Consistent trends in soil moisture content were observed throughout the year. In the rooting zone, or upper 30 cm, the order of increasing soil moisture content was as follows: the mound microsite in the closed canopy, the mound microsite in the gap, pit microsite in the gap, then the pit microsite in the closed canopy. Below the rooting zone at the 80 cm depth, the order of increasing soil moisture content was as follows: the mound

microsite in the closed canopy, the mound microsite in the gap, pit microsite in the closed canopy, then the pit microsite in the gap.

For each time period, linear regression was used to determine if soil moisture was related to characteristics of vine maple gaps. Soil moisture values were not significantly related to gap size in any of the time periods. In the rooting zone (30 cm depth), canopy gap area, aspect, clone size and light environment were significantly related to soil moisture values. With an increasing number of stems on the vine maple clone, soil moisture values in the rooting zone decreased significantly in the fall time periods ($p=0.01$, $r^2=0.81$, $n=6$; $p=0.07$, $r^2=0.61$, $n=6$), in the first winter period ($p=0.02$, $r^2=0.77$, $n=6$), and in the spring ($p=0.10$, $r^2=0.53$, $n=6$) (Figures 2.17a to 2.17d). North-easterly facing gaps had significantly lower soil moisture values at 30 cm than the more south-easterly facing gaps in all seasons (fall: $p=0.05$, $r^2=0.65$, $n=6$ and $p=0.01$, $r2=0.85$, $n=6$; winter: $p=0.10$, $r^2=0.54$, $n=6$ and $p=0.00$, $r^2=0.97$, $n=6$; spring $p=0.01$, $r^2=0.85$, $n=6$; summer $p=0.00$, $r^2=0.94$, $n=6$) (Figures 2.18a to 2.19a). Percentage open sky and the total amount of incoming solar radiation were also significantly related to soil moisture values of the upper horizons in vine maple gaps in the summer: the greater the amount of open sky ($p=0.04$, $r^2=0.69$, $n=6$) and incoming radiation ($p=0.05$, $r^2=0.65$, $n=6$), the lower the amount of soil moisture in the upper 30 cm (Figures 2.19b and 2.19d).

Gap size, slope, elevation and depth of the LFH horizon were not significantly related to soil moisture values at 30 cm depth in the vine maple gap plots. In addition, at 50 and 80 cm depths, none of the gap characteristics, vine maple characteristics, or the topographical parameters measured were significantly related to soil moisture values.

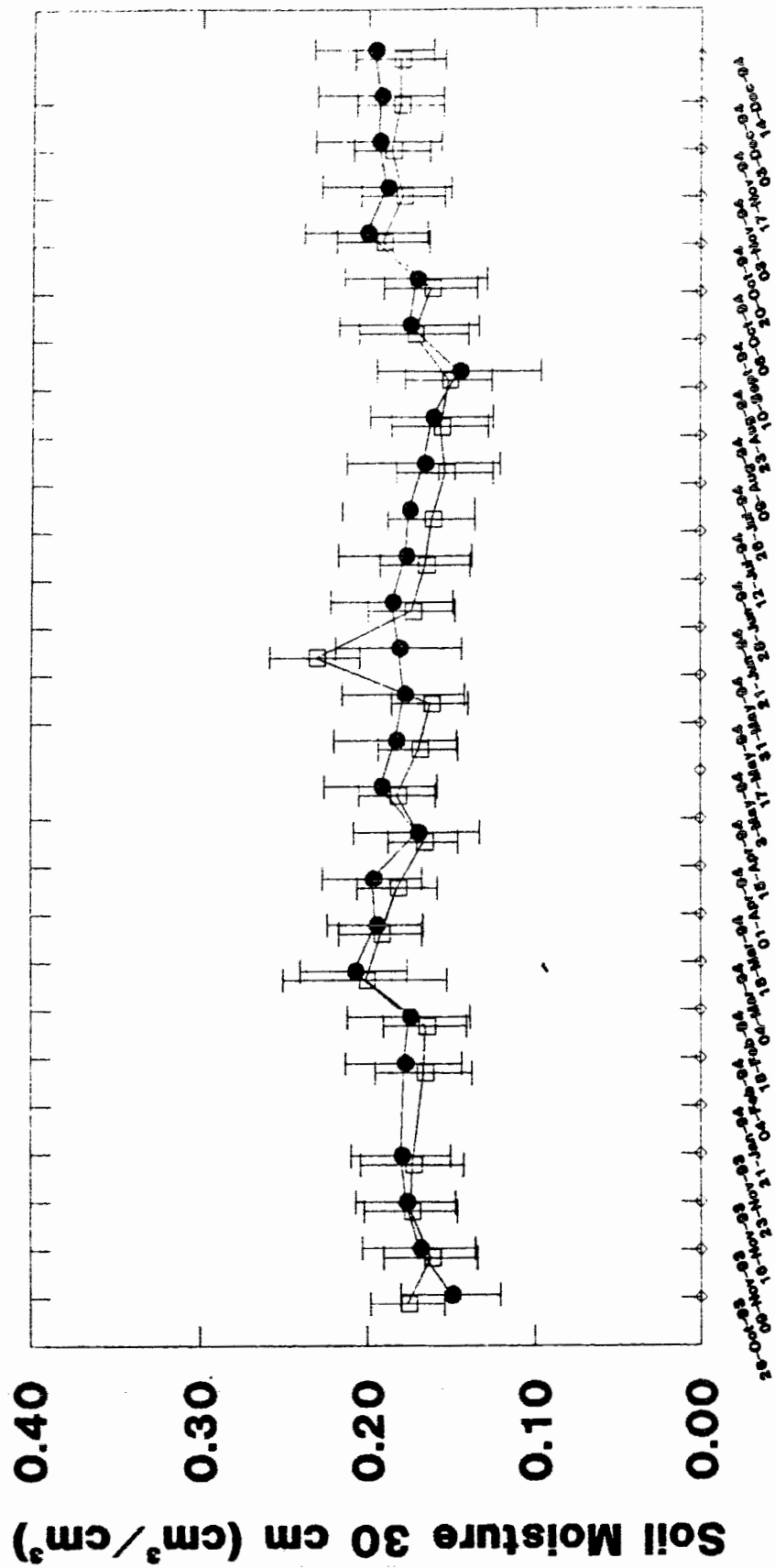

Figure 2.11 Mean soil moisture at 30 cm depth in the soil profile, measured in cm^3/cm^3 on 28 sampling dates from October 1993 to December 1994. The mean for each sampling date was calculated from one measurement in a pit microsite and one measurement in a mound microsite in six plots. Gap plots are designated by the symbol "□" and closed canopy plots are designated by the symbol "●".

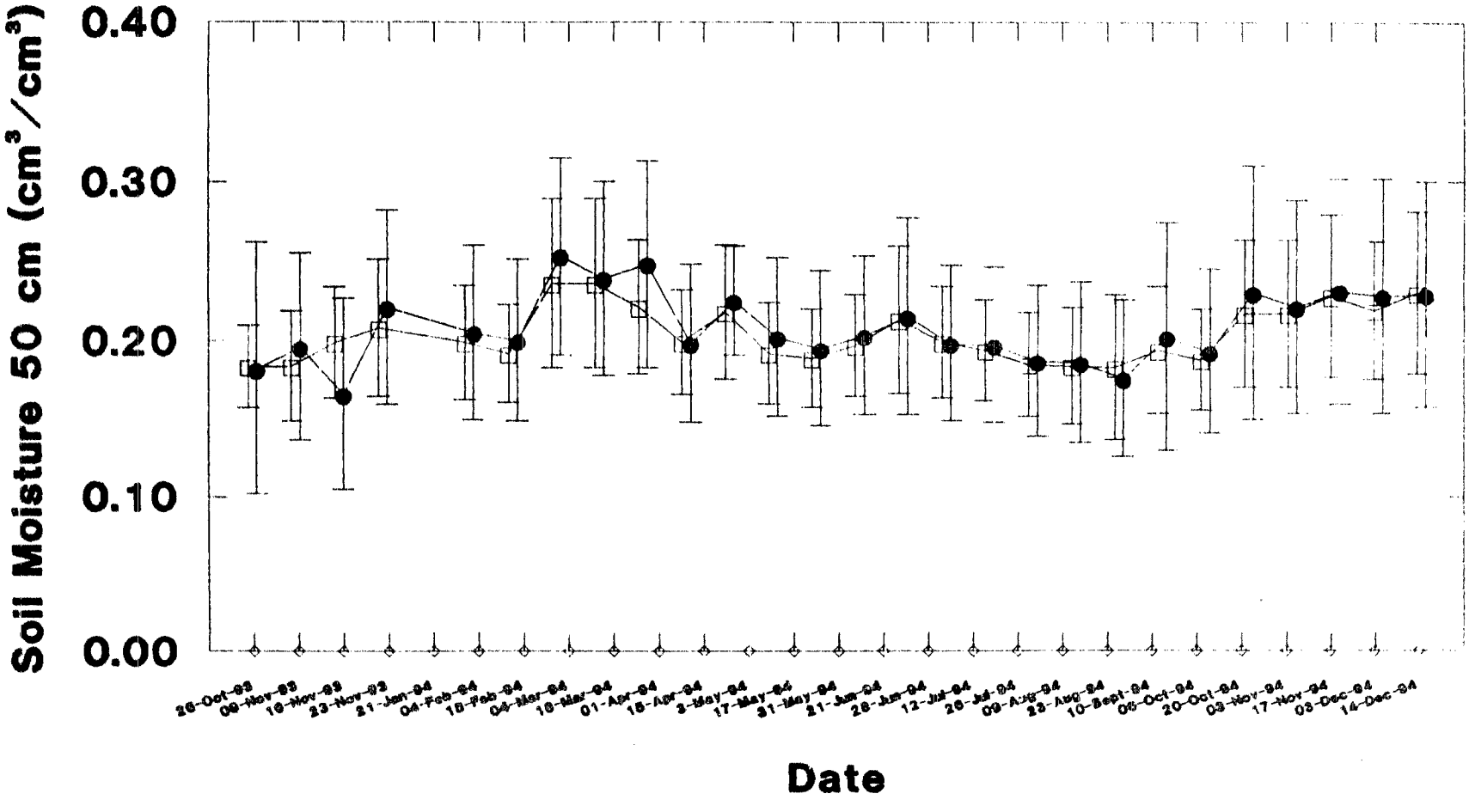

Figure 2.12 Mean soil moisture at 50 cm depth in the soil profile, measured in cm^3/cm^3 on 28 sampling dates from October 1993 to December 1994. The mean for each sampling date was calculated from one measurement in a pit microsite and one measurement in a mound microsite in six plots. Gap plots are designated by the symbol "□" and closed canopy plots are designated by the symbol "●".

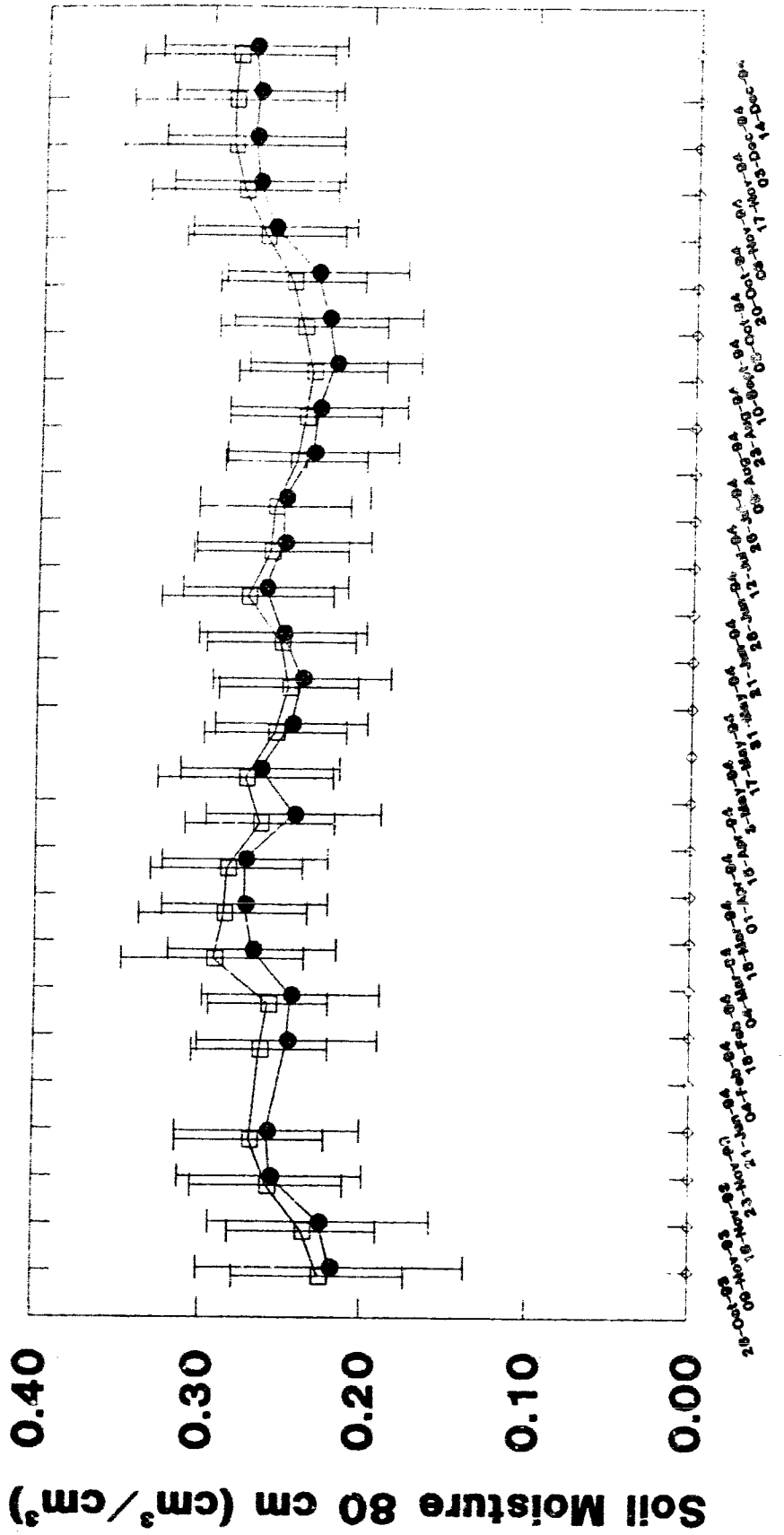

Figure 2.13 Mean soil moisture at 80 cm depth in the soil profile, measured in cm^3/cm^3 on 28 sampling dates from October 1993 to December 1994. The mean for each sampling date was calculated from one measurement in a pit microsite and one measurement in a mound microsite in six plots. Gap plots are designated by the symbol "□" and closed canopy plots are designated by the symbol "●".

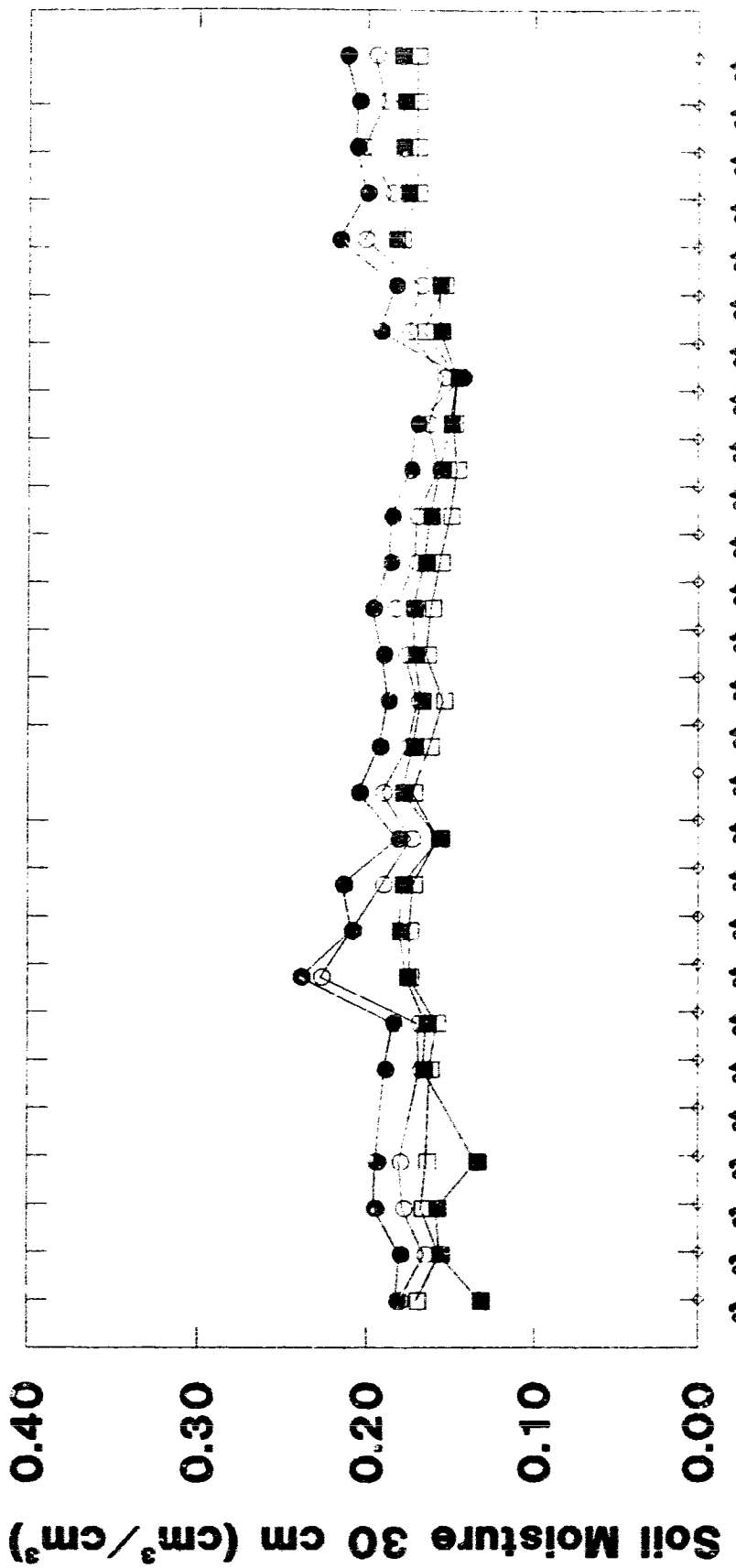

Figure 2.14 Mean soil moisture at 30 cm depth in the soil profile, measured in cm^3/cm^3 on 28 sampling dates from October 1993 to December 1994. The means for each sampling date consists of one measurement in each microsite in six plots. Pit microsites in gap plots are designated by the symbol "○" and pit microsites in closed canopy plots are designated by the symbol "●". Mound microsites in gap plots are designated by the symbol "□" and mound microsites in closed canopy plots are designated by the symbol "■".

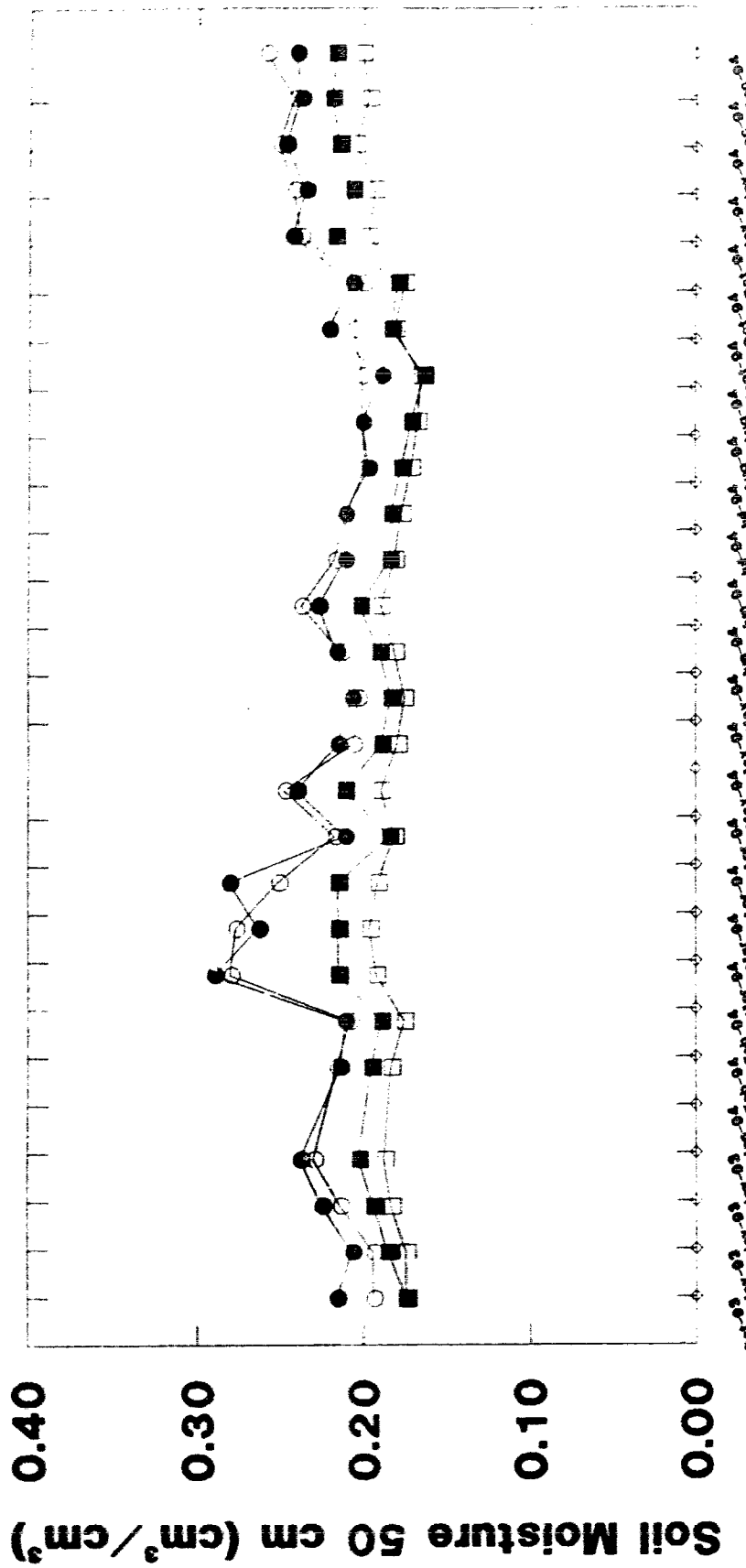

Figure 2.15 Mean soil moisture at 50 cm depth in the soil profile, measured in cm^3/cm^3 on 28 sampling dates from October 1993 to December 1994. The means for each sampling date consists of one measurement in each microsite in six plots. Pit microsites in gap plots are designated by the symbol "o" and pit microsites in closed canopy plots are designated by the symbol "●". Mound microsites in gap plots are designated by the symbol "┐" and mound microsites in closed canopy plots are designated by the symbol "■".

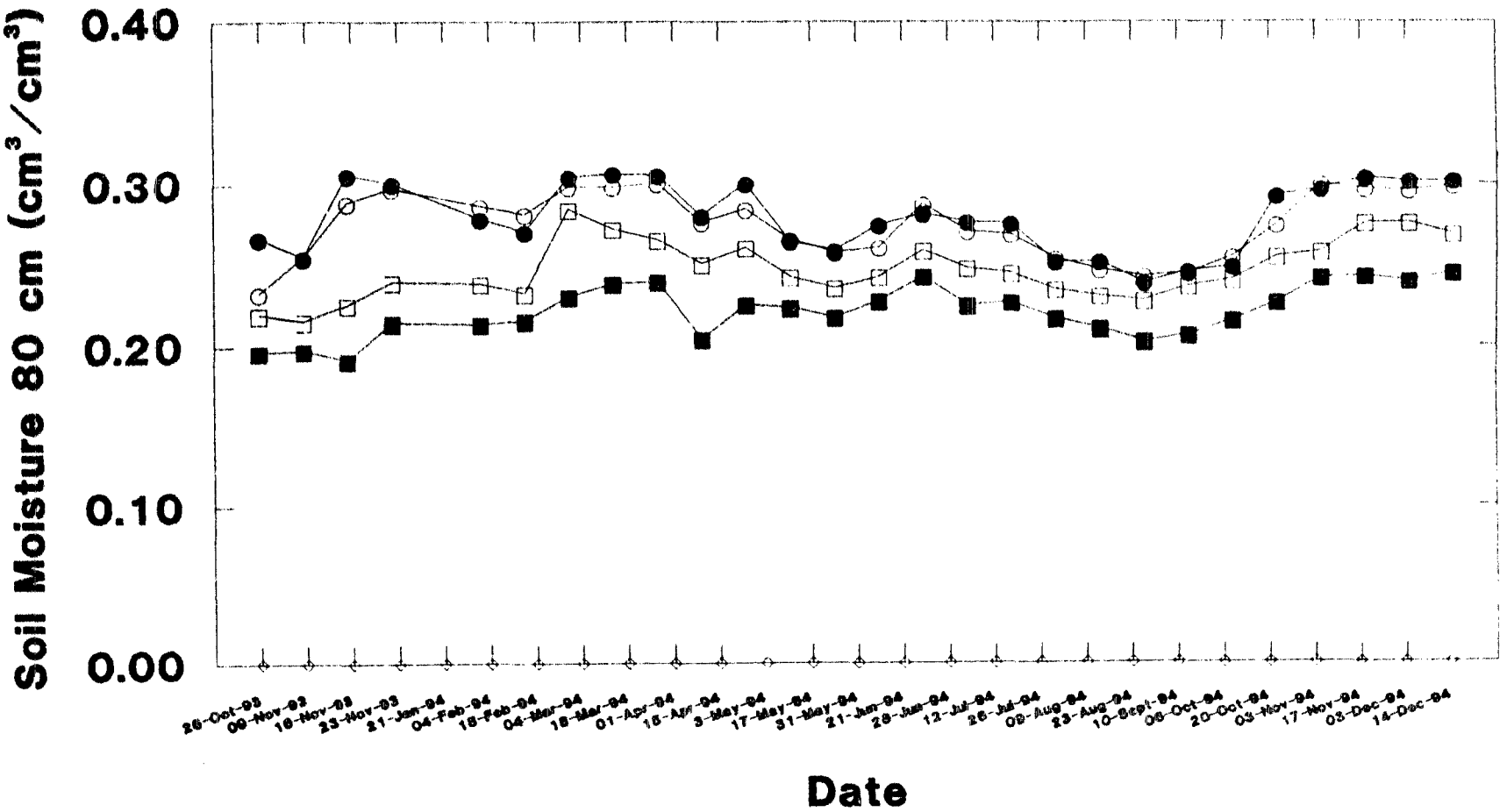

Figure 2.16 Mean soil moisture at 80 cm depth in the soil profile, measured in cm^3/cm^3 on 28 sampling dates from October 1993 to December 1994. The means for each sampling date consists of one measurement in each microsite in six plots. Pit microsites in gap plots are designated by the symbol "o" and pit microsites in closed canopy plots are designated by the symbol "•". Mound microsites in gap plots are designated by the symbol "□" and mound microsites in closed canopy plots are designated by the symbol "■".

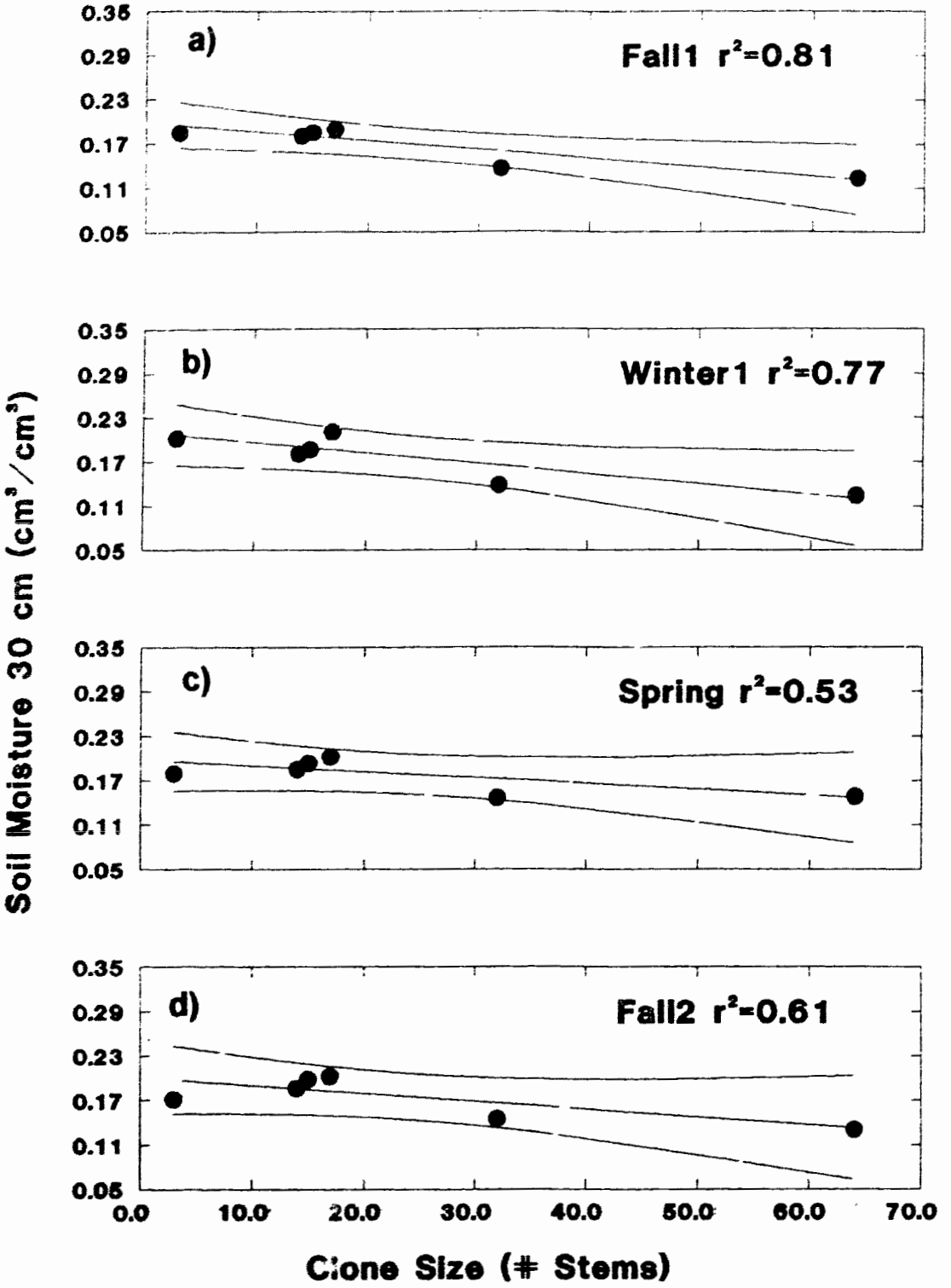

Figure 2.17 A regression of mean soil moisture at 30 cm depth in the profile in gap plots to the number of stems on the vine maple clone for the a) fall1 time period, b) winter1 time period, c) spring time period and d) fall2 time period.

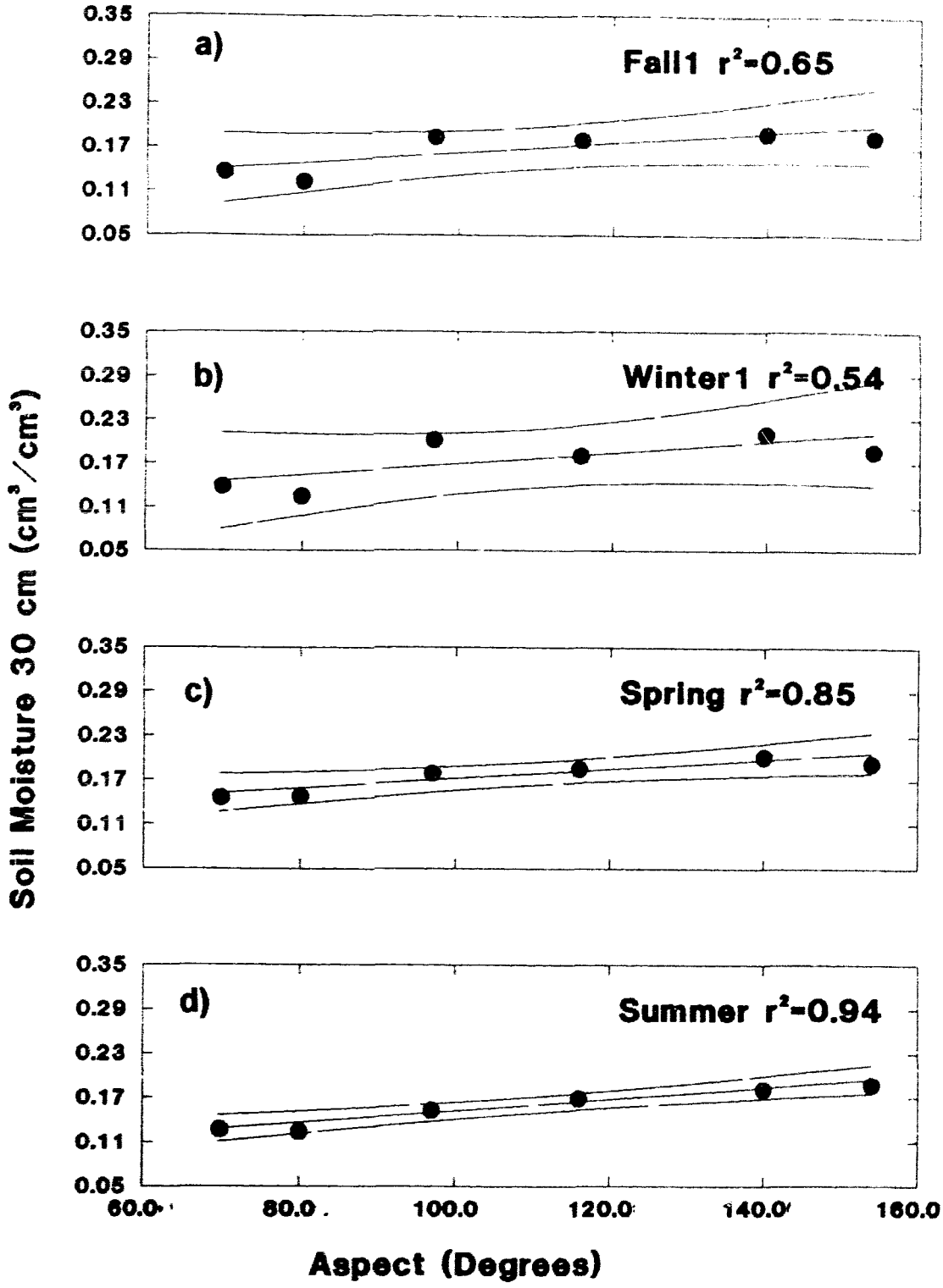

Figure 2.18 A regression of mean soil moisture at 30 cm depth in the profile in gap plots to aspect for the a) fall1 time period, b) winter1 time period, c) spring time period and summer time period.

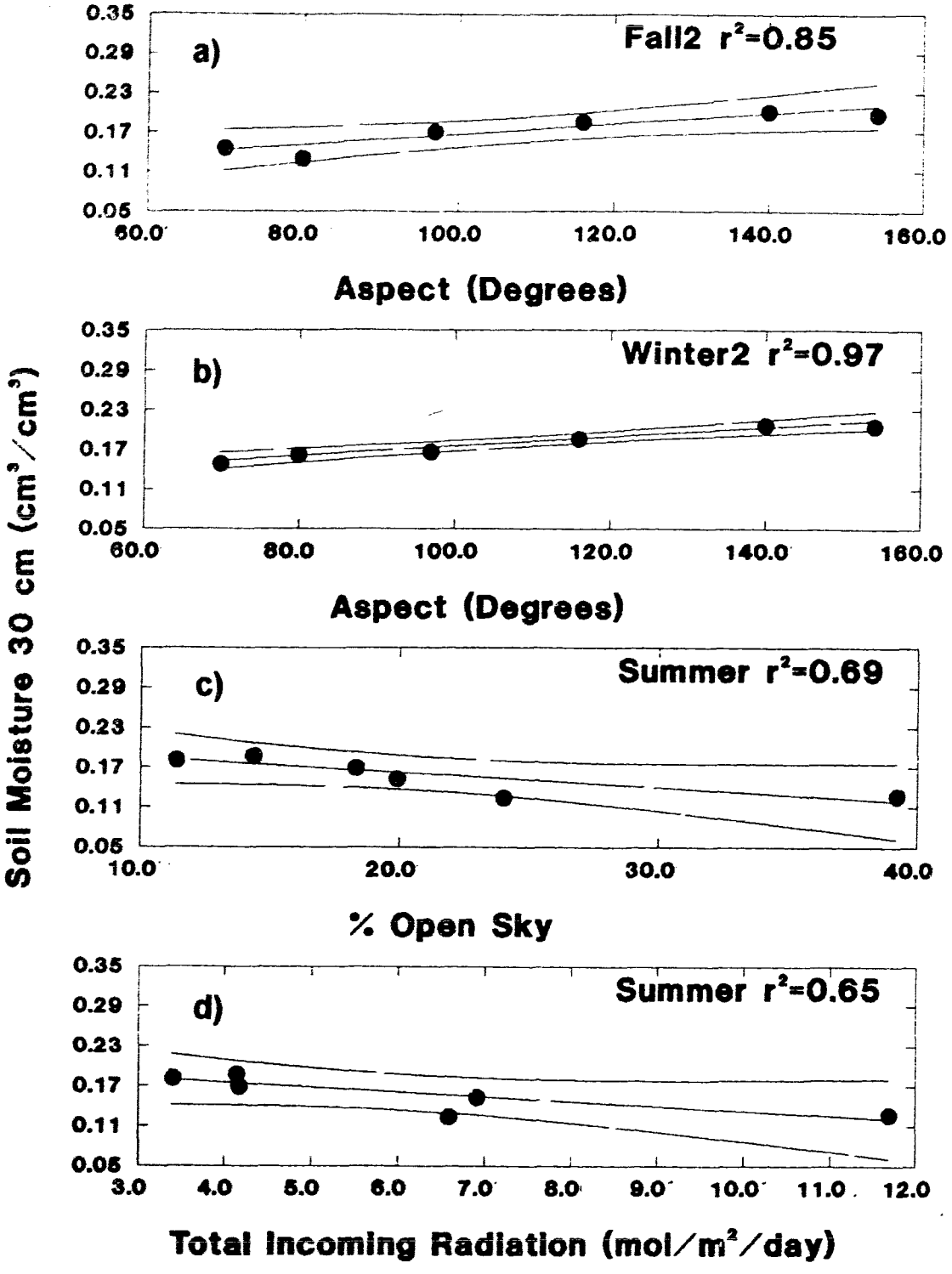

Figure 2.19 a) A regression of mean soil moisture at 30 cm depth in the profile in gap plots to aspect for the fall2 time period and b) winter2 time period. c) A regression of mean soil moisture at 30 cm depth in the profile in gap plots to percent open sky for the summer time period. d) A regression of mean soil moisture at 30 cm depth in the profile in gap plots total incoming direct and diffuse solar radiation for the summer time period.

2.3.5 *Depth to Groundwater Table*

Groundwater table levels showed a remarkable similarity between vine maple gap and closed canopy plots. Groundwater table levels were closer to the soil surface on 19 of 35 sampling dates in the gap plots (not significant), and most of these were in the fall and winter time periods (Figure 2.20). On one sampling date in the fall, gaps had significantly higher water table levels than closed canopy plots ($p=0.05$, $F=6.29$, $df=1$). Pit and mound microtopography had a significant effect on groundwater levels on 24 of 35 sampling dates at the $p=0.10$ level: pits had water table levels closer to the soil surface than mounds.

A comparison was made in groundwater levels between gap and closed canopy plots in similar microsites. For the pit microsites, the groundwater table was closer to the soil surface in the gap plots than in closed canopy plots on 18 of 35 sampling dates, of which only one sampling date in the fall was significant ($p=0.04$, $F=7.14$, $df=1$) (Figure 2.21). A similar trend existed for mound microsites; on 25 of 35 sampling dates, the groundwater table was closer to the surface in the gap plots than the closed canopy plots, of which only one sampling date in the fall was significant ($p=0.09$, $F=4.28$, $df=1$) (Figure 2.39).

To distinguish seasonal trends in the groundwater table levels, mean water table levels were calculated for the gap and closed canopy plots for the seven seasonal time periods outlined in the methodology (Table 2.7). In all seasons, mean seasonal groundwater table levels were closer to the surface in gap plots than closed canopy plots; however, this relationship was significant only in the summer ($p=0.00$, $F=37.97$, $df=1$).

Pits had significantly higher mean seasonal groundwater table levels than mounds in six of seven seasons: the second and third fall time periods ($p=0.00$, $F=19.62$, $df=1$; $p=0.00$, $F=15.99$, $df=1$), winter ($p=0.00$, $F=31.65$, $df=1$; $p=0.00$, $F=29.97$, $df=1$), spring ($p=0.00$, $F=32.53$, $df=1$), and summer ($p=0.05$, $F=5.27$, $df=2$) (Figures 2.22a to 2.22c). Consistent trends in groundwater table levels were also observed throughout the year. The order of increasing water table levels was as follows: the mound microsite in the closed canopy, the mound microsite in the gap, the pit microsite in the closed canopy, and the pit microsite in the gap.

For each time period outlined in the methodology, linear regression was used to determine if groundwater table levels were influenced by vine maple gap characteristics. During certain times of the year, groundwater table levels were found to be related to elevation. In the second fall time period ($p=0.05$, $r^2=0.65$, $n=6$) and winter time periods, ($p=0.01$, $r^2=0.84$, $n=6$; $p=0.01$, $r^2=0.83$, $n=6$), lower elevations had higher groundwater tables (Figures 2.41 and 2.42). Slope, aspect, light regime, clone size and gap size did not significantly influence groundwater table in vine maple gap plots.

2.4 Discussion

Overall, the temperature and moisture regime results obtained in this study did not support the hypothesis that the microclimatic characteristics of vine maple gaps differ significantly from those of the surrounding coastal western hemlock forest. With respect to gap size and clone size, larger vine maple gaps compared to smaller vine maple gaps had significantly higher air temperatures in the summer and fall; significantly higher soil

Table 2.7

Mean groundwater table levels and standard deviations for the seven time periods outlined in Table 2.1, measured in cm below the soil surface, from September 1993 to December 1994. For each individual plot, the mean and standard deviation are from one measurement in a pit microsite and one measurement in a mound microsite for each sampling date within the time period. The overall means and standard deviations for each time period were calculated from the plot means for each sampling date within the time period.

Plot	Fall 1a	Fall 1b	Winter 1	Spring	Summer	Fall 2	Winter 2
1g	100.0 ± 0.0	80.3 ± 19.0	74.3 ± 25.8	86.7 ± 17.2	99.5 ± 1.7	93.1 ± 12.9	68.8 ± 5.7
1c	100.0 ± 0.0	88.6 ± 19.9	88.1 ± 22.5	91.2 ± 16.5	100.0 ± 0.0	96.4 ± 10.3	85.3 ± 16.4
2g	100.0 ± 0.0	83.7 ± 14.7	82.8 ± 16.6	88.5 ± 14.5	98.7 ± 3.2	96.4 ± 7.6	78.8 ± 12.2
2c	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0
3g	100.0 ± 0.0	89.2 ± 17.2	90.3 ± 18.6	90.2 ± 18.0	97.6 ± 8.2	93.2 ± 12.6	86.3 ± 18.0
3c	100.0 ± 0.0	86.2 ± 18.3	82.8 ± 18.7	86.7 ± 16.7	98.4 ± 3.8	93.4 ± 12.5	82.0 ± 19.7
4g	95.6 ± 7.0	68.7 ± 14.1	70.1 ± 11.7	67.8 ± 9.8	82.0 ± 12.5	73.3 ± 17.5	66.8 ± 12.0
4c	96.2 ± 10.8	67.9 ± 23.8	62.0 ± 19.6	69.0 ± 17.4	83.2 ± 15.2	70.6 ± 22.8	61.3 ± 15.4
5g	100.0 ± 0.0	98.5 ± 4.1	99.2 ± 2.3	99.3 ± 1.9	99.3 ± 2.5	98.4 ± 4.4	100.0 ± 0.0
5c	100.0 ± 0.0	95.0 ± 10.2	94.0 ± 12.0	94.9 ± 10.0	100.0 ± 0.0	98.4 ± 4.6	92.3 ± 8.6
6g	100.0 ± 0.0	81.9 ± 24.3	76.1 ± 25.1	85.9 ± 21.2	97.7 ± 7.2	89.8 ± 17.7	70.1 ± 22.1
6c	100.0 ± 0.0	88.8 ± 12.8	88.6 ± 15.1	94.0 ± 10.3	98.5 ± 3.6	93.1 ± 12.9	87.4 ± 13.8
Gap Mean	99.4 ± 2.8	83.7 ± 15.5	82.1 ± 17.4	86.4 ± 14.7	95.8 ± 8.1	90.7 ± 12.0	78.5 ± 12.3
Gap Pit	99.2 ± 3.9	77.7 ± 19.6	74.6 ± 22.0	80.6 ± 20.2	93.6 ± 11.0	85.8 ± 18.4	68.6 ± 16.5
Gap Mound	99.6 ± 1.7	39.8 ± 15.6	89.6 ± 15.2	92.3 ± 11.9	98.1 ± 6.5	95.6 ± 7.9	88.4 ± 10.9
CC Mean	99.4 ± 3.1	87.7 ± 14.4	85.9 ± 15.0	89.3 ± 13.3	96.7 ± 7.1	92.0 ± 13.2	84.7 ± 12.4
CC Pit	98.7 ± 6.2	80.3 ± 21.8	76.3 ± 22.3	82.7 ± 19.3	94.2 ± 11.7	86.9 ± 19.4	73.6 ± 17.0
CC Mound	100.0 ± 0.0	95.1 ± 10.5	95.5 ± 9.9	95.9 ± 8.8	99.1 ± 3.1	97.0 ± 8.2	95.9 ± 9.6

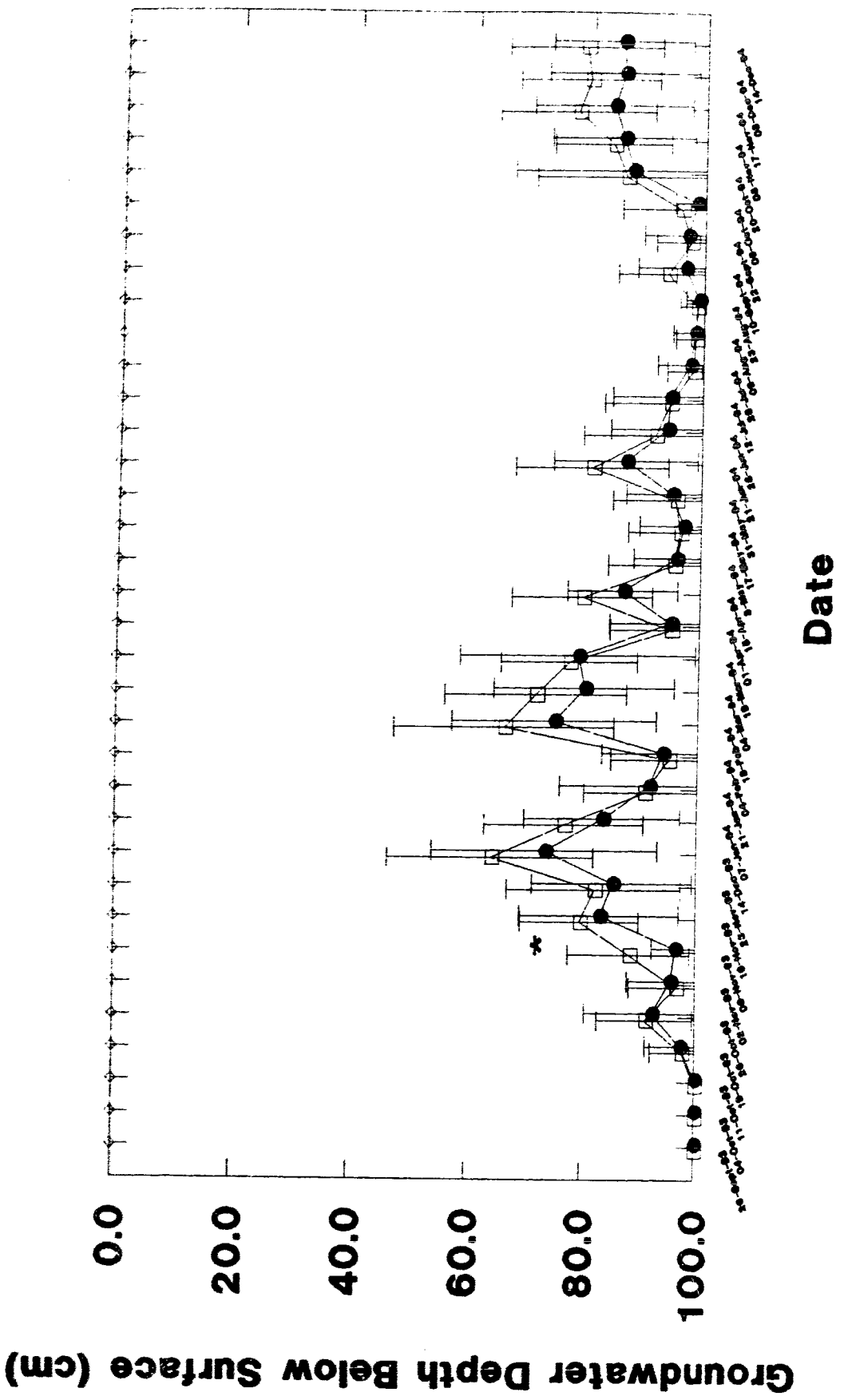

Figure 2.20 Mean groundwater table levels, measured in cm below the soil surface, on 35 sampling dates from September 1993 to December 1994. The mean for each sampling date was calculated from one measurement in a pit microsite and one measurement in a mound microsite in six plots. Gap plots are designated by the symbol "□" and closed canopy plots are designated by the symbol "●".

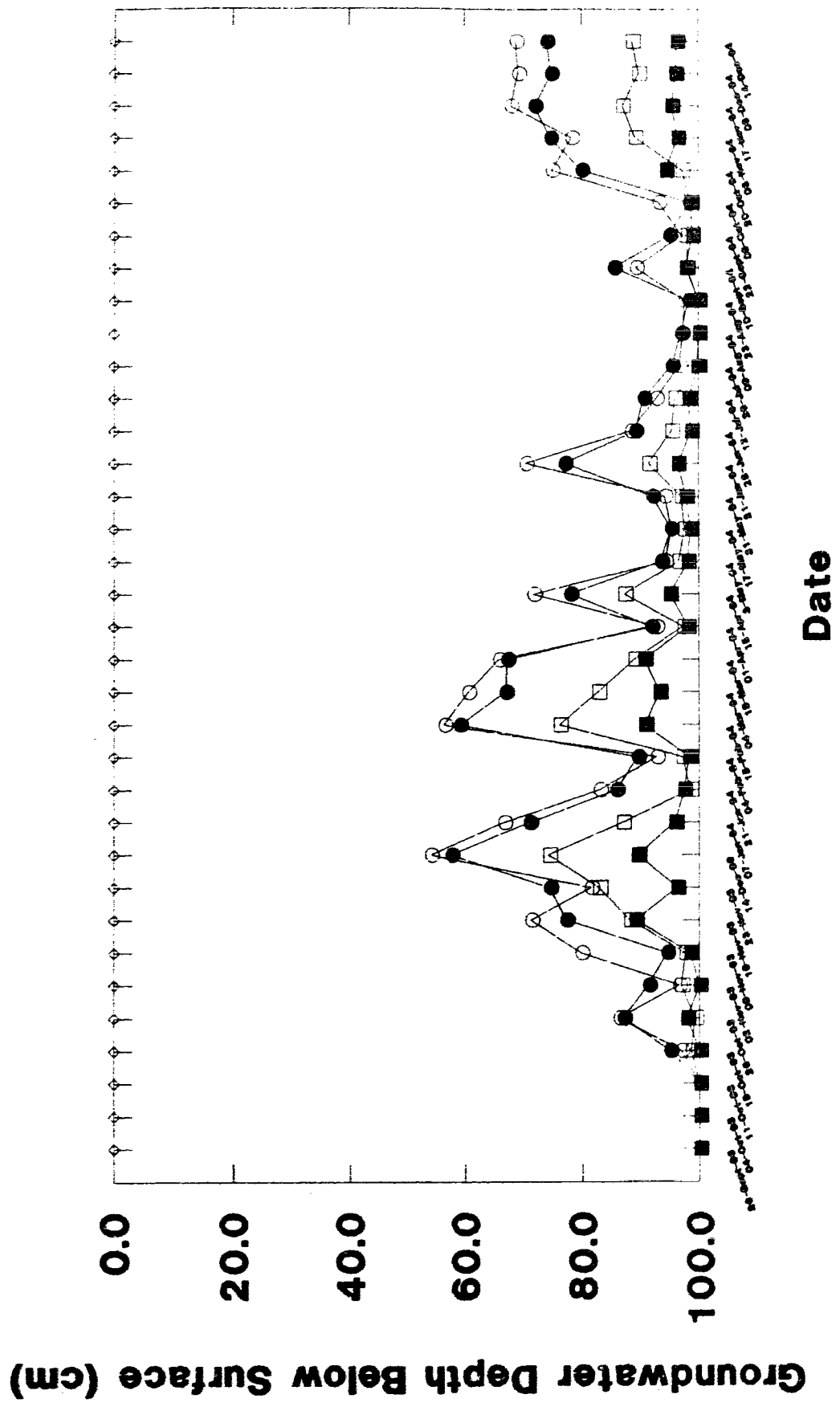

Figure 2.21 Mean groundwater table levels, measured in cm below the soil surface, on 35 sampling dates from September 1993 to December 1994. The mean for each sampling date was calculated from one measurement in each microsite in six plots. Pit microsites in gap plots are designated by the symbol "o" and pit microsites in closed canopy plots are designated by the symbol "•". Mound microsites in gap plots are designated by the symbol "□" and mound microsites in closed canopy plots are designated by the symbol "■".

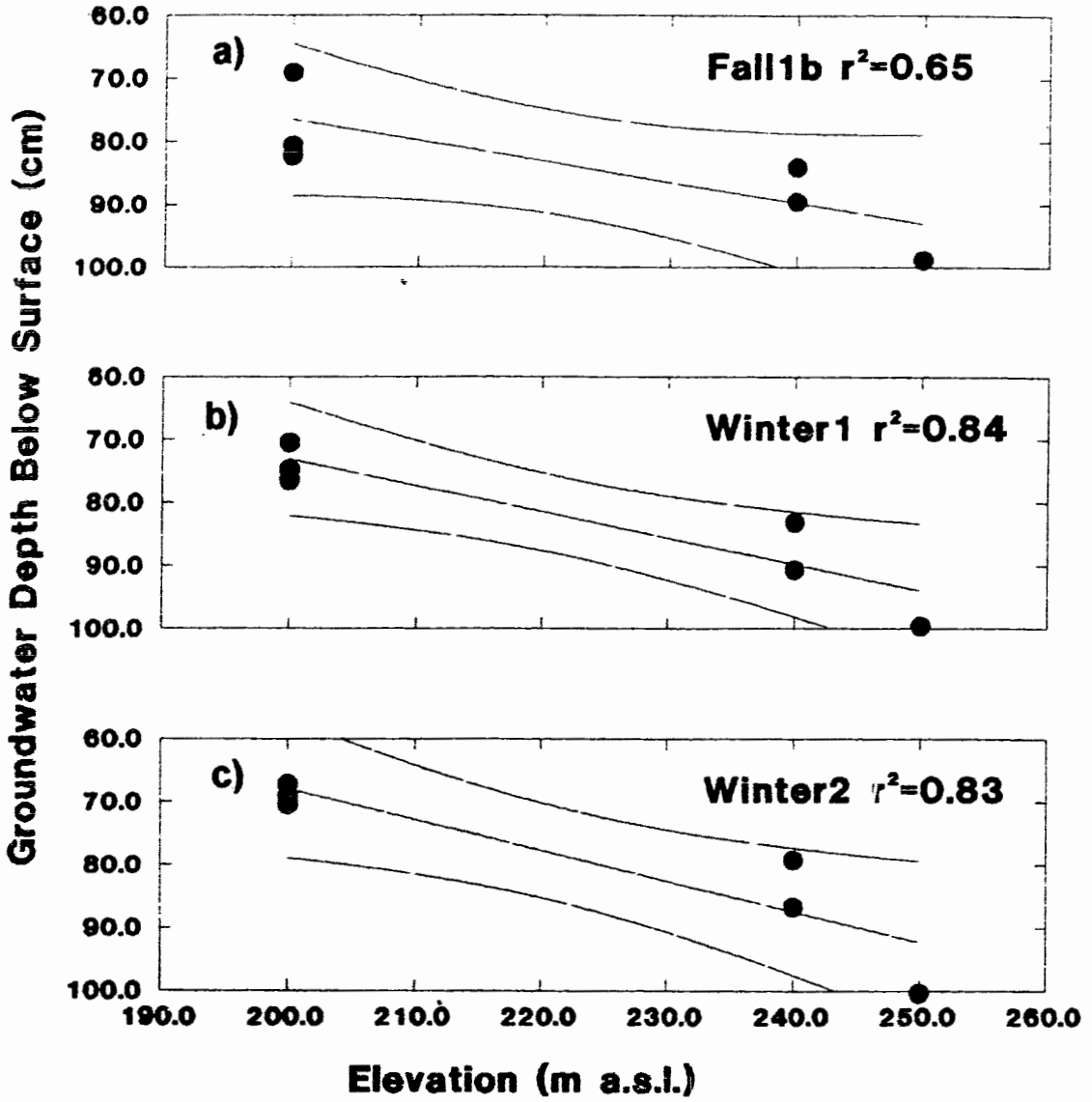

Figure 2.22 a) A regression of groundwater table levels in gap plots to elevation for the fall1b time period. b) A regression of groundwater table levels in gap plots to elevation for the winter1 time period. c): A regression of groundwater table levels in gap plots to elevation for the winter2 time period.

temperatures in the spring, summer and fall; and significantly lower soil moisture content in the upper 30 cm. However, gap size and clone size were not related to groundwater table levels. The additional aspect of this study -- dealing with pit and mound microtopography -- determined that pits and mounds had a consistently significant effect on soil temperature and moisture regimes in the study area. Pits compared to mounds had significantly lower soil temperatures in the summer, significantly higher soil temperatures in the winter, significantly higher soil moisture content at all levels, and significantly higher groundwater table levels.

Because the comparison of temperature and moisture seasonal means between vine maple gaps and the surrounding closed canopy were obtained from data which were temporally pseudoreplicated in order to achieve a larger sample size, the mean seasonal comparisons were not as conclusive as the bi-weekly comparisons. Nevertheless, the mean seasonal comparisons are useful to indicate trends that may not be detected by the bi-weekly comparisons. In the bi-weekly temperature and moisture comparisons, the power of the statistical tests was likely to be quite low due to the small sample size, small effect size and high within-plot sample variability (Toft and Shea 1983). However, some consistent trends in the bi-weekly comparisons -- especially in moisture regimes -- which were not statistically significant may be significant with a larger sample size, and are therefore worth noting as they indicate areas for further study.

2.4.1 *Temperature Regime*

Since light regimes are the same beneath vine maple gap plots and closed canopy plots (McGhee 1996) and vine maple is associated with high transpirational demands resulting in a cooling effect, and since vine maple foliage (which can moderate fluctuations in temperatures) is absent in the winter, surface air temperatures were hypothesized to be cooler throughout the year in vine maple gaps. While mean seasonal air temperatures were significantly lower in the vine maple gap plots as compared to the closed canopy plots in the spring and summer (as were predicted), and were not different in the fall and winter (contrary to what were predicted), few significant differences existed in the bi-weekly mid-day air temperature measurements throughout the year. Therefore, the hypothesis that air temperatures are cooler in gaps in the summer was supported (but not conclusively due to possible pseudoreplication); and the hypothesis that air temperatures in gaps are colder in the winter was not supported.

Two reasons may account for the unexpected finding of similar bi-weekly air temperature measurements in vine maple gaps and the surrounding closed canopy forest. In the first place, the light regime around any individual gap can be strongly modified by understory strata as noted by Canham et al. (1990) and observed by McGhee (1996). McGhee (1996) found that light regimes beneath vine maple clones growing in canopy gaps do not differ from those beneath the closed canopy forest; and, therefore, the amount of solar energy reaching the forest floor is the same. Secondly, the D/H ratios (gap diameter to height of the surrounding canopy) for vine maple gaps were low (0.10-0.35; Table 1.2). Canham et al. (1990) found that, because of low D/H ratio, single tree gaps

in old-growth Douglas-fir/western hemlock forests in Oregon had little effect on understory light regimes. Also, in very small gaps, the development of extremes in surface temperatures is hindered by shade from surrounding trees (Smith 1986).

An explanation for the finding that air temperatures may be cooler in vine maple gaps in the summer is evapotranspirational cooling. Since McGhee (1996) noted that light regime beneath vine maple clones in canopy gaps is the same as the surrounding closed canopy forest, the cooler mean seasonal air temperatures in gaps in the spring and summer are likely due to high transpirational demands of vine maple at this time of year, as observed by Drew (1968), leading to cooler air temperatures.

Since soil temperatures in the surface soil layers vary according to the temperature of the air immediately above (Pritchett and Fisher 1987), mid-day surface soil temperatures were hypothesized to be cooler beneath vine maple gaps than beneath the surrounding forest. Contrary to expectation, soil temperatures did not differ between vine maple gaps and the closed canopy forest throughout the year. Several factors account for this finding. Mid-day air temperatures were not significantly different between vine maple gaps and the surrounding closed canopy (although they may be lower in the gaps in the summer), and light regimes beneath vine maple gaps and closed canopy plots were similar (McGhee 1996). The low D/H ratio of the vine maple gaps also points to the insignificant effect these small gaps had on understory light regimes, similar to findings of Canham et al. (1990). Consequently, the amounts of solar radiation reaching the forest floor are similar in vine maple gaps and closed canopy plots, and produce similar soil temperatures. In contrast, Ash and Barkham (1976), McGee (1976) and Pontailler (1979) found that

soil temperatures in gaps were significantly higher than those beneath the closed forest. The somewhat lower mid-day surface soil temperatures in vine maple gaps in the summer and fall resulted from the influence of surface air temperatures (Pritchett and Fisher 1987).

In developmental gaps in tropical forests (Denslow 1987) and temperate forests (McGhee 1976; Ash and Barkham 1976; Pontailler 1979), canopy openings were observed to have higher maximum (mid-day) surface temperatures than the closed forest due to a localized increase in light levels. Contrary to these findings, surface air and soil temperatures in vine maple gaps did not differ from the surrounding forest. A study on canopy gaps in a tropical forest (Denslow 1987) found that differences between gap and understory light levels were observed to be lower in small gaps than in large gaps; and a study in an old-growth forest in Oregon (Canham et al. 1990) found that as gap size increased, the mean and range of light levels within gaps also increased. Consistent with these findings, mid-day air and soil temperatures in vine maple gaps were related to gap size: mean seasonal air temperatures were significantly lower in smaller gaps than larger gaps in the summer and fall; and mean seasonal surface soil temperatures were significantly lower in smaller gaps than larger gaps in the spring, summer and fall. The effects of gap size may be accounted for by differences in the D/H ratios between small and large gaps: the D/H ratios were higher in larger gaps. Also, the effect of gap size on air and soil temperatures was consistent with the observation of Smith (1986) who notes that the development of extremes in surface temperatures in and around gaps is hindered by side shade; whereas, in larger gaps (two-to-three times the height of surrounding trees) environmental conditions are similar to conditions in larger cleared areas.

2.4.2 *Moisture Regime*

With respect to precipitation, the hypothesis tested was that the amount of precipitation reaching the soil surface throughout the year was greater in vine maple gaps than in the closed canopy. Greater amounts of precipitation in vine maple gaps were expected throughout the year because there is less total leaf area in the gap plots than the closed canopy plots and therefore less interception by vegetation. The results of this study revealed that precipitation levels did not differ significantly between vine maple gap plots and those in closed canopy plots throughout the year, even though precipitation was slightly higher in the vine maple gaps than in the closed canopy plots on almost all of the sampling dates. The results were not consistent with the observation of Pickett and White (1985) who observed that developmental gaps had higher precipitation levels compared to the surrounding closed canopy forest. On the one hand, the discrepancy may have resulted from the two-week collection intervals used in the study during which times evaporation levels may have been higher in gaps than beneath the closed canopy. On the other hand, there may have been no significant difference in precipitation levels since the low D/H ratios of the vine maple gaps suggested that levels of precipitation reaching the forest floor were the same in vine maple gaps as in the surrounding closed canopy forest. Consequently, although the results did not support the hypothesis and the tendency of the data was suggestive of a trend, a more frequent data collection interval and a larger sample size is necessary to make a definitive conclusion.

The biogeoclimatic subzone that the study area is located within is transitional between CWHmm and CWHdm, and while these subzones are characterized by a late

summer dry period, this characteristic was not observed in this study due to similar precipitation levels in all seasons. This coincides with the observation that there was no large seasonal variation in soil moisture content throughout the study area.

Since moisture levels in the upper soil horizons are consistently and significantly higher in developmental gaps than in the adjacent forest (Denslow 1987), and greater amounts of precipitation were expected to reach the forest floor in vine maple gaps compared to the closed canopy forest, surface soil moisture levels in vine maple gaps were hypothesized to be higher than that in the surrounding forest throughout the year. Results from the soil moisture data analyses, however, showed that soil moisture content at all depths was not significantly different between the gap and closed canopy plots in any season. While the result was not consistent with the findings of Denslow (1987) and Lee (1978) for developmental gaps, it was consistent with the finding that vine maple gaps have similar precipitation levels to those of the surrounding forest. Drew (1968) found that vine maple is capable of rapidly depleting soil moisture to a depth of 60 cm during July and August because of its extensive, vigorous root system and high transpiration rate; consequently, the trend observed in this study area in the spring, summer, and fall, was likely the result of the high transpirational demands associated with vine maple. Further evidence of this high transpiration rate was demonstrated in the relationship between clone size and soil moisture: the greater the number of stems on the clone, the lower the soil moisture content within the rooting zone, or upper 30 cm; whereas, below the rooting zone, the size of the vine maple clone was not related to soil moisture values.

Vine maple may have a preference for sites that are inherently wetter since soil moisture contents were higher (not significant) at 80 cm beneath vine maple gaps as compared to those beneath closed canopy plots. However, further study would be required to determine if the location of vine maple gaps is related to inherent soil moisture.

Consistent with the general observations of Pickett and White (1985), the percentage of open sky and the total amount of incoming solar radiation in vine maple gaps were related to soil moisture values in the upper 30 cm soil zone in the summer: the greater the amount of open sky and incoming radiation, the lower the amount of soil moisture in the upper 30 cm. The result may be explained by the fact that larger vine maple gaps have higher evapotranspirational demands than smaller vine maple gaps (Drew 1968).

Since less interceptional and transpirational surface area results in an increase in water table levels, due to greater amounts of precipitation reaching the forest floor and less total leaf area to intercept precipitation (Pritchett and Fisher 1990), groundwater table levels were hypothesized to be higher in vine maple gaps than beneath the closed canopy throughout the year. Consistent with the findings of no differences in precipitation levels as noted above, results from groundwater table level measurements revealed no significant differences in groundwater table levels between gaps and closed canopy plots. However, the readings for groundwater table levels were higher in the gap plots, especially in the fall and winter months (during the rainy season) when vine maple was not in leaf and was not actively transpiring. In contrast to the results for vine maple gaps, Pritchett and Fisher (1990) note that large canopy openings have higher groundwater table levels than the

surrounding forest. No studies were found in the literature concerning the relationship between small developmental gaps and groundwater table levels or the effects of gap size on groundwater table levels. Gap size and clone size were not related to groundwater table levels in vine maple gaps. Groundwater table levels were likely related more to subsurface drainage patterns than to vine maple gap size. Further evidence of the effects of subsurface drainage was the finding that groundwater table levels in the fall and winter were related to elevation: plots located at lower elevations had significantly higher groundwater table levels than plots at higher elevations. This result was attributable to sub-surface drainage from higher elevations to lower elevations.

2.4.3 *Pit and Mound Microtopography*

In this study, the hypotheses tested were that, throughout the year, pits are wetter than mounds; that pits are warmer than mounds in winter, and cooler than mounds in summer; and that the groundwater table levels are higher in pits than mounds. Consistent with the findings of Beatty and Stone (1985) that mounds have significantly warmer soil temperatures in summer and colder temperatures in winter (thus giving mounds a greater amplitude of temperature fluctuation than pits), and that mounds are drier than pits, all hypotheses of the study were confirmed: pit microsites are less extreme in their soil temperature regimes than mound microsites (pits compared to mounds had significantly cooler mid-day soil temperatures in the summer and warmer mid-day soil temperatures in the winter); pit microsites have significantly higher soil moisture values and higher groundwater table levels than mound microsites. The results were also consistent with

those of Peterson et al. (1990) who found that soil temperatures are higher in mounds, and that soil moisture levels are higher in pits.

When the soil temperature, soil moisture and groundwater regimes of pits under vine maple gaps were compared to those of pits under the closed canopy, no significant differences were observed. Similarly, when the same parameters for mounds under vine maple gaps were compared to those of mounds under the closed canopy, no significant differences were observed. However, significant differences in soil temperature, soil moisture, and groundwater were observed between pits and mounds, yet no significant differences were observed for these parameters between vine maple gaps and the closed canopy plots. In the study area, pit and mound microtopography, therefore, had a significant effect on soil temperature and moisture regimes; whereas, vine maple gaps did not significantly effect soil moisture and temperature regimes. The results suggest that the soil temperature and moisture differences between pits and mounds are independent of the forest cover whether canopy gaps or closed forest.

Chapter 3

Soil physical and chemical properties of persistent canopy openings occupied by vine maple in a coastal western hemlock forest

Chapter 3
Soil physical and chemical properties of persistent canopy openings occupied by vine maple in a coastal western hemlock forest

3.1 Introduction

In coastal British Columbia ecosystems, hardwood species typically colonize early successional stages in stand development, and persist into later successional stages only in disturbed areas and riparian zones (Haeussler et al. 1990). Canopy openings containing the hardwood species *Acer circinatum* Pursh. (vine maple) are common to coastal B.C. forests. Vine maple has been observed to persist and be self-maintaining over long periods of time in these canopy gaps, some of which are characterized by the absence of a gapmaker (McGhee 1996; Spies et al. 1990).

McGhee (1996) proposed two alternative hypotheses to explain the origin of persistent vine maple gaps, *edaphic gaps* and *priority gaps*. Under the edaphic gap hypothesis, vine maple has a competitive advantage due to unique inherent soil properties or site characteristics of the gap; whereas, under the priority gap hypothesis, vine maple has been able to resist the regeneration of taller canopy dominants and subsequent canopy closure by establishing a dense mat of stems early in stand development that is large enough to prevent invasion of the site by conifers. In this study, the inherent soil properties of vine maple gaps were compared to those of the surrounding forest, to determine if vine maple gaps are edaphic or priority in origin. This component of the study also sought to determine the effects of vine maple gaps on soil properties. The effect of

persistent vine maple gaps on soil properties was expected to be significant because the influence of the species was prolonged throughout stand development.

Very little information is available concerning the soil properties of forest canopy openings, and even less information is available on soil properties associated with the canopy gaps in Pacific Northwest temperate rainforests. Most research on nutrient dynamics in forest openings has focused on large disturbances such as clearcuts or burned areas; few studies have focused on nutrient dynamics within developmental gaps, which are created by tree mortality. Developmental gaps may increase temporarily the availability of soil nutrients due to the reduction in rates of uptake of resources (because of the loss of biomass), and to the increase in rates of decomposition and mineralization of nutrients held in organic matter (because of increased availability of energy and moisture) (Pickett and White 1985). However, Vitousek and Denslow (1986) report that, in a lowland tropical rainforest, the rates of N availability and cycling are not greatly affected at the forest level (in the short-term) by the presence of treefall gaps; and concludes that the increase in light availability within treefall gaps is a more important shift in resources than changes in nutrient availability. Since nutrient availability is controlled by a number of interacting factors (Gorham et al. 1979), it is difficult to predict whether or not nutrient availability will increase in all gaps (Pickett and White 1985).

Although there have been no formal studies on soil properties beneath vine maple, some general observations have been made. Vine maples are often found on moist, rich, rocky sites along stream banks, in damp woods, in depressions, and in meadows (Haeussler et al. 1990; UBC Bot. Garden 1976). The vigorous, shallow, and fibrous

rooting system of vine maple is believed to give it an advantage over other species on talus slopes, shallow soils, and rock bluffs, that may explain its dominance on many of these sites (Anderson 1969). Due to a high transpiration rate, vine maples are water demanding (Drew 1968). Vine maple can be an edaphic climax shrub in both the Coastal Western Hemlock and Coastal Douglas-fir biogeoclimatic zones (Krajina et al. 1982).

Vine maples have been observed to be very strong competitors on nutrient rich sites (Krajina et al. 1982). Vine maple has high nutritional requirements for Ca, Mg and N; and it efficiently returns nutrients to the soil through litterfall (Haeussler et al. 1990). The heavy annual litterfall and the rich nutrient content of vine maple leaves are believed to result in relatively higher rates of nutrient cycling compared to other understory species (Russell 1973). Vine maple leaves are thought to decompose faster than coniferous needles due to lower lignin and higher N contents (Haeussler et al. 1990). Unlike coniferous needles, the composition of vine maple litter does not promote soil acidity (Haeussler et al. 1990).

Due to the return of nutrients to the site through litterfall, Moder humus, which is favourable to the growth of Douglas-fir and western redcedar, has been observed to form beneath vine maples (Krajina et al. 1982). Soil organism activity is greater in Moder humus forms than in Mor humus forms, the latter being the least biologically active of humus forms (Ministry of Forests 1981). Mors occur beneath coniferous forests; are characterized by high levels of acidity, slow decomposition rates, and high C/N ratios; and develop under conditions which are unfavourable for the development of more biologically active humus forms. Moders develop beneath deciduous overstory or understory

vegetation, both of which yield easily decomposable litter. Moders are characterized by a higher pH level, lower C/N ratio, lower total carbon, higher total nitrogen, and higher base saturation than Mor humus forms (Ministry of Forests 1981; Pritchett and Fisher 1987). The C/N ratio is usually a better index of N availability than total N concentration (Watts 1983). A low C/N ratio (near or below 15) suggests that soil N is rapidly being made available by mineralization; whereas, a high C/N ratio (greater than about 25) suggests low N availability due to predominant immobilization (Watts 1983). In Mor humus forms, the C/N ratio of H horizons is generally above 25, and of F horizons commonly exceeds 40.

Soils in forests of the Coastal Western Hemlock zone, in which the study area was located, are dominantly Orthic Humo-Ferric Podzols grading (with increasing precipitation) into Ferro-Humic Podzols, with Mors as the dominant humus form. Leaching of nutrients from the mineral soil is rapid in this wet climate, and many soils are derived from acidic parent materials which are low in clay minerals and poor in nutrients (Watts 1983). Therefore, the storage of nutrients in vegetation and surface organic layers is extremely important in the maintenance of ecosystem productivity, especially on the coarse textured, nutrient-poor soils that are characteristic of the study area (Meidinger and Pojar 1991).

This study examined the relationship between vine maple gaps and the physical and chemical properties of the forest floor and surface mineral soil horizons. Soil properties in vine maple gaps were compared to those in paired plots with similar

topographical characteristics in the surrounding western hemlock forest. The following hypotheses were tested in this component of the study:

1. The concentration of bases in the forest floor of gap plots is expected to be higher than that of closed canopy plots since leaf litter of vine maple is believed to provide a rich supply of nutrients to the site (Krajina et al. 1982).

2. Since the study area is overlain by a layer of glacial till, soil texture and gravel content values are expected to be similar throughout the gap and closed canopy plots.

3. Since vine maples return nutrients efficiently to the soil through rapid litter decomposition, are associated with rapid rates of nutrient cycling (Haeussler et al. 1990), and may be associated with greater levels of soil organism activity, it is expected that compared to closed canopy plots, bulk density will be lower in gap plots; and that pH, organic matter concentration, and total N will be higher in gap plots.

4. The C/N ratio of the upper mineral soil is expected to be lower in gap plots due to the rapid decomposition rates of vine maple litter and the high concentration levels of nitrogen associated with hardwood litter (Haeussler et al. 1990).

3.2 Methodology

3.2.1 *Sample Collection*

Across level topography, a three-meter long transect line was installed at the centre of each plot. Samples were collected at one meter intervals along the transect line, and sampling in pit or mound microsites was avoided. On the vine maple plots, the centre of the transect was located beneath the vine maple foliage.

3.2.2 *Forest Floor Properties*

3.2.2.1 *Depth and Weight of the Forest Floor*

In each of the gap plots and closed canopy plots, the forest floor (LFH horizons) was collected by measuring an approximately 20 cm^2 area that was removed by inserting a shovel down to the mineral-organic soil interface. Sampling in pits and mounds was avoided. Once removed, mineral soil was brushed off the LFH sample, and the sample was placed into a square aluminum container. The depths of the L, F and H horizons were measured, and the exact length and width of each sample was measured. The sample was then placed inside a plastic bag and taken to the lab. The samples were oven-dried overnight at 105°C and were then weighed. Prior to weighing, any excess mineral soil still remaining on the sample was removed.

3.2.2.2 *Nutrient Concentrations in the Forest Floor*

Nutrient concentrations for the samples taken from the forest floor (LFH horizons) were determined using the methods of Parkinson and Allen (1975). In the LFH samples, analyses were conducted to determine the concentration levels of N, P, Ca, Mg, K, Mn, Fe, Zn, and Al. Although Al is not a nutrient, its concentration levels were measured; and Al is treated as a nutrient within the text. Samples were fine ground with a coffee grinder, and a representative, 0.25 g sub-sample was placed in a digestion tube along with 5 ml of concentrated H_2SO_4. One ml of lithium-sulfate-peroxide mixture (prepared the day prior to digestion and consisting of 7 g Li_2SO_4, 0.21 g Se powder and 175 ml 30% H_2O_2) was then added to each tube. After the reaction ceased, the sample was placed on a

digestion block for three minutes and allowed to cool until white gas was no longer being produced. This step was repeated four times. The samples were then heated on a digestion block for one hour at 360 ^{o}C after which they were removed from the block and allowed to cool. One-half ml H_2O_2 was added to each sample and the samples were returned to the block for another 30 minutes. This step was repeated twice. Once digestion was complete, the samples were removed from the digestion block and cooled for one hour. Approximately 20 ml of distilled water was added to the sample, and the sample was shaken using a silicon stopper. The sample was then diluted to 100 ml with distilled water.

Total N and P concentrations were measured using a LaChat Auto analyzer; and Ca, Mg, K, Fe, Mn, Zn and Al concentrations were measured using an Atomic Absorption Spectophotometer. Accuracy was ensured by the use of standardized reference samples, blanks and repeats. Using the data on the weight of LFH per unit of surface area, the concentration values were converted into kg/ha to give an indication of the total amount of each nutrient contained within the LFH layer.

3.2.3 *Physical Soil Properties*

3.2.3.1 *Sample Collection*

Bulk soil samples from 5 and 20 cm beneath the soil surface were collected in the summer of 1994. The 5 and 20 cm mineral soil samples were collected by removing an approximately 0.5 m^2 section of soil beneath the LFH sample location. The first 0-10 cm of soil was removed and placed onto a plastic sheet. The soil was manually mixed to

homogenize the sample, and approximately 1 L of soil was collected and placed into a plastic bag. Similarly, the 20 cm soil sample was collected by removing the next 20 cm of soil, placing it onto a second plastic sheet, homogenizing it, and collecting a 1 L sample. The samples were taken to the lab and were oven-dried at 105 ^{O}C overnight.

Four bulk soil samples from approximately 50 and 100 cm depths were collected from each site in the summer of 1993. In each of the gap plots and closed canopy plots, two samples were located in a pit and two in a mound corresponding to the locations of the hydroprobe access tubes and groundwater wells described in Chapter two. Where possible, holes were drilled into the ground to the depth of 1m using an auger. The 50 and 100 cm depths beneath the surface were measured by marking the auger with masking tape. When it was not possible in a plot to get down to 1 m, the depth of the sample collection was noted. Samples were placed in plastic bags and taken to the lab where they were air-dried.

3.2.3.2 *Gravel Content*

Gravel content was determined from the bulk mineral soil samples collected at 5, 20, 50 and 100 cm below the soil surface. Cobbles and stones (>7.5 cm diameter) within the samples were discarded. Each sample was put through a 2 mm sieve; and, the percentage of gravel in the sample was determined by weighing the portion of the sample greater than 2 mm in size, and comparing that to the total weight of the sample.

3.2.3.3 *Particle Size Distribution*

Soil texture was determined using the hydrometer method (Klute 1986). Particle size analysis was carried out for the samples collected at 20, 50 and 100 cm depths. A 40 g representative subsample of air-dried and sieved soil was soaked for 15 minutes in a beaker containing 250 ml water and 50 ml of dispersing agent (50 g of Calgon -- sodium hexametaphosphate -- per litre of water). The sample was then transferred to a dispersing cup and mixed for 10 minutes with an electric mixer. Iso-amyl alcohol was used as an anti-foam agent when necessary. Once mixed, the suspension was transferred to a sedimentation cylinder and the volume was increased to 1 L using water. A control was also prepared containing 50 ml of dispersing agent and 950 ml water. The suspensions were allowed to sit overnight to allow temperatures to equilibrate.

A plunger was inserted into the cylinder to place all of the particles into suspension. Once mixing was complete, the hydrometer was lowered into the suspension, and readings were taken at 30 seconds, 1, 3, 10, 30, 60 and 90 minutes, and 24 hours after settling began. The hydrometer was placed in solution 10 seconds before the reading was to be taken and was removed immediately after so as to not disturb the settling process. The temperature of the solution was recorded when each reading was taken. Textural class and percentages of sand, silt and clay were determined using a computer software package obtained from the UBC Department of Soil Science.

3.2.3.4 *Bulk Density*

Bulk density of the top 10 cm of mineral soil was determined in three locations on each site using a bulk density cylinder. Care was taken to ensure that the sample was not collected where there was a large cobble or tree root present.. Samples were oven dried at 105^0C for 24 hours and weighed, and the volume of the collection cylinder was calculated.

3.2.4 *Chemical Soil Properties*

3.2.4.1 *Sample Collection*

The methodology for collecting soil samples for chemical analysis was the same as that for collecting soil samples for physical analysis that is outlined in section 3.2.3.1

3.2.4.2 *pH*

For the LFH and the soil samples collected at 5, 20, 50 and 100 cm depths at each site, the pH was determined using the glass electrode-calomel electrode pH meter method (Kalra and Maynard 1991). For mineral soil samples, exchange acidity was measured using a 1:2 soil-water slurry ratio; and for the LFH samples, a 1:10 soil-water slurry ratio was used. Ten g of soil (5g of LFH) were mixed with 20 ml of 0.01M $CaCl_2$ solution (50 ml for LFH), mixed intermittently for 30 minutes, and then left to settle for 30 minutes.

3.2.4.3 *Organic Matter Concentration*

For samples collected from the 5 and 20 cm depths from each site, organic matter concentration was determined using the mass-loss-due-to-ignition technique (Kalra and Maynard 1991). After cleaning a porcelain crucible by heating it at 375^{0}C for one hour, a 5 g, (less than 2 mm size) oven-dried sample was placed into the crucible and heated at 375^{0}C for 16 hours, the sample was allowed to cool to 150^{0}C, and then it was placed in a desiccator for 30 minutes. The difference in weight of the sample before and after ignition provided an estimate of organic matter weight.

3.2.4.4 *Total Nitrogen - Mineral Soil*

To determine the total N content of the mineral soil at the 5 and 20 cm depths, the Kjeldahl method was used (Kalra and Maynard 1991). Samples were sieved before analysis, and then a representative, 0.50 g sub-sample was placed in a digestion tube along with 1 g of digestion mix powder (composed of 100 g K_2SO_4 - $5H_20$ for every 1g of Se). For digestion to occur, the sample was heated on a digestion block for 1 1/$_2$ hours at 360 ^{O}C with 5 ml concentrated H_2SO_4. After a sample was removed from the digestion block, it was allowed to cool for one hour, then approximately 20 ml of distilled water was added to the sample, and the sample was shaken using a silicon stopper. The sample was then diluted to 100 ml with distilled water and total N concentration was measured using a LaChat Auto Analyzer.

3.2.4.5 *C/N Ratio*

Using the organic matter and total nitrogen concentration values, the C/N ratios for mineral soil samples from the 5 and 20 cm depths below the surface were determined. Organic carbon content values were calculated from the organic matter values determined by the mass-loss-due-to-ignition method; organic matter contains approximately 58% organic carbon.

3.2.5 *Statistical Design*

For each of the soil parameters, the data were analyzed as a split-plot design following the procedure outlined in section 2.2.5. The six paired plots constituted the whole plots and the paired plots were subdivided into gap and closed canopy sub-plots. Because of the small sample size and the exploratory nature of the study, a significance level of $p=0.10$ was used in testing for significant differences. Statistical power was not calculated because of the complex experimental design; however, the power of the statistical tests is likely to be low due to small sample size, small effect size, and the high within-plot sample variability (Toft and Shea 1983). In the figures, error bars represent one standard deviation from the mean. Regression analysis was performed to determine if the gap characteristics -- such as gap size and clone size -- were significantly related to soil properties.

3.3 Results

3.3.1 *Forest Floor Properties*

3.3.1.1 *Forest Floor Depths and Weights*

Depth and weight per unit area were calculated to give an indication of the relative amount of organic matter resting on the soil surface. The mean weight of the forest floor (LFH horizons) per unit area ranged from 0.17 to 0.42 g/cm^2. The LFH weights were lower (not significant) beneath the gap plots (0.29 g/cm^2) than beneath the closed canopy plots (0.39 g/cm^2) (Figure 3.1a). While the LFH depth in the plots in the study area ranged from 1.6 to 4.3 cm (Figure 3.1b), the depth of the forest floor was significantly lower in vine maple gaps (2.0 cm) than beneath the closed canopy (3.0 cm) ($p=0.10$, $F=4.12$, $df=1$). The greatest difference in depth was seen in the F horizon, which averaged 1.2 cm on gap plots and 2.0 cm on closed canopy plots.

The weight per unit surface area of LFH in vine maple gaps was not significantly related to either gap size or clone size. The depth of the LFH in vine maple gaps was strongly influenced by both canopy gap size ($p=0.02$, $r^2=0.80$, $n=6$) and clone size ($p=0.03$, $r^2=0.72$, $n=6$): the larger the gap (the larger the clone), the thicker the LFH (Figure 3.1c and 3.1d).

3.3.1.2 *Nutrient Concentrations in the Forest Floor*

Total nutrient concentrations of Ca ($p=0.03$, $F=8.36$, $df=1$), Mg ($p=0.002$, $F=34.38$, $df=1$), K ($p=0.08$, $F=4.94$, $df=1$), and Al ($p=0.09$, $F=4.56$, $df=1$) were found to

be significantly higher in the LFH beneath the gap than those beneath the closed canopy. Total N and Fe were higher (not significantly) in the gap than in the closed canopy, while the P and Zn concentrations were approximately the same (Figures 3.2 and 3.3).

Linear regression was performed to determine if nutrient concentrations in the LFH of vine maple gaps were related to the weight of the LFH, clone size and thickness of the LFH horizons. Results showed that: the greater the weight per unit surface area of LFH, the lower the concentration of Mg ($p=0.03$, $r^2=0.74$, $n=6$), Mn ($p=0.04$, $r^2=0.69$, $n=6$), and Al ($p=0.01$, $r^2=0.83$, $n=6$); the larger the clone size, the lower the concentration of P ($p=0.06$, $r^2=0.64$, $n=6$) and K ($p=0.04$ $r^2=0.70$, $n=6$), and the higher the concentration of Ca ($p=0.000$, $r^2=0.98$, $n=6$); the greater the depth of the LFH, the lower the concentration of P ($p=0.01$, $r^2=0.82$, $n=6$) and K ($p=0.03$, $r^2=0.74$, $n=6$), and the higher the concentration of Ca ($p=0.02$, $r^2=0.77$, $n=6$) (Figures 3.4 and 3.5).

The weight of the forest floor in combination with nutrient concentrations can give an indication of the total amount of nutrients stored within the forest floor. The mean total amounts of N, P, Mg, K, Fe, and Al stored in the LFH were lower (not significantly) beneath the gap plots than beneath the closed canopy plots: and the total amounts of Ca and Mn were higher (not significantly) beneath the gap than beneath the closed canopy plots (Figures 3.6 to 3.7). The total amounts of each nutrient stored in the LFH were not significantly influenced by the size of the vine maple clone, gap size, or the depth of the LFH horizons.

Table 3.1

Nutrient concentrations in the forest floor (LFH horizons), measured in g/kg, for gap and closed canopy plots. The individual plot means and standard deviations consist of three samples per plot. The overall means and standard deviations for the gap and closed canopy were calculated from the means of the individual plots.

Plot	N	P	Ca	Mg	K	Fe	Mn	Zn	Al
1g	20.09 ± 2.81	0.68 ± 0.36	1.19 ± 0.52	0.49 ± 0.08	1.43 ± 0.08	3.88 ± 2.14	0.30 ± 0.06	0.06 ± 0.02	3.71 ± 2.30
1c	23.09 ± 1.35	0.63 ± 0.17	1.68 ± 0.17	0.39 ± 0.05	0.91 ± 0.15	2.09 ± 0.23	0.25 ± 0.02	0.07 ± 0.01	2.43 ± 0.30
2g	24.80 ± 1.52	0.64 ± 0.03	2.29 ± 0.17	0.41 ± 0.07	1.08 ± 0.19	1.43 ± 0.26	0.17 ± 0.08	0.06 ± 0.01	1.61 ± 0.26
2c	17.42 ± 3.83	0.64 ± 0.17	1.01 ± 0.37	0.26 ± 0.06	0.63 ± 0.11	1.49 ± 0.09	0.09 ± 0.04	0.06 ± 0.01	1.62 ± 0.09
3g	21.17 ± 6.18	0.75 ± 0.26	2.20 ± 1.24	0.72 ± 0.32	1.16 ± 0.14	6.56 ± 5.75	0.59 ± 0.06	0.08 ± 0.00	4.73 ± 3.16
3c	21.05 ± 2.01	0.75 ± 0.08	2.05 ± 1.00	0.56 ± 0.06	0.92 ± 0.13	3.65 ± 2.05	0.34 ± 0.26	0.08 ± 0.01	3.13 ± 1.17
4g	23.14 ± 0.77	0.65 ± 0.16	2.21 ± 0.33	0.47 ± 0.11	1.01 ± 0.05	1.75 ± 0.18	0.25 ± 0.11	0.07 ± 0.01	1.89 ± 0.17
4c	20.79 ± 0.16	0.43 ± 0.14	0.91 ± 0.02	0.35 ± 0.07	0.90 ± 0.11	1.50 ± 0.40	0.08 ± 0.01	0.07 ± 0.02	1.85 ± 0.42
5g	23.89 ± 3.55	0.67 ± 0.31	2.84 ± 1.22	0.58 ± 0.12	1.01 ± 0.10	2.94 ± 1.12	0.76 ± 0.28	0.09 ± 0.00	3.70 ± 2.47
5c	22.95 ± 1.77	0.85 ± 0.33	1.12 ± 0.86	0.52 ± 0.15	0.80 ± 0.05	3.07 ± 1.44	0.57 ± 0.54	0.07 ± 0.01	2.83 ± 0.91
6g	17.91 ± 2.05	0.53 ± 0.24	4.51 ± 3.61	0.71 ± 0.04	0.83 ± 0.24	2.74 ± 0.61	0.77 ± 0.07	0.06 ± 0.00	3.65 ± 0.83
6c	21.02 ± 1.25	0.72 ± 0.25	0.79 ± 0.65	0.44 ± 0.05	1.00 ± 0.12	3.21 ± 1.01	0.17 ± 0.02	0.07 ± 0.00	3.70 ± 1.39
Gap	21.84 ± 2.60	0.65 ± 0.07	2.51 ± 1.12	0.56 ± 0.13	1.08 ± 0.20	3.02 ± 1.86	0.47 ± 0.29	0.07 ± 0.01	3.12 ± 1.21
CC	21.05 ± 2.05	0.66 ± 0.15	1.26 ± 0.50	0.42 ± 0.11	0.86 ± 0.13	2.50 ± 0.93	0.25 ± 0.18	0.07 ± 0.01	2.59 ± 0.79

Table 3.2

Total nutrient amounts in the forest floor (LFH horizons), measured in kg/m^2, for gap and closed canopy plots. The individual plot means and standard deviations consist of three samples per plot. The overall means and standard deviations for the gap and closed canopy were calculated from the means of the individual plots.

Plot	N	P	Ca	Mg	K	Fe	Mn	Zn	Al
1g	5.20 ± 1.22	0.18 ± 0.11	0.31 ± 0.17	0.13 ± 0.02	0.37 ± 0.06	0.96 ±0.43	0.08 ± 0.02	0.02 ± 0.01	0.91 ± 0.46
1c	8.84 ± 1.30	0.25 ± 0.09	0.65 ± 0.17	0.15 ± 0.02	0.34 ± 0.03	0.79 ±0.06	0.10 ± 0.01	0.03 ± 0.01	0.92 ± 0.06
2g	12.89 ± 6.74	0.34 ± 0.22	1.25 ± 0.83	0.23 ± 0.17	0.58 ± 0.37	0.71 ±0.27	0.10 ± 0.11	0.03 ± 0.01	0.80 ± 0.32
2c	6.74 ± 1.31	0.23 ± 0.03	0.38 ± 0.09	0.10 ± 0.02	0.25 ± 0.06	0.61 ±0.22	0.04 ± 0.02	0.02 ± 0.01	0.65 ± 0.20
3g	4.31 ± 3.50	0.15 ± 0.14	0.44 ± 0.38	0.10 ± 0.06	0.14 ± 0.15	0.41 ±0.22	0.09 ± 0.10	0.01 ± 0.01	0.36 ± 0.28
3c	7.45 ± 5.21	0.28 ± 0.21	0.67 ± 0.52	0.20 ± 0.13	0.34 ± 0.22	1.23 ±0.84	0.08 ± 0.01	0.03 ± 0.02	1.08 ± 0.65
4g	8.64 ± 0.89	0.24 ± 0.05	0.83 ± 0.51	0.18 ± 0.05	0.29 ± 0.05	0.66 ±0.11	0.09 ± 0.04	0.02 ± 0.00	0.71 ± 0.11
4c	8.48 ± 0.88	0.17 ± 0.06	0.37 ± 0.05	0.14 ± 0.04	0.37 ± 0.09	0.63 ±0.23	0.03 ± 0.00	0.03 ± 0.01	0.77 ± 0.25
5g	5.19 ± 1.97	0.15 ± 0.11	0.65 ± 0.44	0.12 ± 0.03	0.21 ± 0.04	0.59 ±0.17	0.15 ± 0.02	0.02 ± 0.01	0.71 ± 0.29
5c	7.78 ± 2.35	0.27 ± 0.00	0.38 ± 0.35	0.17 ± 0.05	0.27 ± 0.08	0.95 ±0.18	0.22 ± 0.25	0.02 ± 0.01	0.90 ± 0.14
6g	3.14 ± 1.03	0.10 ± 0.06	0.75 ± 0.61	0.12 ± 0.03	0.15 ± 0.08	0.47 ±0.16	0.13 ± 0.03	0.01 ± 0.00	0.62 ± 0.18
6c	8.82 ± 2.36	0.31 ± 0.15	0.34 ± 0.33	0.18 ± 0.05	0.41 ± 0.09	1.31 ± 0.45	0.07 ± 0.01	0.03 ± 0.01	1.54 ± 0.74
Gap	6.56 ± 3.60	0.19 ± 0.09	0.71 ± 0.32	0.15 ± 0.05	0.31 ± 0.17	0.65 ± 0.20	0.11 ± 0.03	0.02 ± 0.01	0.71 ± 0.19
CC	8.02 ± 0.84	0.25 ± 0.05	0.46 ± 0.15	0.16 ± 0.04	0.33 ± 0.06	0.92 ± 0.30	0.09 ± 0.07	0.03 ± 0.00	0.98 ± 0.31

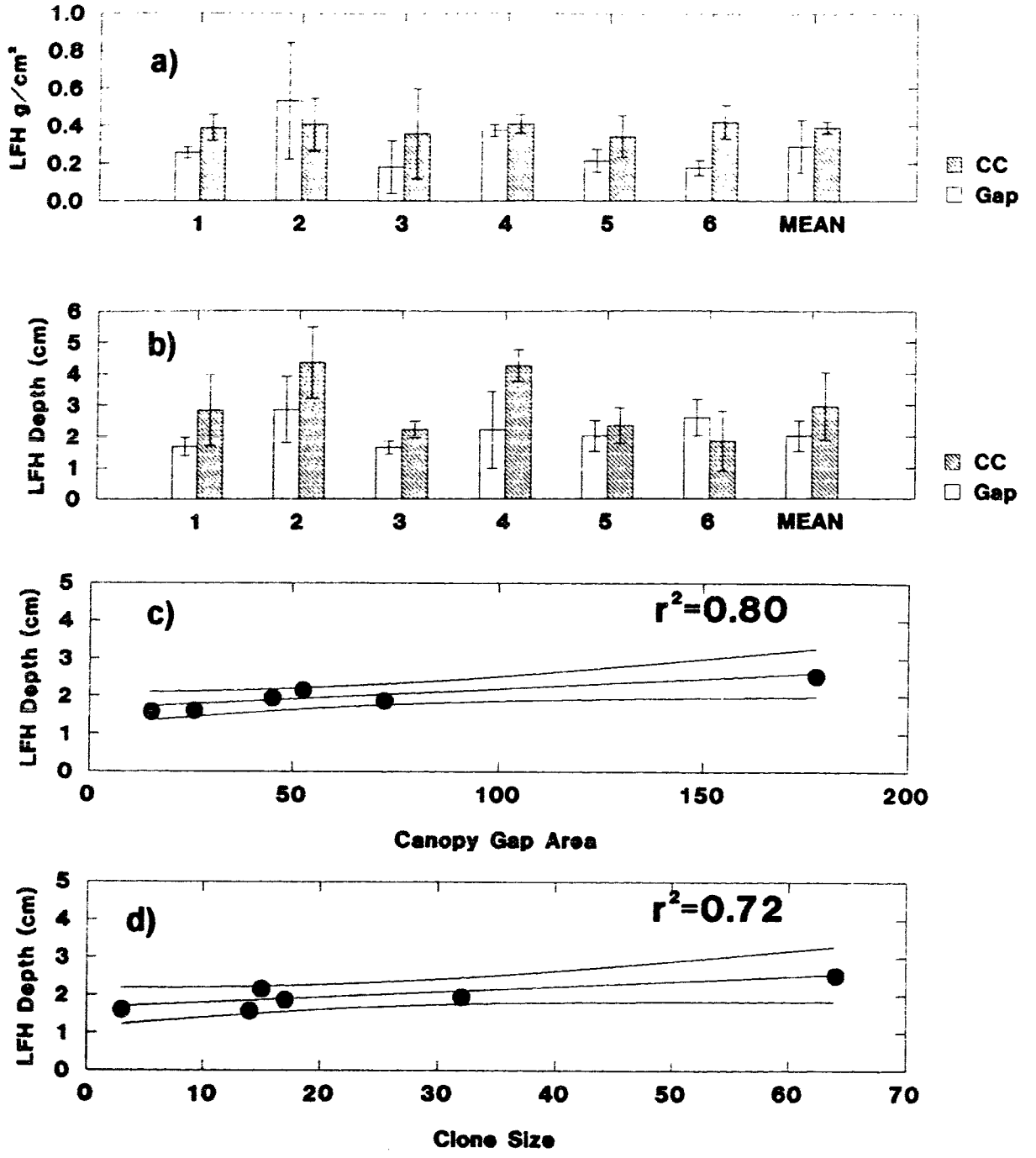

Figure 3.1 a) Weight of LFH per unit area measured in g/cm^2. b) Depth of LFH in gap and closed canopy plots measured in cm. c) A regression of gap size to depth of LFH. d) A regression of depth of LFH to the number of stems on the vine maple clone in gap plots.

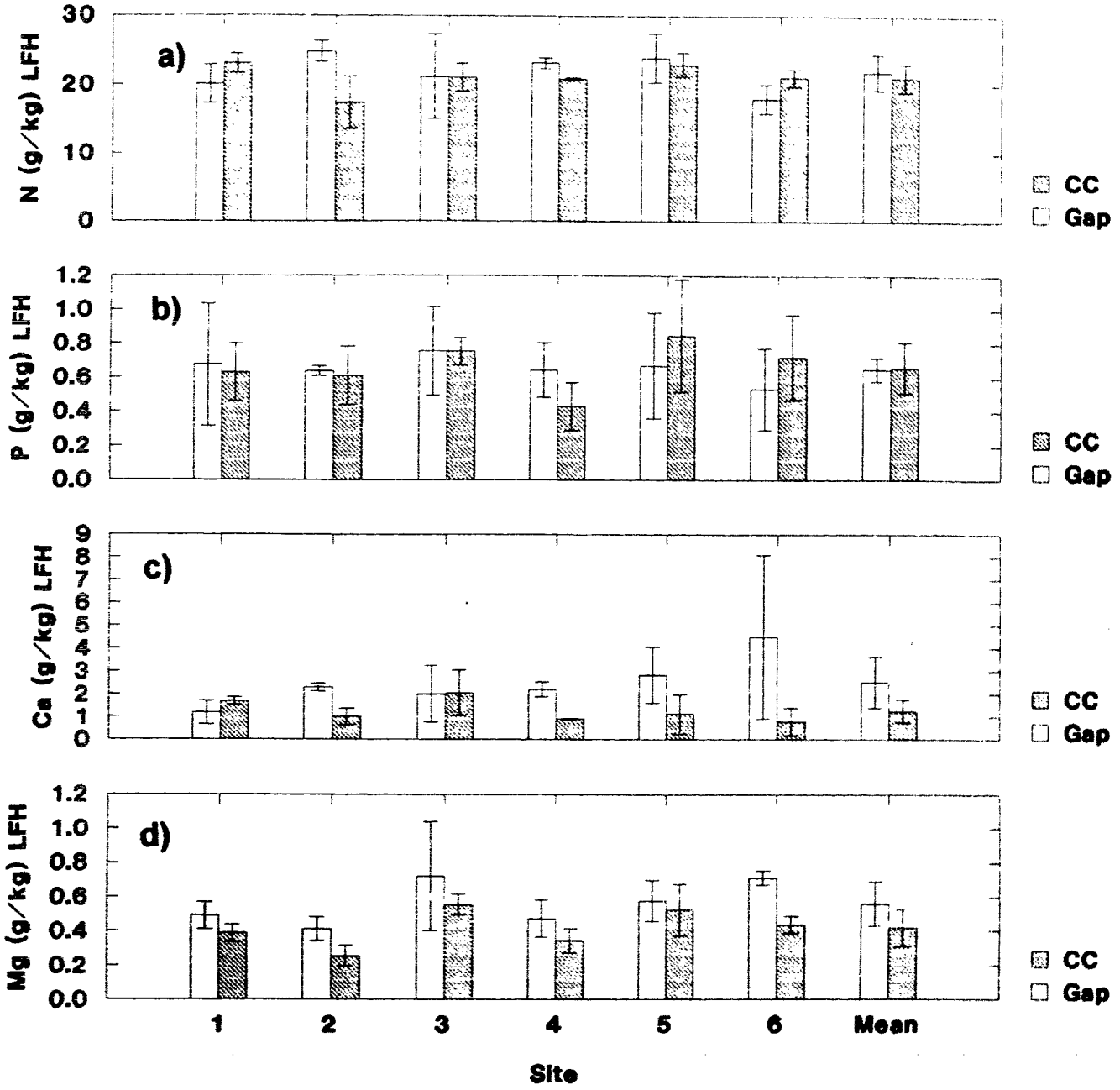

Figure 3.2 a) N, b) P, c) Ca and d) Mg concentrations in the LFH, measured in g/kg.

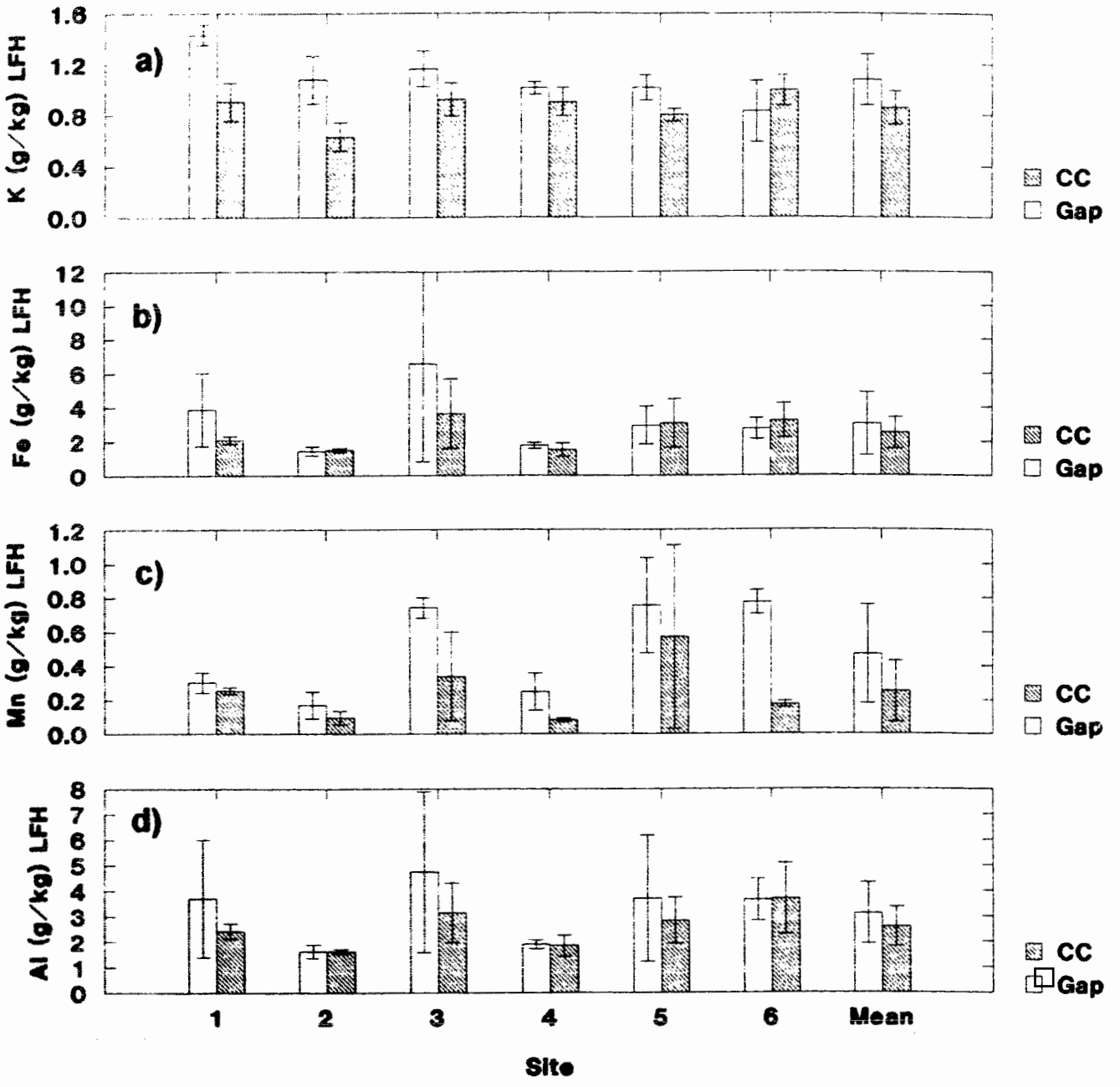

Figure 3.3 a) K, b) Fe, c) Mn and d) Al concentrations in the LFH, measured in g/kg.

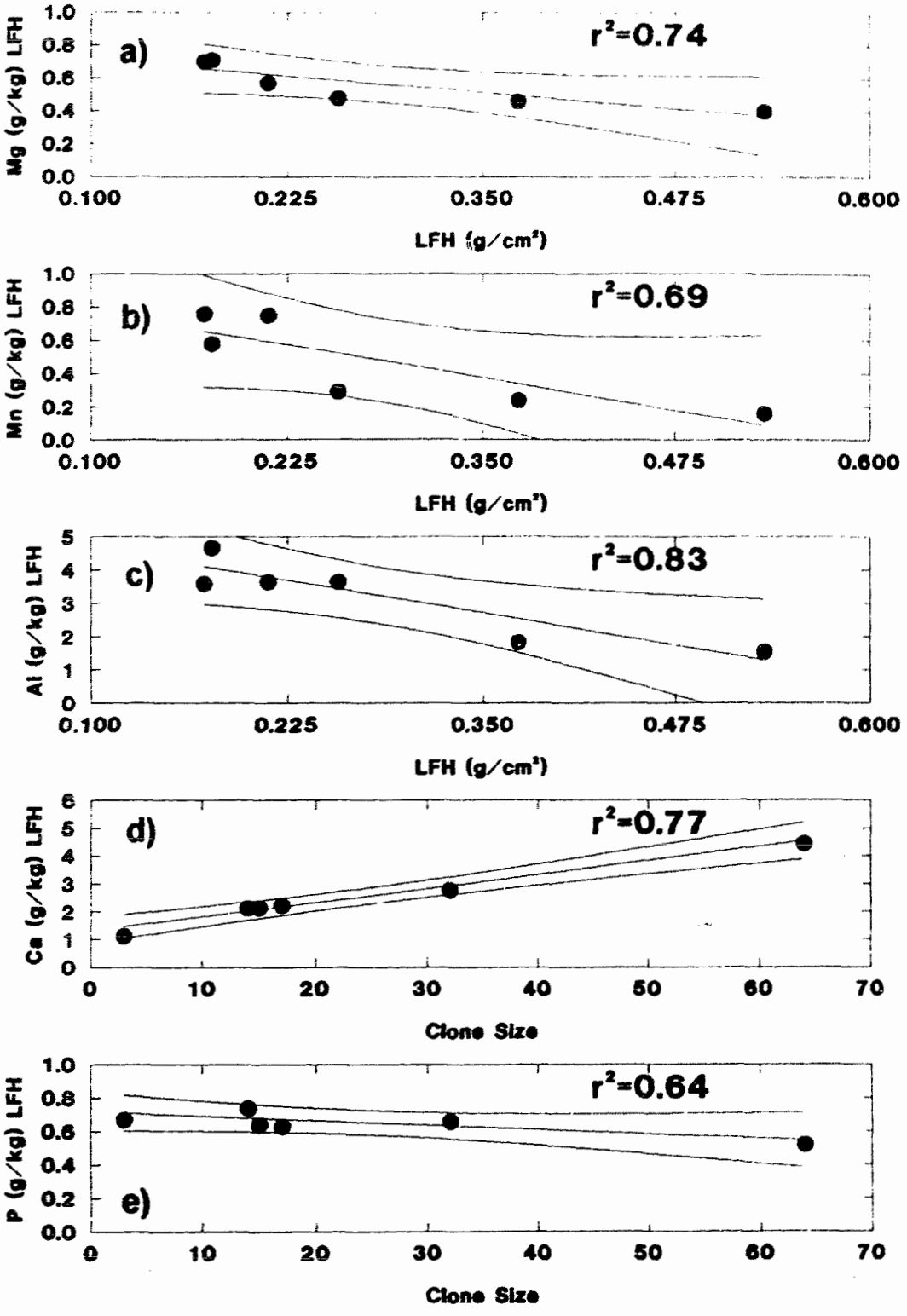

Figure 3.4 A regression of weight of LFH per unit surface area to a) Mg, b) Mn and c) Al concentrations in the LFH. A regression of clone size to d) Ca and e) P concentrations in the LFH.

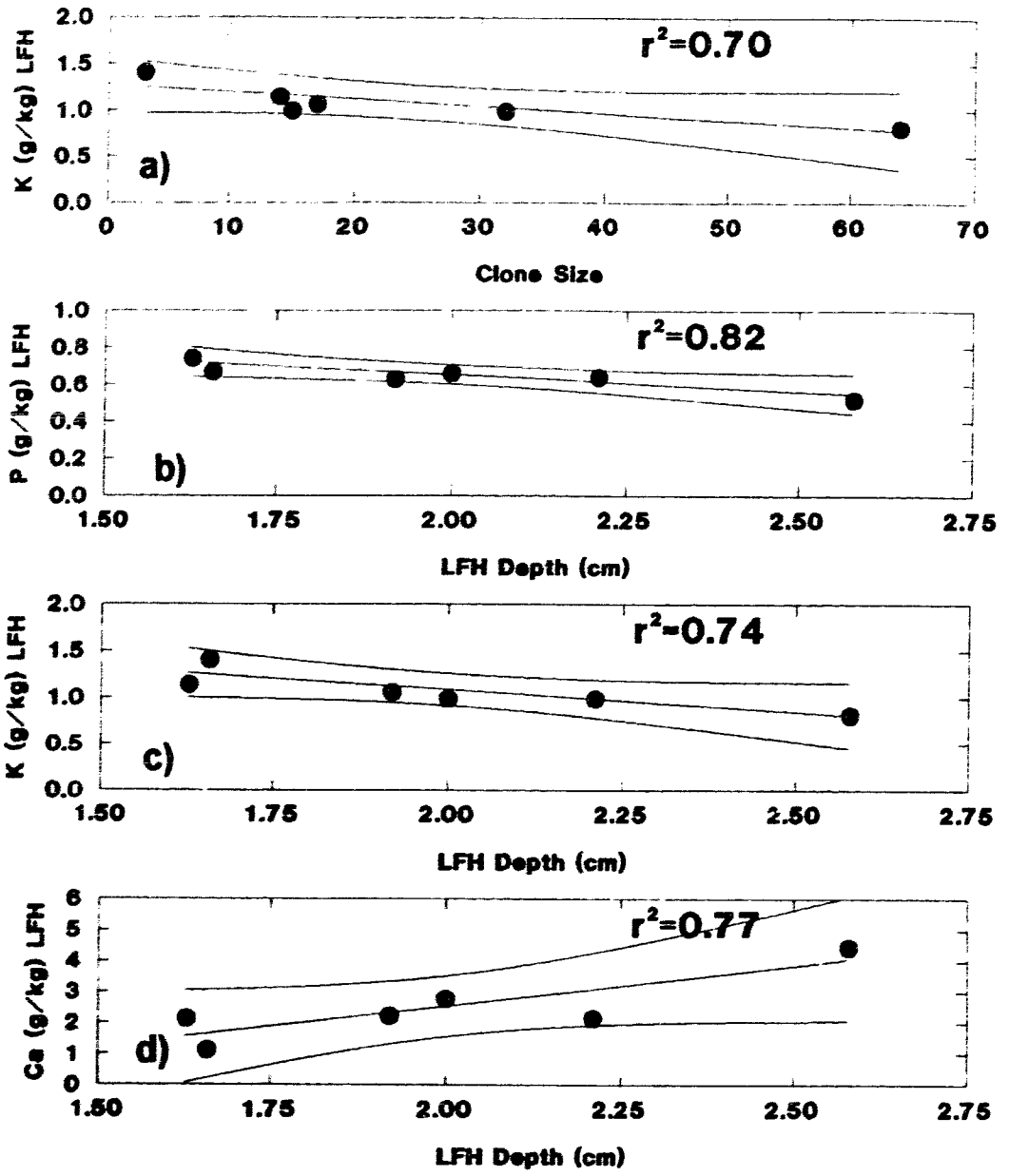

Figure 3.5 a) A regression of clone size to K concentration in the LFH. A regression of the depth of the LFH horizon to b) P, c) K, and d) Ca concentrations in the LFH.

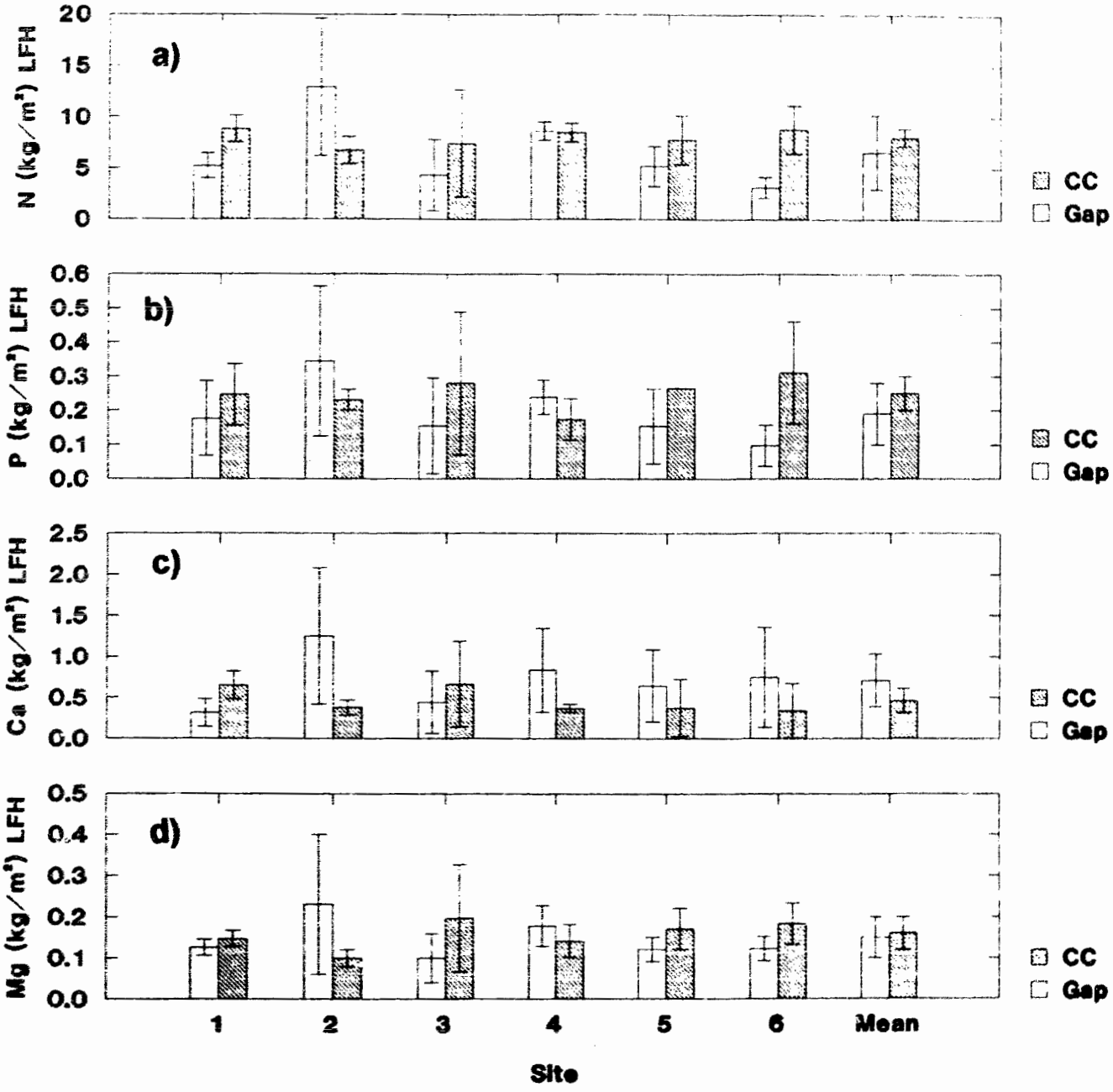

Figure 3.6 Total amount of a) N, b) P, c) Ca and d) Mg stored in the LFH horizons, measured in kg/m^2.

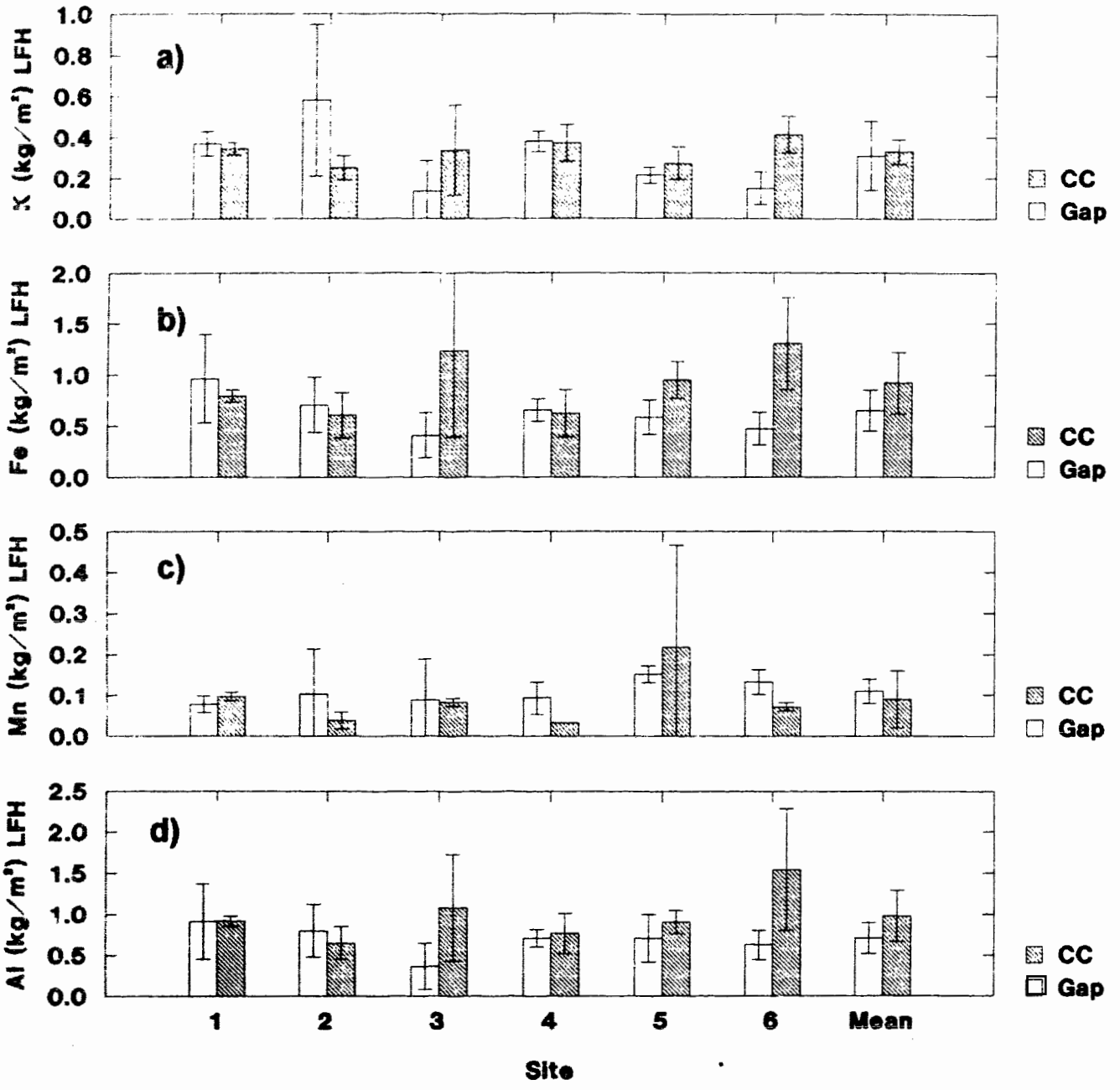

Figure 3.7 Total amount of a) K, b) Fe, c) Mn and d) Al stored in the LFH horizons, measured in kg/m^2.

3.3.2 *Physical Soil Properties*

3.3.2.1 *Gravel Content*

The mean gravel content in the study area ranged from 10 to 40%. Gravel content was not significantly different between gap and closed canopy plots at the 5, 50 and 100 cm depths in the soil profile; however, mean gravel content was 4% lower in the gap plots than in the closed canopy plots at 20 cm ($p=0.06$, $F=5.63$, $df=1$) (Figures 3.8a to 3.8d). Linear regression demonstrated that gravel content of the upper mineral soil was not significantly related to the size of the vine maple clone. Gravel content was not significantly related to soil moisture values at any depth in the profile in either the summer or winter.

3.3.2.2 *Particle Size Distribution*

Almost all of the samples collected within the study area were within the loamy sand textural class. Compared to the closed canopy plots, the mean percentage by weight of the sand content was found to be 1-3% higher (not significantly) in the gap plots, silt content was 0.5-2% lower (not significantly) in gap plots, and clay content was 0.5% lower (not significantly) in the gap plots. Linear regression showed that the greater the clay content at 20 cm, the larger the vine maple clone ($p=0.03$, $r^2= 0.75$, $n=6$) (Figure 3.9a); and the greater the sand content at 50 cm, the larger the vine maple clone ($p=0.04$, $r^2= 0.69$, $n=6$) (Figure 3.9b).

Table 3.3

Means and standard deviations of physical soil properties for the paired plots. The individual plot means and standard deviations consist of three or four samples per plot (refer to section 3.2). The overall means and standard deviations for the gap and closed canopy were calculated from the means of the individual plots.

Plot	Gravel 5 cm (%)	Gravel 20 cm (%)	Gravel 50 cm (%)	Gravel 100 cm (%)	Sand 20 cm (%)	Clay 20 cm (%)	Sand 50 cm (%)	Clay 50 cm (%)	Sand 100 cm (%)	Clay 100 cm (%)	Bulk Density 5 cm (g/cm^3)	LFH g/cm^2 surface area	LFH Depth (cm)
1g	20.2 ± 9.5	33.6 ± 11.1	25.2 ± 4.8	35.1 ± 18.9	80.4 ± 5.0	1.3 ± 0.5	75.9 ± 4.2	2.0 ± 1.6	77.9 ± 4.0	1.6 ± 1.1	0.59 ± 0.06	0.26 ± 0.03	1.7 ± 0.3
1c	30.2 ± 15.7	38.6 ± 23.6	34.2 ± 10.1	35.4 ± 8.4	79.0 ± 5.4	1.0 ± 0.6	73.9 ± 5.9	1.8 ± 2.4	72.3 ± 3.6	1.9 ± 1.7	0.49 ± 0.26	0.39 ± 0.07	2.8 ± 1.1
2g	15.5 ± 2.2	24.0 ± 14.6	18.9 ± 2.6	26.6 ± 9.1	84.7 ± 2.6	1.3 ± 0.0	78.6 ± 2.9	1.2 ± 1.1	75.7 ± 4.2	1.2 ± 0.4	0.57 ± 0.13	0.53 ± 0.31	1.9 ± 1.1
2c	16.5 ± 4.9	28.6 ± 10.0	43.0 ± 13.4	32.0 ± 17.7	88.4 ± 1.5	0.7 ± 0.1	76.3 ± 8.0	1.9 ± 2.0	79.4 ± 8.6	2.4 ± 0.7	0.69 ± 0.07	0.41 ± 0.14	3.3 ± 1.1
3g	23.0 ± 18.1	15.2 ± 8.3	29.4 ± 6.6	27.9 ± 6.5	75.5 ± 2.2	1.0 ± 0.4	73.4 ± 4.2	2.0 ± 1.1	73.9 ± 1.1	1.7 ± 0.8	0.57 ± 0.09	0.18 ± 0.14	1.6 ± 0.2
3c	17.1 ± 1.9	18.4 ± 11.9	15.2 ± 3.4	15.7 ± 5.4	74.8 ± 7.9	2.1 ± 0.6	75.7 ± 2.7	1.7 ± 2.0	79.7 ± 4.2	1.4 ± 0.8	0.56 ± 0.20	0.36 ± 0.24	2.2 ± 0.3
4g	13.5 ± 15.5	17.8 ± 6.5	20.2 ± 7.1	27.4 ± 6.5	74.5 ± 4.2	1.6 ± 0.4	73.5 ± 2.0	1.1 ± 1.3	70.0 ± 4.2	1.2 ± 0.9	0.55 ± 0.16	0.37 ± 0.03	2.2 ± 1.2
4c	11.2 ± 2.7	15.2 ± 2.2	19.9 ± 2.0	16.9 ± 7.1	73.8 ± 2.0	2.2 ± 0.5	75.2 ± 3.0	1.7 ± 1.6	76.2 ± 5.1	1.6 ± 1.0	0.50 ± 0.21	0.41 ± 0.05	4.3 ± 0.5
5g	18.7 ± 2.8	22.7 ± 3.3	22.7 ± 3.0	26.6 ± 5.6	78.1 ± 1.3	1.3 ± 0.7	78.9 ± 2.7	1.2 ± 1.8	77.4 ± 1.7	1.6 ± 0.7	0.64 ± 0.13	0.21 ± 0.06	2.0 ± 0.5
5c	20.6 ± 4.8	24.3 ± 5.1	37.4 ± 5.3	31.4 ± 7.1	76.4 ± 4.1	2.0 ± 0.3	77.2 ± 3.0	2.1 ± 1.8	76.0 ± 3.9	1.6 ± 0.8	0.70 ± 0.09	0.34 ± 0.11	2.3 ± 0.6
6g	14.7 ± 14.7	10.1 ± 7.3	21.1 ± 5.0	33.0 ± 6.5	75.2 ± 4.1	3.0 ± 0.3	82.9 ± 2.9	1.5 ± 1.5	81.3 ± 3.2	1.6 ± 0.6	0.46 ± 0.27	0.17 ± 0.04	2.6 ± 0.6
6c	21.6 ± 4.6	20.7 ± 4.6	23.4 ± 4.6	24.5 ± 6.6	70.0 ± 3.2	4.1 ± 1.1	69.9 ± 6.3	2.8 ± 0.6	68.9 ± 7.6	2.3 ± 1.6	0.59 ± 0.43	0.42 ± 0.09	1.8 ± 1.0
Gap	19.3 ± 3.7	20.4 ± 8.2	22.9 ± 3.9	29.4 ± 3.7	78.1 ± 3.9	1.6 ± 0.7	77.3 ± 3.7	1.5 ± 0.4	76.0 ± 3.8	1.5 ± 0.2	0.56 ± 0.06	0.29 ± 0.14	2.0 ± 0.5
CC	19.5 ± 6.4	24.3 ± 8.4	28.1 ± 9.8	25.3 ± 9.4	77.1 ± 6.3	2.0 ± 1.2	74.7 ± 1.7	2.1 ± 0.3	73.1 ± 7.3	2.0 ± 0.6	0.59 ± 0.09	0.39 ± 0.03	3.0 ± 1.1

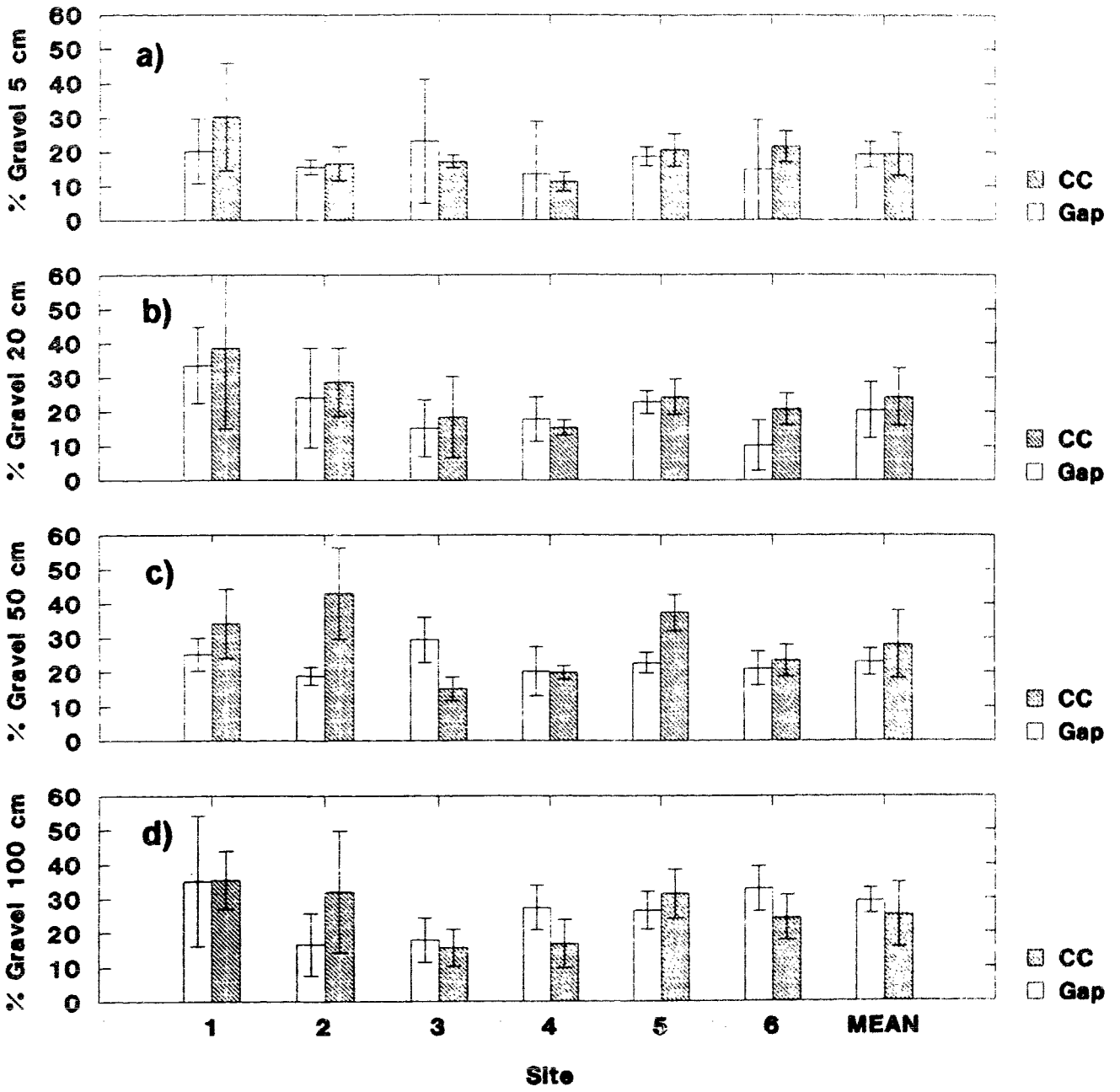

Figure 3.8 Gravel content (%) at a) 5 cm, b) 20 cm, c) 50 cm and d) 100 cm depths in the soil profile.

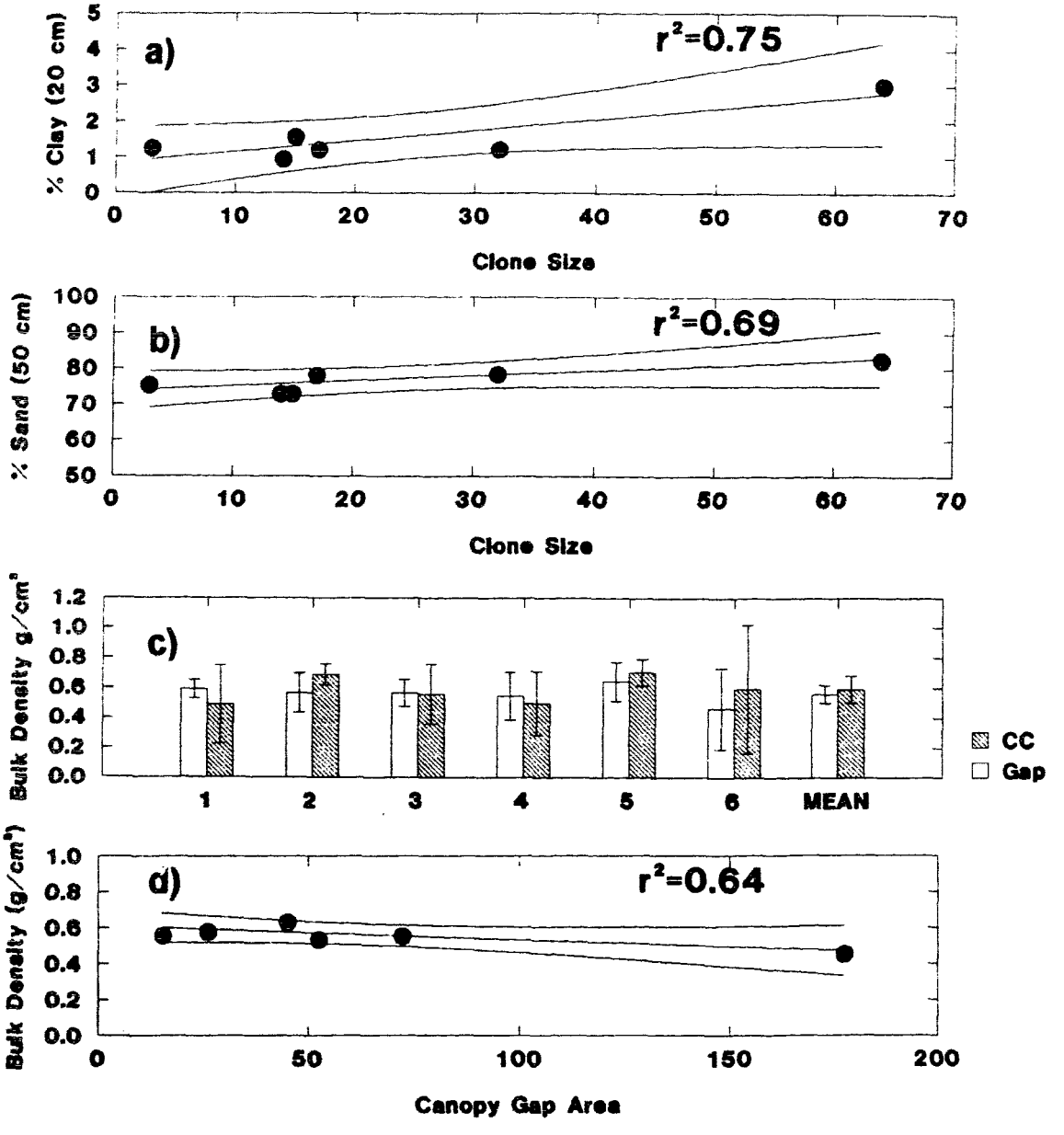

Figure 3.9 A regression of the number of stems on the vine maple clone to a) clay content at 20 cm depth in the soil profile and b) sand content at 50 cm depth in the soil profile. c) Bulk density at 5 cm depth in the mineral soil, measured in g/cm^3. d) A regression of bulk density of the surface mineral soil to canopy gap size.

3.3.2.3 *Bulk Density*

Surface soil bulk density (Db) values throughout the study area were quite low, ranging from 0.46 to 0.69 g/cm^3 (Figure 3.9c); however, mean bulk density values were slightly lower (not significantly) in the gap (Db=0.56 g/cm^3) compared to the closed canopy (Db=0.59 g/cm^3) at 5 cm depth in the soil profile. Linear regression demonstrated a relationship between bulk density and canopy gap size (the larger the canopy gap, the lower the bulk density) ($p=0.06$, $r^2=0.64$, $n=6$) (Figure 3.9d); however, bulk density was not related to the size of the vine maple clone.

3.3.3 *Chemical Soil Properties*

3.3.3.1 *pH*

The mean pH levels of the LFH in the study area ranged from 3.1 to 4.8 (Figures 3.10 to 3.11a), and from 3.8 to 4.6 in the mineral soil. The pH levels of the forest floor (LFH horizons) was significantly higher in vine maple gap plots than in closed canopy plots where the mean pH level of the forest floor in gap and closed canopy plots was 4.05 and 3.43 respectively ($p=0.02$, $F=10.60$, $df=1$); however, the pH levels of the mineral soil at 5, 20, 50 and 100 cm depths were higher (not significant) beneath vine maple gap plots than beneath the closed canopy Linear regression demonstrated that the pH levels of both the mineral soil and the LFH in vine maple gaps were not significantly related to canopy gap size or the size of the vine maple clone.

3.3.3.2 *Organic Matter Concentration*

The range in organic matter concentration of the surface mineral soil (0-30 cm) in the study area was from 10 to 20%. At the 5 and 20 cm depths, the organic matter concentrations were nearly identical beneath vine maple gaps compared to that beneath the closed canopy (Figures 3.11b and 3.11c). Linear regression demonstrated no significant relationships between the organic matter concentrations at 5 and 20 cm depths in the soil profile, and either gap size or clone size.

3.3.3.3 *Total Nitrogen - Mineral Soil*

The mean concentration of total N in the upper layers of mineral soil throughout the twelve research plots ranged from 2.1 to 5.0 g/kg. Although mean total N concentration was found to be 0.7 g/kg higher in the gap at 5 cm depth, total N concentrations at 5 and 20 cm depths in the soil profile were not significantly different in soils beneath vine maple gaps compared to those in soils beneath the closed canopy (Figure 3.12a and 3.12b). Significant relationships, however, were revealed at the 20 cm level between the total N content and the number of stems on the vine maple clone (the greater the number of stems, the greater the N content) ($p=0.08$, $r^2=0.59$, $n=6$); and between the total N content at the 20 cm level and the weight per unit surface area of LFH (the lower the weight per unit surface area of LFH, the higher the N content) ($p=0.09$, $r^2=0.57$, $n=6$) (Figure 3.13a and 3.13b).

Table 3.4

Means and standard deviations of chemical soil properties for the paired plots. The individual plot means and standard deviations consist of three or four samples per plot (refer to section 3.2). The overall means and standard deviations for the gap and closed canopy were calculated from the means of the individual plots.

Plot	pH LFH	pH 5 cm	pH 20 cm	pH 50 cm	pH 100 cm	Organic Matter 5 cm (g/kg)	Organic Matter 20 cm (g/kg)	Total N 5 cm (g/kg)	Total N 20 cm (g/kg)	C/N Ratio 5 cm	C/N Ratio 20 cm
1g	4.02 ± 0.8	4.29 ± 0.1	4.62 ± 0.1	4.65 ± 0.2	4.14 ± 0.1	179.9 ± 41.6	123.6 ± 13.4	4.3 ± 1.9	2.9 ± 0.7	26.1 ± 5.6	25.2 ± 3.2
1c	3.39 ± 0.0	4.06 ± 0.1	4.31 ± 0.4	4.65 ± 0.1	4.08 ± 0.2	207.4 ± 62.9	213.1 ± 145.2	4.3 ± 1.9	4.4 ± 3.2	30.0 ± 4.3	29.0 ± 2.7
2g	3.47 ± 0.4	4.00 ± 0.4	4.57 ± 0.2	4.44 ± 0.3	3.76 ± 0.0	188.4 ± 28.8	130.1 ± 25.5	5.0 ± 1.4	2.7 ± 0.9	21.7 ± 2.8	29.2 ± 4.7
2c	3.15 ± 0.2	3.47 ± 0.2	4.50 ± 0.1	4.26 ± 0.4	3.86 ± 0.6	169.7 ± 51.7	144.8 ± 37.3	4.1 ± 1.3	2.4 ± 0.6	24.0 ± 1.1	34.4 ± 1.4
3g	4.34 ± 0.2	4.31 ± 0.3	4.51 ± 0.1	4.58 ± 0.2	3.85 ± 0.4	140.9 ± 48.3	134.0 ± 25.5	3.1 ± 0.9	3.2 ± 0.5	26.3 ± 3.7	24.8 ± 4.3
3c	3.76 ± 0.3	4.10 ± 0.2	4.17 ± 0.6	4.37 ± 0.4	4.03 ± 0.2	136.0 ± 86.1	201.6 ± 155.5	3.0 ± 1.3	4.2 ± 2.7	24.4 ± 6.2	27.2 ± 4.7
4g	3.91 ± 0.1	3.87 ± 0.2	4.17 ± 0.1	4.53 ± 0.1	4.00 ± 0.3	198.3 ± 61.2	180.0 ± 61.5	4.3 ± 1.3	3.2 ± 1.3	26.4 ± 3.3	33.1 ± 1.9
4c	3.12 ± 0.3	4.04 ± 0.1	4.50 ± 0.1	4.18 ± 0.3	3.84 ± 0.3	200.0 ± 7.6	142.5 ± 13.7	4.3 ± 0.1	2.7 ± 0.3	27.1 ± 0.7	30.7 ± 2.6
5g	3.83 ± 0.3	4.15 ± 0.6	4.49 ± 0.2	4.49 ± 0.3	3.91 ± 0.3	126.7 ± 29.2	150.0 ± 9.4	4.0 ± 0.7	3.2 ± 0.8	25.0 ± 0.8	27.9 ± 5.0
5c	3.82 ± 0.5	4.19 ± 0.4	4.61 ± 0.1	4.60 ± 0.1	4.05 ± 0.1	134.4 ± 7.5	117.4 ± 12.7	2.6 ± 0.8	2.1 ± 0.2	30.5 ± 7.6	32.5 ± 1.0
6g	4.76 ± 0.2	4.73 ± 0.0	4.88 ± 0.1	4.69 ± 0.2	4.19 ± 0.0	179.0 ± 96.0	157.4 ± 17.3	5.2 ± 2.9	3.4 ± 0.6	19.9 ± 0.2	27.7 ± 8.9
6c	3.37 ± 0.0	4.24 ± 0.9	4.37 ± 0.7	3.49 ± 0.8	3.21 ± 1.1	147.4 ± 2.4	102.7 ± 42.7	2.7 ± 1.1	2.5 ± 0.7	34.3 ± 11.5	23.7 ± 8.8
Gap	4.05 ± 0.4	4.23 ± 0.3	4.58 ± 0.2	4.56 ± 0.1	4.01 ± 0.2	168.9 ± 28.4	145.8 ± 21.0	4.2 ± 1.0	3.1 ± 0.3	24.2 ± 2.8	28.0 ± 3.0
CC	3.43 ± 0.3	4.02 ± 0.3	4.41 ± 0.2	4.33 ± 0.5	3.86 ± 0.4	165.8 ± 32.0	153.7 ± 44.6	3.5 ± 0.8	3.0 ± 1.0	28.3 ± 4.0	29.6 ± 3.9

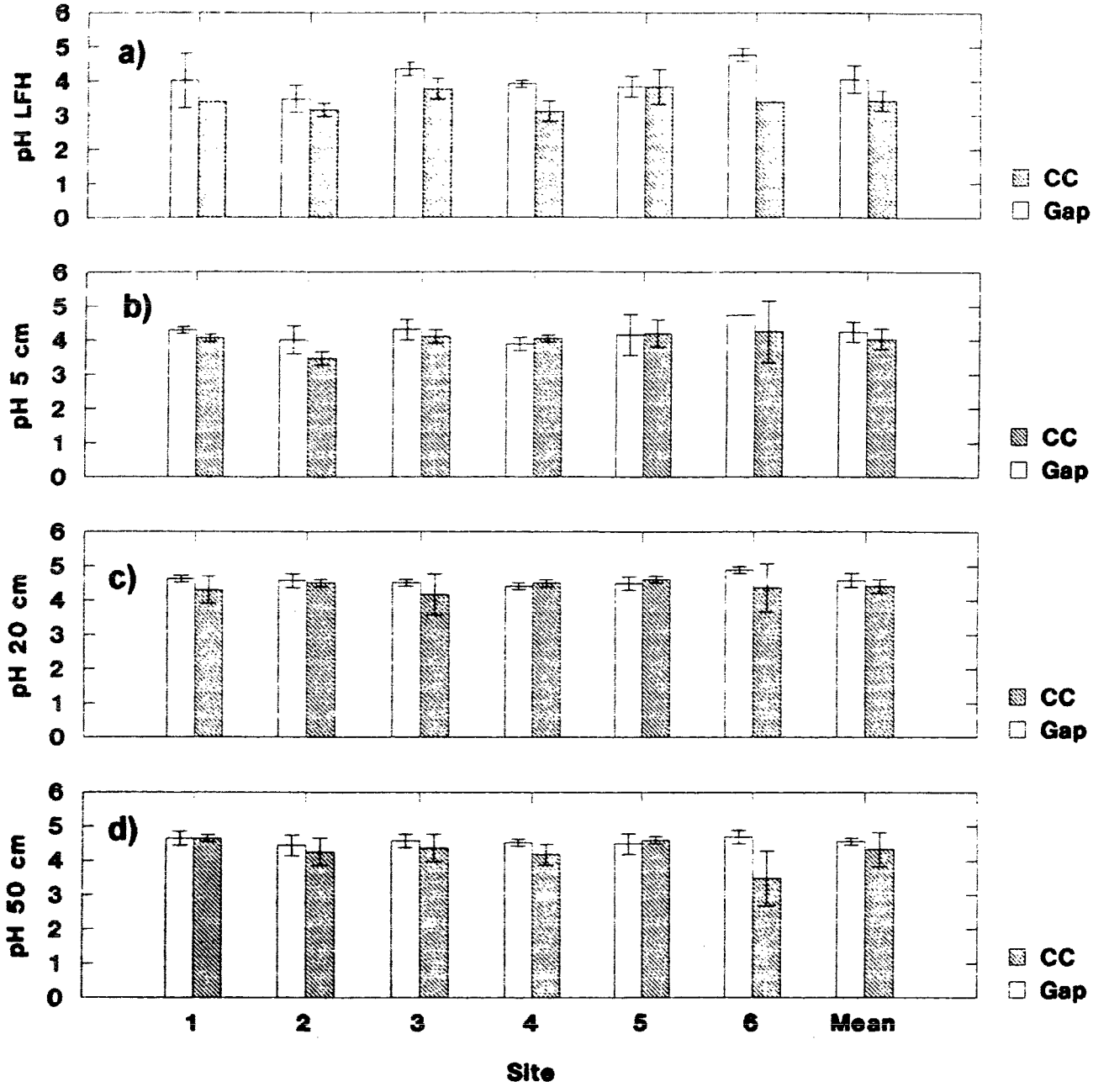

Figure 3.10 pH of the a) LFH layer, b) 5 cm, c) 20 cm and d) 50 cm depth in the soil profile.

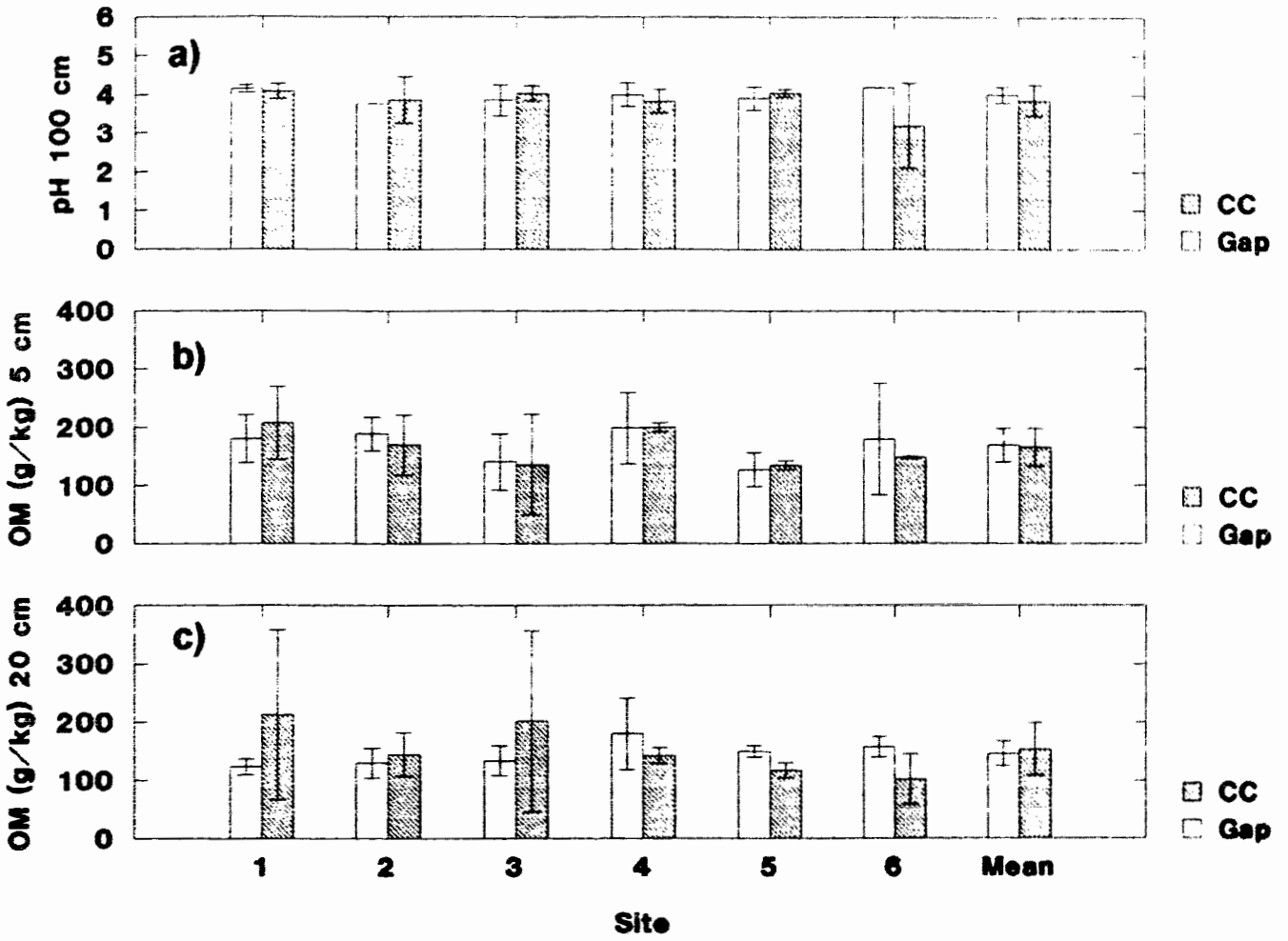

Figure 3.11 a) pH at 100 cm depth in the soil profile. Organic matter concentration at b) 5 cm and c) 20 cm depth in the soil profile, measured in g/kg.

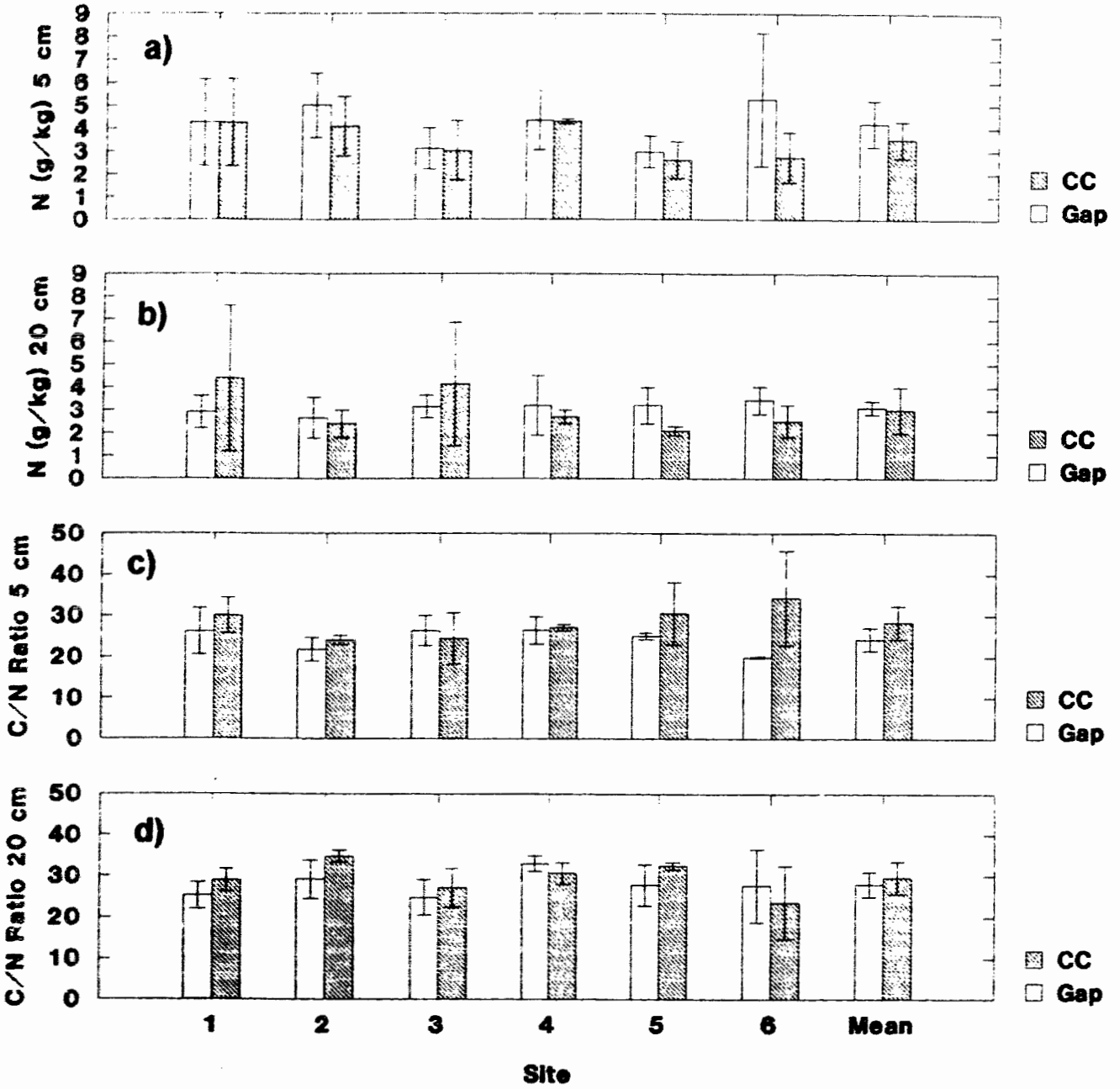

Figure 3.12 Total N concentration at a) 5 cm and b) 20 cm depth in the soil profile, measured in g/kg. C/N ratio at c) 5 cm and d) 20 cm depth in the soil profile.

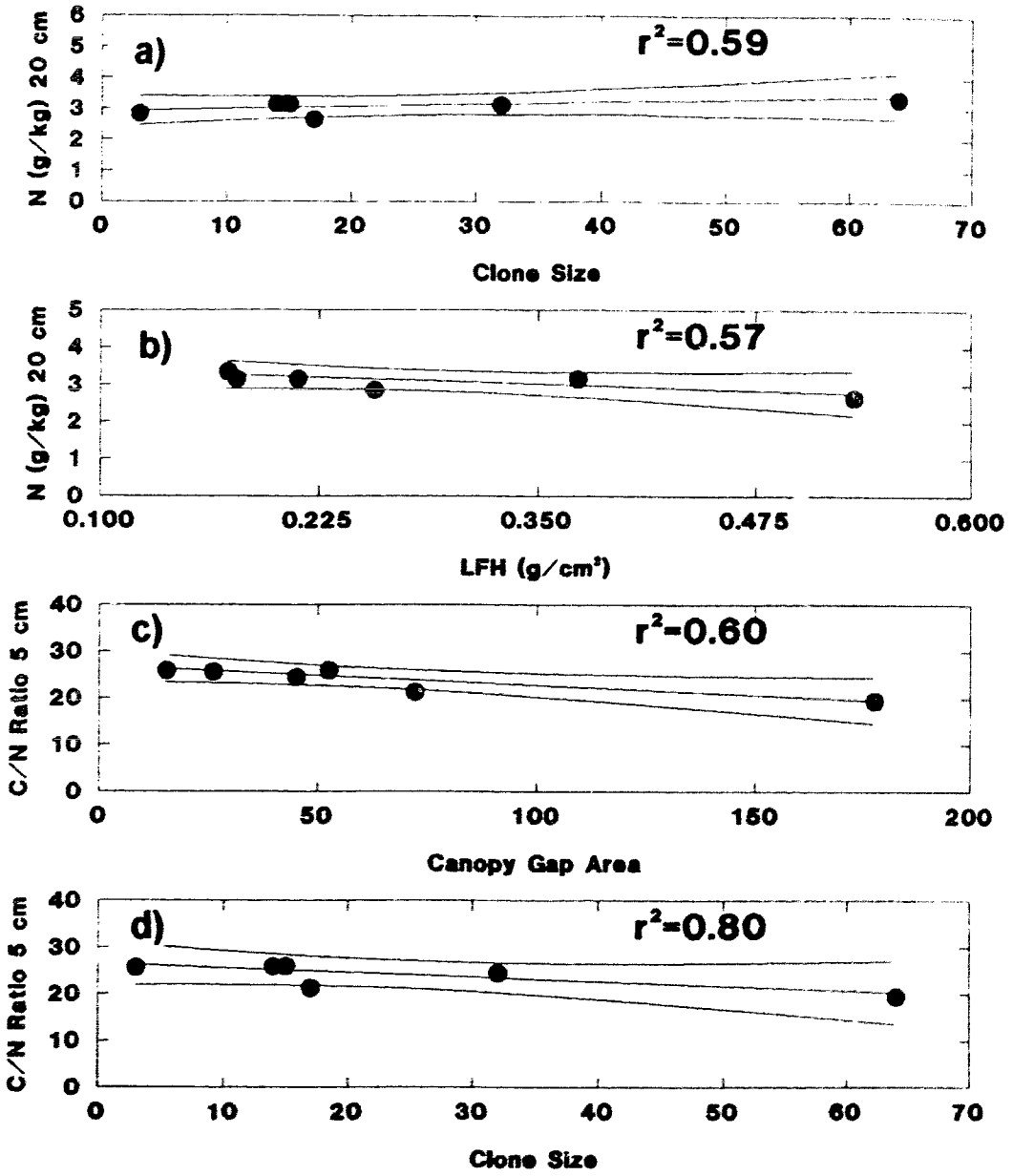

Figure 3.13 A regression of total N content at 20 cm depth in the soil profile tc a) the number of stems on the vine maple clone in the gap plots and b) the weight of LFH per unit surface area. A regression of C/N ratio of the upper 10 cm of mineral soil to c) canopy gap size and d) the size of the vine maple clone.

3.3.3.4 *C/N Ratio*

Mean C/N ratio values in the upper layers of soil throughout the twelve research plots ranged from 19 to 35. At the 5 and 20 cm depths in the soil profile, C/N ratios were lower (not significantly) beneath vine maple gap plots than those beneath closed canopy plots (Figures 3.12c and 3.12d). The mean C/N ratio for gap plots was 24 at the 5 cm level, and 28 at the 20 cm level; whereas, the mean C/N ratio for closed canopy plots was 28 at the 5 cm level, and 30 at the 20 cm level.

Within the upper 10 cm of mineral soil, linear regression demonstrated significant relationships between C/N ratio and the size of the vine maple clone (the larger the clone size, the lower the C/N ratio) ($p=0.07$, $r^2=0.60$, $n=6$), and between the C/N ratio and the size of the canopy gap (the larger the gap, the lower the C/N ratio) ($p=0.02$, $r^2=0.80$, $n=6$) (Figures 3.13c and 3.13d). However, at 20 cm depth, neither gap size nor clone size was significantly related to the C/N ratio.

3.4 Discussion

In this component of the study, physical and chemical soil properties in coastal western hemlock forests containing vine maple gaps were examined to determine if significant differences existed between the soils beneath the gaps compared to soils beneath the surrounding closed canopy forest. Comparisons in the concentrations of nutrients in the forest floor, depth of the forest floor, soil texture, gravel content, bulk density, pH levels, organic matter concentration, total N concentration, and C/N ratios were made between the soils beneath vine maple gaps and those beneath the surrounding

closed canopy forest. Few of the differences in physical soil properties between vine maple gaps and closed canopy plots were statistically significant, even at the p=0.10 level. However, while not always statistically significant, several of the chemical soil properties showed trends which were consistent with previous observations of soil properties beneath vine maple.

Vine maples are associated with the development of Moder humus forms, rapid rates of nutrient cycling, rapid rates of litter decomposition, and high concentrations of bases in the litterfall (Haeussler et al. 1990; Krajina et al. 1982). In this study, the soils in vine maple gaps compared to those in closed canopy forest were found to have significantly thinner forest floors (LFH horizons), significantly higher Ca, Mg, K and Al concentrations in the LFH, significantly higher pH in the LFH horizons, and higher (but not significantly) C/N ratios in the surface mineral soils. No statistically significant differences in organic matter concentration in the upper mineral soil; total N concentration in the upper mineral soil; pH levels of the mineral soil; or N, P, Mn, Zn and Fe concentrations in the LFH, were found. Likewise, no significant differences in the total amounts of nutrients stored in the LFH were found between the gap plots and the closed canopy plots.

The storage of nutrients in vegetation and surface organic layers is extremely important in the maintenance of ecosystem productivity in soils in the Coastal Western Hemlock biogeoclimatic zone in which the study area is located (Watts 1983). Tree growth is believed to be improved in areas where deciduous hardwood species promote the development of Moder humus forms due to more rapid rates of nutrient cycling, higher

pH levels and higher base saturation (Watts 1983; Ministry of Forests 1981). However, Binkley (1995) found that soils can dramatically differ under different species of trees but also observed that many of the traditional beliefs, that conifers degrade soils and hardwoods improve soils, are based on weak evidence. This study on soil properties beneath vine maple agrees with the findings of Binkley (1995) that no species uniformly pushes all soil variables in favourable (or unfavourable) directions.

In this study, the power of the statistical tests was likely quite low, due to the small sample size, small effect size, and the high within-plot sample variability (Toft and Shea 1983). Furthermore, many soil properties (that were not significantly different between the gap and closed canopy) were found to be significantly related to the size of the vine maple clone and the size of the canopy gap among vine maple gap plots. Some of the differences, therefore, between gap and closed canopy plots which were not found to be statistically significant may in fact be significant with a larger sample size. Consequently, many of the statistically insignificant trends found in this study were worth noting as they indicated areas for further research.

3.4.1 *Forest Floor Properties*

Since vine maples are associated with rapid rates of nutrient cycling, rapid litter decomposition, and possibly greater levels of soil organism activity, the weight and depth of the forest floor on gap plots were expected to be lower than those on closed canopy plots. Results showed that the weight of the forest floor beneath the gap plots was less than that beneath the closed canopy plots (although not significantly), while the depth of

the forest floor was significantly thinner beneath the gap plots than that beneath the closed canopy plots. These results are consistent with previous observations that relatively thin forest floors of Moder humus forms develop beneath vine maples, and, thicker forest floors of Mor humus forms develop beneath coniferous canopy (Haeussler et al. 1990). The forest floor of Moder humus forms is thinner than the forest floor of Mor humus forms due to the more rapid incorporation of organic material into the mineral soil in Moder humus types (Ministry of Forests 1981). The greatest difference in depth seen in the F horizon (averaging 1.18 cm on gap plots and 1.99 cm on closed canopy plots), was likely a reflection of faster decomposition rates and/or less input of litterfall in the gap plots than in the closed canopy plots. The weight of LFH in vine maple gaps was not found to be significantly related to either gap size or clone size; however, the depth of the LFH in gap plots was significantly influenced by both gap size and clone size (the larger the gap and the larger the clone, the thicker the LFH). This result provides indirect evidence that larger clones have higher rates of litterfall than smaller clones.

The concentration of nutrients in the forest floor (LFH horizons) of gap plots was expected to be higher than that of closed canopy plots since leaf litter of vine maple in the gap plots provides a rich supply of nutrients to the forest floor (Krajina et al. 1982). In the comparison of mean total nutrient concentrations for vine maple gap plots to those for closed canopy plots in the LFH, total Ca, Mg, K, Al were found to be significantly higher in the LFH beneath the gap; whereas, N and Fe, though somewhat higher, were not significantly different. P and Zn concentrations were approximately the same in the LFH beneath both the gap plots and closed canopy plots. The mean total amounts of nutrients

stored in the LFH of gap plots and closed canopy plots were not found to be significantly different, which was likely the result of the LFH horizons being significantly thinner in gap plots than in closed canopy plots. In addition, the amount of the soluble Fe and Al cations stored in the LFH were lower in gap plots (although not significantly so), which was possibly evidence of greater amounts of leaching in gap plots than in closed canopy plots.

In a similar study on bigleaf maples, Fried et al. (1990) found no consistent differences in the concentrations or amounts of P, K, Ca, or Mg in the upper mineral soils beneath bigleaf maples compared to those in the upper mineral soils beneath Douglas-fir. He postulated that the lack of differences in the amounts of nutrients stored in the soils could be explained by nutrients being cycled more rapidly in the bigleaf maple systems, and that the rates of uptake of nutrients by bigleaf maple roots and the storage of nutrients in woody tissues could be sufficient to utilize the additional input of nutrients from litter. Also, Fried suggested that, since above- and below-ground woody tissues of bigleaf maples might have greater concentrations of nutrients than conifers, there may be more nutrients stored in the biomass of maples than conifers. Fried et al. (1990) also noted that the lack of consistent differences in nutrients in soils beneath bigleaf maples and conifers may be related to the uncertainty about the length of time that bigleaf maples have had to bring about changes in the soils.

3.4.2 *Physical Soil Properties*

Particle size and gravel content can have a large influence on the nutrient and water holding capabilities of soil, which in turn can have a large influence on the growth

and vigor of the vegetation on a site (Pritchett and Fisher 1987). Since similar parent materials cover the entire study area (glacial till), soil texture and gravel content were expected to be similar throughout the gap and closed canopy plots. As hypothesized, gravel content and soil texture were quite similar throughout the paired plots, resulting from the relatively homogenous layer of glacial till covering the study area. Almost all of the samples collected from the study area were within the loamy sand textural class. Within a textural class, differences in texture are unlikely to be biologically significant in terms of the water and nutrient holding capabilities of the soil.

Soil moisture values were not significantly related to gravel content at any depth in the profile in either the summer or winter months. This result is not suprising since gravel content was quite similar throughout the study area. As noted in the previous chapter, surface soil moisture values in vine maple gaps are believed to be related to the high transpiration rates of vine maple. At depth, moisture values were believed to be related more to larger-scale subsurface flow patterns, since gravel content and soil texture were relatively homogenous throughout the study area. In gap plots, clay content was significantly related to soil moisture only at the lower depths in the soil profile where soil moisture values increased with increasing clay content. In addition, in the upper profile in gap plots, it was found that the higher the clay content, the larger the vine maple clone. This may be a reflection of vine maple having a competitive advantage on soils (with clay-sized particles) that have high nutrient and water holding capabilities.

Vine maple litter decomposes more easily than conifer litter (Haeussler et al. 1990), and the Moder humus forms associated with vine maples are generally more

biologically active than Mor humus forms found beneath the conifer canopy (Ministry of Forests 1981). For these reasons, vine maple gaps were hypothesized to encourage greater levels of mixing and aeration of the surface soil horizons which would be evident by lower bulk densities. In this study, mean bulk density values of the surface mineral soil, though slightly lower, were not significantly lower in the gaps than those in the closed canopy. The unexpected results may be explained by the finding that the organic matter concentrations of the surface mineral soils did not significantly differ between vine maple gaps and closed canopy plots. Similarly, in the study of bigleaf maple, Fried et al. (1990) found that bulk densities were not significantly lower under maple than under Douglas-fir; but attributed the high variability in bulk density values to small mammal activity.

Bulk density values were significantly related to gap size: the larger the canopy gap, the lower the bulk density. This finding can be explained by the fact that larger gaps had larger clones, and larger clones had greater amounts of vine maple litterfall (which was rapidly decomposed and incorporated into the surface mineral soil) than smaller clones; however, bulk density was not found to be significantly related to the size of the vine maple clone. Therefore, it was possible to conclude that the lower bulk densities in larger vine maple gaps compared to smaller vine maple gaps were the result of either vine maple gaps creating a more favourable environment for soil organism activity resulting in greater mixing and aeration of the surface soil horizons; or, of greater amounts of energy and moisture reaching the forest floor, resulting in higher rates of decomposition (and therefore greater incorporation of organic matter into the surface soil).

3.4.2 *Chemical Soil Properties*

Since vine maple litter has been observed to have a high concentration of bases (Haeussler et al. 1990), pH levels were expected to be higher beneath vine maple gaps than those beneath closed canopy plots. The pH levels were found to be significantly higher beneath vine maple gap plots than those beneath the closed canopy in the LFH horizons; but not significantly higher at 5, 20, 50 and 100 cm depths in the mineral soil. In the upper layers of the soil profile, the higher pH levels in the gaps were likely a reflection of the higher base content of the decomposing vine maple litter. Similarly, pH levels in the upper 10 cm of mineral soil have been observed to be higher (not significantly) under bigleaf maple than under Douglas-fir (Fried 1990). At greater depths in the soil profile, pH levels are usually a reflection of parent material characteristics: low pH's are generally associated with quartz-rich or silicate-rich parent materials, particularly in the cool rainy climates found within the study area (Watts 1983). In the study area, mean pH levels ranged from 3.1 to 4.8 in the LFH, and from 3.8 to 4.6 in the mineral soil, both ranges being below the optimum 5.0-5.5 level for most conifers. Within the range of pH levels in the study area, Mo availability is low and P deficiency may occur in conifer trees which lack mycorrhizae due to the low solubility of these nutrients below pH=5 (Watts 1983). Under these conditions, any increase in pH levels would likely be beneficial to the growth of conifers.

In the study area, the organic matter concentration in the upper layers of the mineral soil ranged from 10 to 20%, indicating that the soils in this area are relatively rich

in organic matter. Due to the rapid rate of litter decomposition associated with vine maple litter, and possibly greater soil organism activity beneath vine maple resulting in rapid incorporation of organic material into the mineral soil, it was expected that organic matter concentrations of the upper mineral soil would be higher beneath vine maple gap plots than beneath closed canopy plots. The results indicated that, at the 5 cm depth, organic matter concentrations were nearly identical between vine maple gaps and closed canopy plots; and, at the 20 cm depth, organic matter concentrations were somewhat lower beneath the gaps than the closed canopy plots. In contrast, Fried et al. (1990) found that total C concentrations (an index of organic matter) were significantly greater under bigleaf maple, which is probably due to the large amount of litter produced by bigleaf maples. That organic matter concentrations of the surface soil horizons were lower beneath vine maple gaps than beneath the closed canopy was due likely to less total input of litterfall to the site. However, linear regression demonstrated that the organic matter concentration of the upper 30 cm of the soil profile in vine maple gaps was not significantly related to clone size or gap size.

The total N concentration levels were hypothesized to be higher beneath gap plots than those beneath closed canopy plots since leaf litter of vine maple is believed to provide a rich supply of nutrients to the site (Krajina et al 1982). Total N concentration levels were higher in the gaps at the 5 cm depth (although not significantly), and were at approximately equal levels at the 20 cm depth. In contrast, under bigleaf maple, Fried et al. (1990) found that N concentrations were significantly greater at the 10 cm depth, probably due to the large amount of litter produced by bigleaf maples. That total N

concentrations of the surface mineral soil were not significantly different under vine maple gaps compared to closed canopy plots may be explained by similar organic matter concentrations at these depths. According to Watts (1983), if the N concentration level in the surface 15 cm of the mineral soil exceeds 0.1%, the soil is likely to supply adequate available N for good tree growth. Since the mean total N values in the upper layers of soil throughout the twelve research plots ranged from 0.21% to 0.50%, it was unlikely that any of the research plots were deficient in N. However, the total N concentration of the fine fraction is a crude index of available N supply, and the C/N ratio is usually a better indicator of N availability (Watts 1983). In the study, the total N content at the 20 cm level significantly increased with increasing clone size; and significantly increased with decreasing weight per unit surface area of LFH. Compared to smaller clones, larger clones were likely associated with greater levels of soil organism activity, greater incorporation of organic material into the mineral soil horizons, and therefore higher N availability.

The C/N ratio of the upper mineral soil was expected to be lower in gap plots due to the higher concentration of nitrogen arising from the rapid decomposition rates of vine maple litterfall (Haeussler et al. 1990). While at the 5 and 20 cm depths in the soil profile, the C/N ratios were lower beneath vine maple gap plots than those beneath closed canopy plots, the differences were not statistically significant. Fried et al. (1990) found no consistent difference in the C/N ratios in the surface mineral soil beneath bigleaf maple and Douglas-fir. The unexpected C/N ratio results in this study were attributable to similar concentrations of N and C in the mineral soils beneath vine maple gaps and closed canopy plots. The mean C/N ratio for gap plots was 24 at 5 cm, and 28 at 20 cm; whereas, the

mean C/N ratio for closed canopy plots was 28 at 5 cm, and 30 at 20 cm. Because ratios above 25 suggest low N availability due to immobilization (Watts 1983), the C/N ratio differences between vine maple gaps and the surrounding forest may be biologically significant, but that would be apparent only in a larger sample size. Finally, in the upper 10 cm of mineral soil, larger gaps and larger clones had significantly lower C/N ratios and therefore had higher N availability than smaller gaps and smaller clones. It appears that larger vine maple gaps may have a greater influence on nutrient availability than smaller vine maple gaps.

Chapter 4

Litterfall and litter decomposition in persistent canopy openings occupied by vine maple in a coastal western hemlock forest

Chapter 4
Litterfall and litter decomposition in persistent canopy openings occupied by vine maple in a coastal western hemlock forest

4.1 Introduction

The hardwood forest resources of British Columbia have historically been underestimated or ignored in both their ecological and economic dimensions (Massie et al. 1994). In the past decade, several factors have contributed to a change in the status of hardwood species, including a better understanding of the silvicultural and ecological importance of hardwood species, an increased scientific and public concern over the sustainability of natural resources, and a concern for the conservation of biodiversity. Greater attention is now being given to hardwoods in research and forest resource management in B.C. and elsewhere (Massie et al. 1994). Broad-leafed trees play a significant role in enhancing wildlife habitat, promoting biodiversity, vegetating riparian areas, and colonizing early successional stages (Haeussler et al. 1990). After disturbances, hardwoods are also believed to maintain ecosystem resilience by establishing quickly, retaining soil nutrients, and reducing soil erosion (Perry and Maghembe 1989). In terms of soil physical and chemical properties little is known, however, about the benefits conferred to the sites upon which hardwood species grow. Also, the relationship between hardwood species and long-term site productivity in B.C. forests is poorly understood.

The abundance of the hardwood species, vine maple, throughout the successional time frame in coniferous forests of the Pacific Northwest has been observed to follow a bi-modal distribution in which early abundance after clearcutting is followed by near-extinction at 40 years of age (Russel 1973). However, in a recent study, vine maple was

found to inhabit persistent openings in the forest canopy not created by treefall (McGhee 1996). These gaps are characterized by the ability of vine maple to resist the regeneration of taller canopy dominants and subsequent canopy closure by establishing a dense mat of stems early in stand development that is large enough to prevent invasion of the site by conifers. Consequently, the impact of these gaps on soil properties (due to perceived differences in litterfall accumulation and litter decomposition) is likely to be significant because the influence of vine maple is prolonged over a greater period of time than is usual in the successional time frame.

Litterfall accumulation and litter decomposition account for a large amount of the nutrient cycling that occurs during forest stand development (Fogel and Cromack 1976). In a 450-year old Douglas-fir forest, up to 72% of the aboveground nutrient return is in litterfall (Abee and Lavender 1972). If litter decomposition is slow, considerable biomass and nutrient capital can accumulate in the forest floor. Nitrogen deficiency in many northern coniferous forests has been linked to the slow release of available nitrogen from the forest floor (Williams 1972). High litter decomposition rates have been correlated with low lignin content, low C/N ratios, and high N availability (Fogel and Cromack, 1976; Prescott, 1995). Decomposition rates are also influenced by moisture, temperature, and the type of microorganisms and soil fauna active in the decomposition process (Pritchett and Fisher 1987).

Hardwood litter generally decomposes more rapidly than conifer litter due to its higher nutrient content, lower lignin content, and higher proportion of surface area to mass (Assman 1970; Perry 1970; Fried et al. 1990). The higher rate of nutrient turnover

associated with hardwoods is postulated to enhance the productivity of conifer stands (Assman 1970; Perry 1970; Fried et al. 1990). In Oregon, coniferous forests cycle nutrients differently when mixed with hardwoods than when existing in pure stands (Perry et al. 1987): stands with hardwoods returned 10 kg/ha/year more N in leaf litter than pure stands and stands without hardwoods contained 520 kg/ha more N in mineral soil, mineralized 20% more N from soil, and had a lower soil C/N ratio than mixed stands. Fried et al. (1990) found that litterfall weight and nutrient content were significantly greater under bigleaf maple than under Douglas-fir, and that turnover rates for forest floor biomass and nutrients were significantly faster under maple.

Litter from vine maple decomposes faster than conifer litter due to a lower lignin content and a higher nitrogen concentration (Triska and Sedell 1976). The heavy annual litterfall and rich nutrient content of vine maple litter is believed to result in high rates of nutrient cycling (Russell 1973). The composition of vine maple litter does not promote soil acidity as does the composition of conifer needles (Haeussler et al. 1990). Due to the return of nutrients to the site through litterfall, Moder humus tends to form beneath vine maples, creating an environment favorable to the growth of Douglas-fir and western redcedar (Krajina et al. 1982) since Moder humus forms provide more available nutrients than do Mor humus forms (Ministry of Forests 1981). Mors, which are relatively biologically inactive, are the most common humus form in the forests within the study area, and are characterized by high levels of acidity, slow decomposition rates, and high C/N ratios (Ministry of Forests 1981; Watts 1983).

A number of scientists have studied the effects of vegetation on soils by observing differences in soil properties caused by different tree and understory species in forest stands (Alban 1969; Tarrant and Miller 1963; Fried et al. 1990). Some studies have focused on differences in the chemical composition of litter and forest floors under different species to better understand the influence of species on nutrient dynamics (Tarrant et al. 1951; Gessel and Turner 1974; Fried et al. 1990). The objective of this component of the study was to compare the rates of litterfall accumulation and litter decomposition of persistent vine maple gaps to those in the surrounding closed canopy of a western hemlock forest in the Coastal Western Hemlock biogeoclimatic zone. The purpose of this comparison was to determine the influence of persistent vine maple gaps on the nutritional status of sites in coastal B.C. forests. If the properties of litterfall and decomposition in vine maple gaps differ from those in the surrounding forest, vine maple may influence the nutritional status of the gaps. These properties may also give an indication of how vine maple gaps influence site productivity, and may help to explain the long-term impact of persistent vine maple gaps on forest soils. In this study, the following hypotheses were tested:

1. The concentration of nutrients in the litterfall of vine maple gap plots is higher than that of closed canopy plots.

2. Rates of litterfall are lower in vine maple gap plots compared to closed canopy plots.

3. Decomposition rates in vine maple gap plots are higher than those in closed canopy plots.

4. Vine maple litter has higher decomposition rates than those of a mix of western hemlock and Douglas-fir litter.

4.2 Methodology

4.2.1 *Litterfall Collection*

Ten litter traps were placed on each of the twelve plots to collect litterfall from August 24, 1993 to September 20, 1994. Following the method of litter collection of Prescott et al. (1988), the litter traps consisted of greenhouse trays (approximately 5 cm tall, 20 cm wide and 50 cm long), each lined with 1 mm nylon mesh and fitted with holes in the bottom to allow for drainage. The litterfall was collected by removing the mesh and emptying its contents into a bag. Samples from each tray on each plot were stored separately. The litter was allowed to air dry, then was oven-dried, and the oven-dry weight was recorded.

Litterfall was collected during four time periods: Aug. 24 - Oct. 11, 1993 (period a, early fall); Oct. 12 - Nov. 16, 1993 (period b, late fall); Nov. 17, 1993 - June 13, 1994 (period c, winter and spring); and June 14 to Sept 20, 1994 (period d, summer). Litterfall collection extended over a period of thirteen months rather than twelve months, due to unforseeable circumstances (illness). Because the commencement of litterfall collection on Aug 24, 1993 and the termination of collection on September 29, 1994 were both dates that occurred before vine maple foliage started to fall, the extra month had no effect on the total annual vine maple litterfall measurements. In this study therefore, the total litterfall is referred to as annual litterfall even though it covered a thirteen month collection period. Since nutrient analysis was to be performed on these samples, collections from periods a and b were made weekly to minimize nutrient losses due to leaching.

Samples from periods a and b were sorted into three components: coniferous needles, vine maple leaves, and 'other' debris. Due to the large number of samples and the length of time required to sort a sample, samples from time periods c and d were not sorted. The 'other' debris component consisted of small twigs, cone scales, cedar litter and any other material smaller than 10 cm in size. The amount of the 'other' component of the litterfall was relatively small during time periods a and b (less than 10%). The amount of cedar litter in litter traps on approximately half of the plots was determined for time periods a and b; and because the amount of the cedar component of the litterfall was also small during these time periods (less than 5%), it was not given further consideration. The oven-dry weight of the needle and vine maple components from all plots were recorded. For each plot, the total amount of litterfall in time periods a and b (excluding the 'other' debris) was calculated by adding the weight of vine maple litter plus the weight of the needle litterfall. In a similar manner, the total amount of litterfall for periods c and d (including the 'other' debris) was recorded. Total annual litterfall was calculated for each plot by adding the total oven-dry weight recorded for each of the four time periods.

4.2.2 *Nutrient Concentrations in Litterfall*

Similar to the analysis performed on the LFH samples described in the previous chapter (section 3.2.2.2), the Parkinson and Allen Method was used to determine the nutrient concentrations of the litterfall samples. In the litterfall samples, analyses were conducted to determine the concentration levels of N, P, Ca, Mg, K, Mn, Fe, Zn, and Al. Although Al is not a nutrient, its concentration levels were measured; and Al is treated as

a nutrient within the text. The chemical properties of litterfall in vine maple gaps and in closed coniferous canopy plots were compared using a composite sampling technique to provide an estimate of the mean value of subsamples without having to analyze each sample individually. The lower cost and greater efficiency of composite sampling, however, was done at the expense of gaining information on within-plot variability (Carter and Lowe 1985). Since the goal of this study was to determine differences in nutrient concentrations in litterfall between gap plots and canopy plots, information on the variability within plots was not necessary.

For each of the time periods a and b, three composite samples of vine maple litter from each of the gap plots, and three composite samples of conifer litter from both the gap and closed canopy plots, were analyzed. To create a composite sample, the litterfall from each trap in each time period was ground in a coffee grinder, and an equal amount of sample from each trap was taken to give a 0.25 g representative sub-sample. Due to time constraints, nutrient analysis was not performed on litterfall from time periods c and d.

4.2.3 *Litter Decomposition*

The method of measuring decomposition rates resembled that used by Prescott et al. (1993) and Taylor et. al (1991). Standardized samples were collected from littertraps placed beneath one site supporting predominantly western-hemlock and some Douglas-fir, and beneath two sites supporting vine maple. To eliminate all fallen debris except vine maple leaves on vine maple sites, and hemlock and Douglas-fir needles on the conifer site, the litterfall was sorted. The ratio of western hemlock needles to Douglas-fir needles was

approximately 3:1. After litter samples were oven-dried, 2 gram samples of vine maple were placed into 12 cm by 15 cm bags, and 2 gram samples of the hemlock/Douglas-fir were placed into 6 cm by 12 cm bags. The bags were made of 2-ply 1 mm fiberglass mesh. To examine decomposition rates, ten bags of each litter type were placed on each site on November 16, 1993. Each bag was tagged and pinned to the forest floor; and, for the vine maple bags, the origin of the sample was recorded in case there was a difference in the litter quality from the two vine maple collection sites.

Taylor et. al (1991) retrieved samples at six month intervals to determine mass loss due to decomposition; whereas, Prescott et al (1993) retrieved samples annually. In this study, collections were made at time intervals of six months (May 1994), one year (November 1994), and two years (November 1995). For each of these sampling periods, three samples of both litter types were removed from each site. The litter bags were oven-dried and then gently shaken to remove any mineral soil that had entered into the bag. Each litter sample was then removed from the bag, rinsed under a gentle stream of water above a nest of sieves (700 μm and 50 μm) to prevent any material from being washed down the drain, and then oven-dried and weighed.

4.2.4 *Statistical Analysis*

For each of the parameters, the data were analyzed as a split-plot design following the procedure outlined in section 2.2.5. The six paired plots constituted the whole plots, and the paired plots were subdivided into gap and closed canopy sub-plots. Because of the small sample size and the exploratory nature of the study, a significance level of $p=0.10$

was used in testing for significant differences. Statistical power was not calculated because of the complex experimental design; however, the power of the statistical tests is likely to be low due to small sample size, small effect size, and the high within-plot sample variability (Toft and Shea 1983). In the figures, error bars represent one standard deviation from the mean. Regression analysis was performed to determine if gap characteristics, such as gap size and clone size, had an effect on litterfall and litter decomposition.

4.3 Results

4.3.1 *Litterfall*

Encompassing the fall of 1993, time periods a and b correspond to the period of total vine maple litterfall. In the gap plots in the fall, the mean total amount of vine maple litterfall was four times less than the amount of needle litterfall over the same fall time periods ($p=0.001$, $f=34.02$, $df=1$). The total amount of vine maple litterfall for the six plots ranged from 34 to 197 kg/ha. The order of decreasing amount of litterfall was: plot 6g (197 kg/ha), plot 5g (154 kg/ha), plot 2g (133 kg/ha), plot 4g (85 kg/ha), plot 3g (48 kg/ha), and plot 1g (34 kg/ha). The order of decreasing amount of litterfall corresponded to the decreasing order of clone size.

The mean total amount of needle litterfall was one-and-one-half times greater in the closed canopy plots than in the vine maple gap plots over the fall time periods ($p=0.02$, $F=11.15$, $df=1$). Over the winter and spring (time period c), the total amount of litterfall was virtually the same beneath the gap plots compared to the closed canopy plots.

In time period d (summer), total litterfall was somewhat greater (but not significantly) beneath the closed canopy plots than beneath the gap plots. With respect to total annual litterfall, there was no significant difference between the gap plots and the closed canopy plots (Figures 4.1-4.2).

A significant relationship between vine maple litterfall and clone size existed over time periods a and b: the larger the clone, the greater the amount of vine maple litterfall ($p=0.02$, $r^2=0.79$, $n=6$) (Figures 4.3a). However, the amount of needlefall reaching the forest floor beneath gaps were not related to canopy gap size. The amounts of vine maple litterfall were significantly related to the concentrations of P, K, Ca and Mn: the greater the amount of vine maple litterfall, the lower the concentrations of P ($p=0.06$, $r^2=0.64$, $n=6$) and K ($p=0.03$, $r^2=0.71$, $n=6$), the higher the concentration of Ca in the LFH ($p=0.01$, $r^2=0.82$, $n=6$), and the greater the amount of Mn stored in the LFH (Figures 4.3b to 4.4b). The C/N ratio of the upper 10 cm of mineral soil was significantly related to the amount of vine maple litterfall in vine maple gaps: the greater the amount of vine maple litterfall, the lower the C/N ratio of the surface mineral soil ($p=0.04$, $r^2=0.70$, $n=6$) (Figure 4.4c). The total amount of litterfall in the vine maple gap plots was not related to nutrient concentrations in the LFH, the total amount of nutrients stored in the LFH, or the C/N ratio of the upper mineral soil.

Table 4.1

Litterfall rates measured in kg/ha. The individual plot means and standard deviations consist of ten samples per plot. The overall means and standard deviations for the gap and closed canopy were calculated from the means of the individual plots.

Plot	Vine[1] Maple Period a	Vine[1] Maple Period b	Needle[1] Period a	Needle[1] Period b	Total[1] Litterfall Period a	Total[1] Litterfall Period b	Total[2] Litterfall Period c	Total[2] Litterfall Period d	Total[2] Annual Litterfall
1g	33 ± 26	2 ± 3	210 ± 25	56 ± 20	428 ±588	58 ± 19	611 ± 264	410 ± 85	1307 ± 338
1c			367 ±48	235 ± 74	367 ± 49	235 ± 77	710 ± 161	431 ± 59	1744 ± 234
2g	31 ± 27	103 ± 52	360 ± 34	63 ± 25	391 ± 54	166 ± 55	748 ± 275	894 ± 235	2171 ± 359
2c			309 ± 23	88 ± 25	309 ± 23	88 ± 25	809 ± 488	623 ± 126	1809 ± 320
3g	8 ± 7	40 ± 36	338 ± 34	463 ±108	346 ± 34	503 ±116	798 ± 270	498 ± 97	2102 ± 343
3c			277 ± 20	682 ± 79	277 ± 20	682 ± 79	795 ± 149	317 ± 101	2024 ± 174
4g	39 ± 18	45 ± 31	167 ± 30	29 ± 11	206 ± 22	74 ± 26	552 ± 214	316 ± 129	1135 ± 334
4c			354 ± 13	44 ± 10	354 ± 13	44 ± 10	648 ± 209	551 ± 141	1577 ± 269
5g	40 ± 36	113 ± 73	342 ± 44	306 ±125	382 ± 63	419 ±111	1171 ± 491	377 ± 93	2310 ± 642
5c			314 ± 20	607 ±110	314 ± 20	607 ±110	958 ± 193	391 ± 133	2223 ± 168
6g	26 ± 12	171 ± 32	182 ± 20	43 ± 24	208 ± 19	214 ± 42	733 ± 283	335 ± 95	1469 ± 264
6c			393 ± 27	231 ± 76	393 ± 27	231 ± 76	691 ± 237	538 ± 49	1822 ± 278
Gap	29 ± 12	79 ± 61	266 ± 89	160 ±181	295 ± 87	239 ±183	769 ± 217	472 ± 217	1742 ± 460
CC			336 ± 43	315 ± 299	336 ± 43	314 ±267	769 ± 112	480 ± 112	1890 ± 243

[1] Measurement does not include other debris

[2] Measurement includes other debris

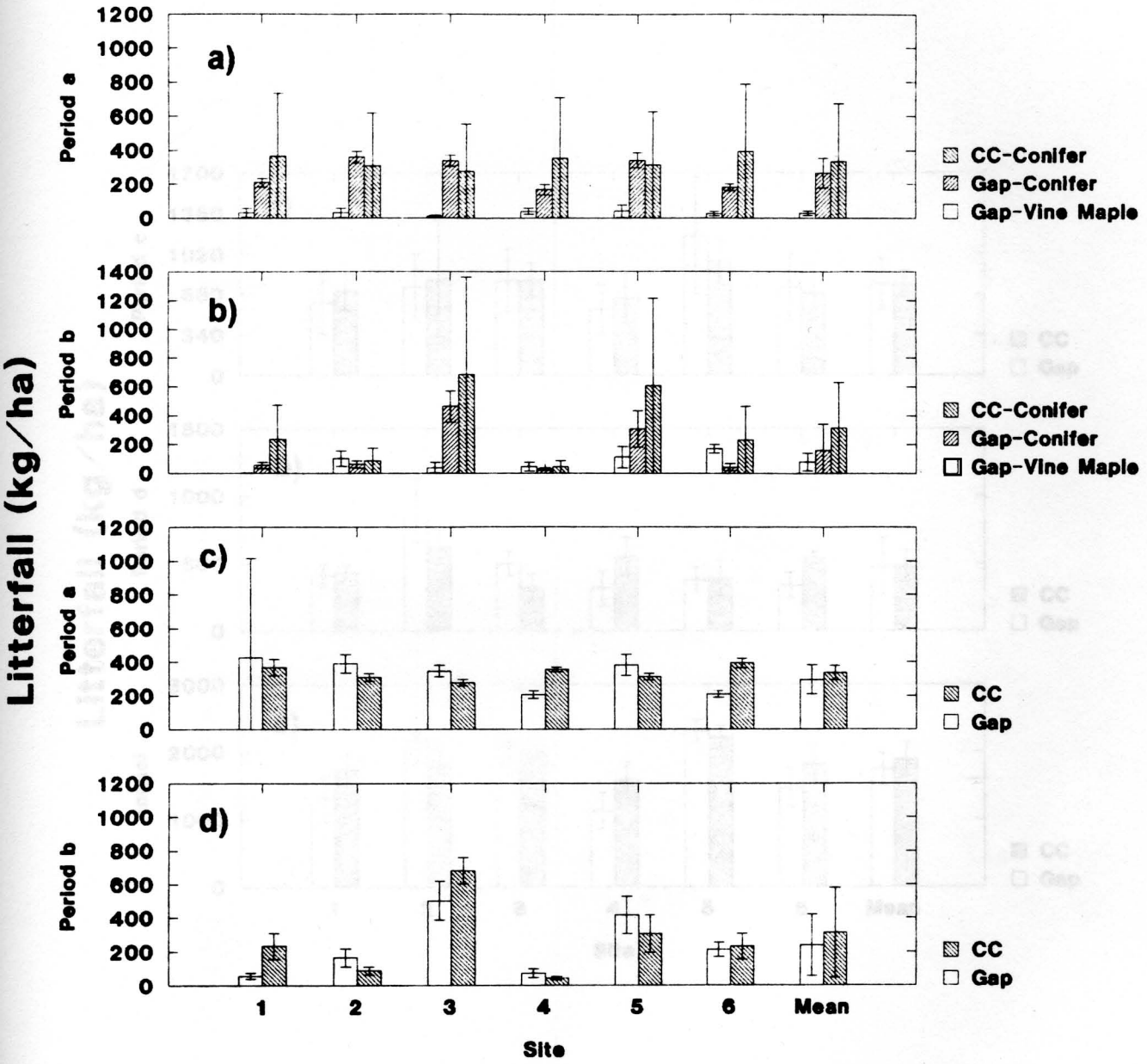

Figure 4.1 Vine maple and conifer litterfall in a) early fall (time period a) and b) late fall (time period b) (kg/ha). Total litterfall in c) early fall (time period a) and d) late fall (time period b) (kg/ha).

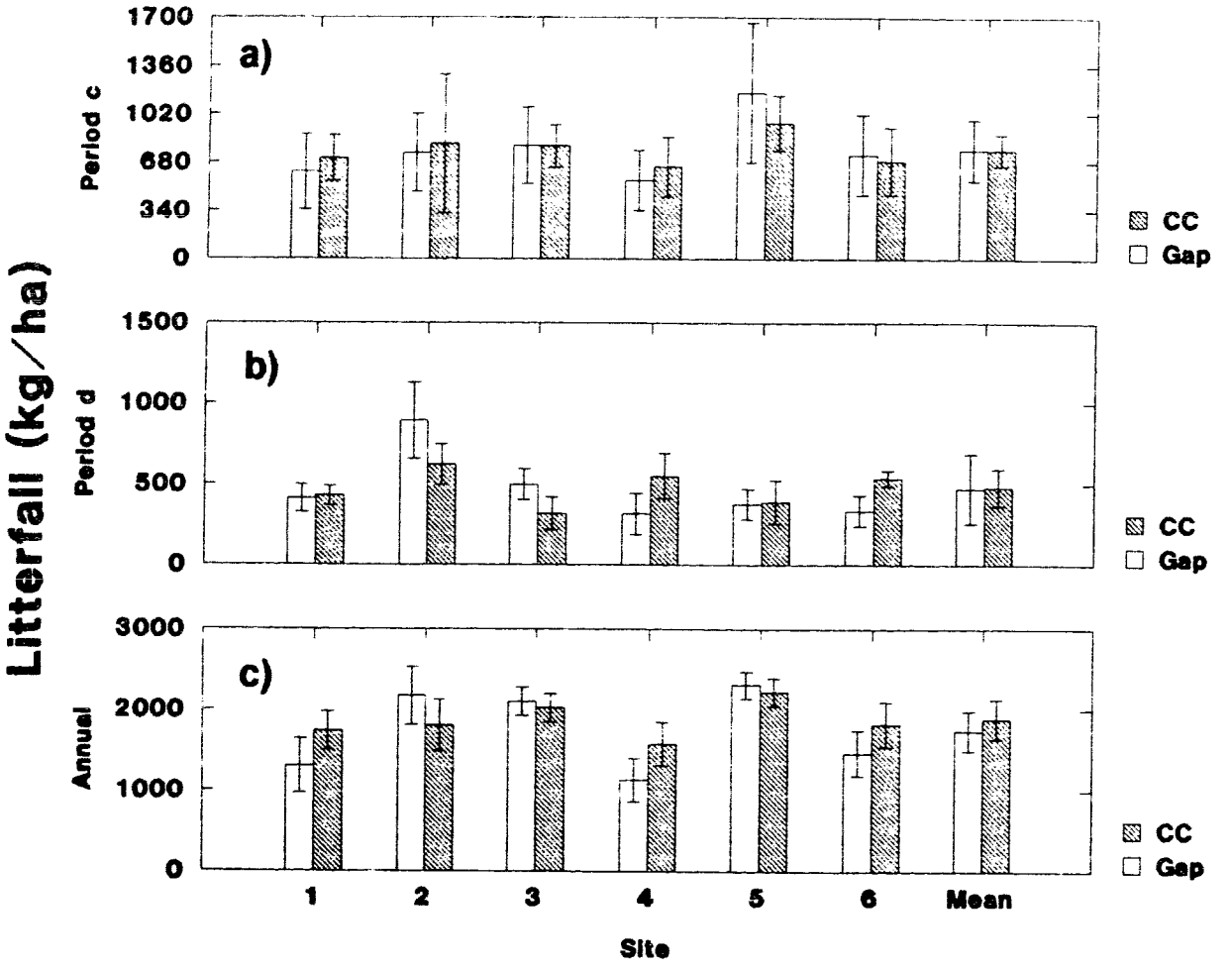

Figure 4.2 Total litterfall in a) the winter and spring (time period c) and b) the summer (time period d) (kg/ha). c) Total annual litterfall (kg/ha).

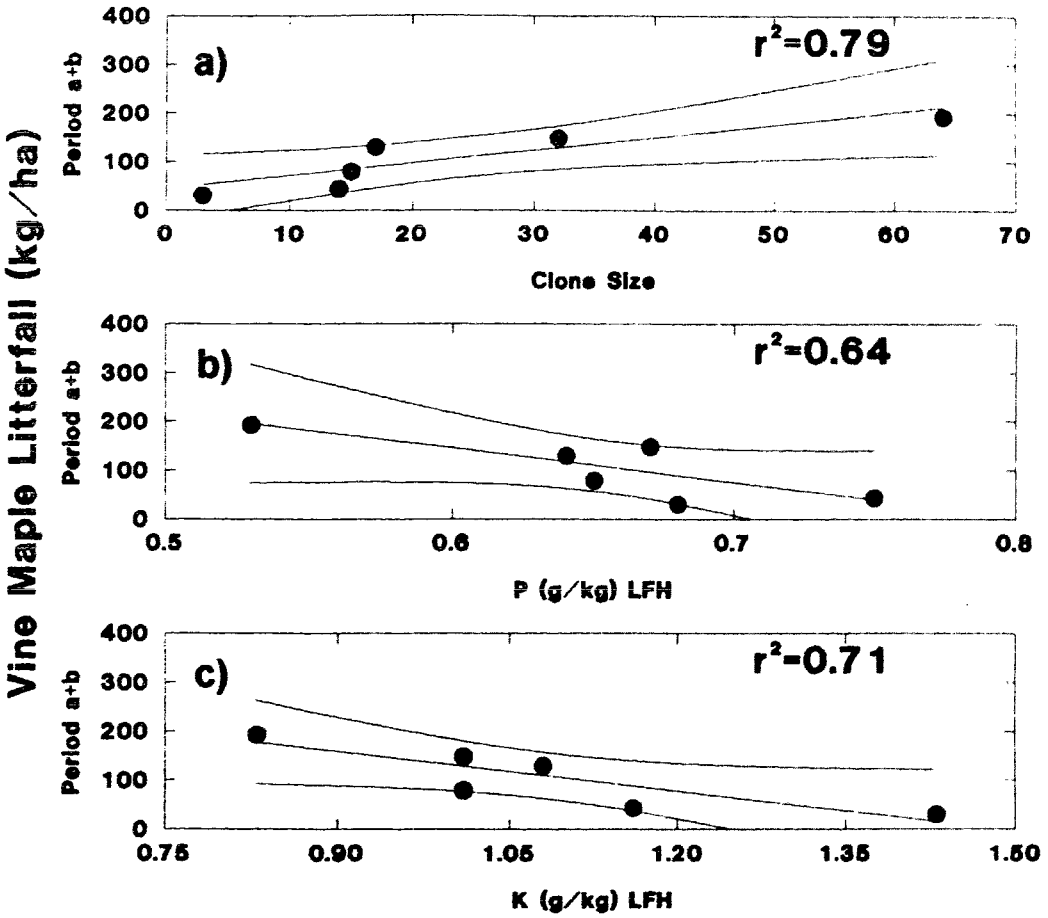

Figure 4.3 a) A regression of the total annual amount of vine maple litterfall in vine maple gaps to the size of the vine maple clone. A regression of the total amount of vine maple litterfall in vine maple gaps to b) P and c) K concentrations in the LFH.

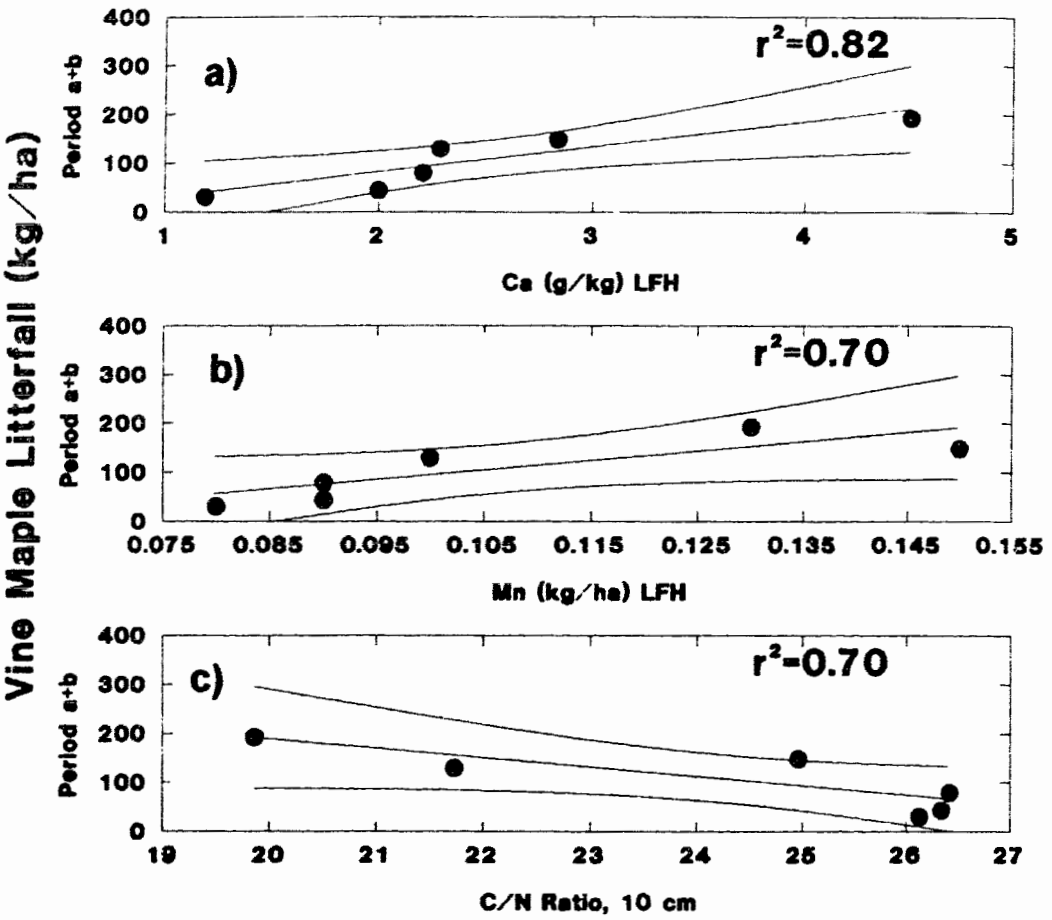

Figure 4.4 A regression of the total amount of vine maple litterfall in vine maple gaps to a) the concentration of Ca in the LFH, b) the amount of Mn stored in the LFH and c) the C/N ratio of the upper 10 cm of mineral soil.

4.3.2 *Litterfall Nutrient Concentrations*

Compared to concentrations in the needle litterfall, vine maple litterfall had significantly higher concentrations of almost all of the nutrients tested (Tables 4.2 and 4.3). Concentrations of N ($p=0.001$, $F=12.37$, $df=1$), P ($p=0.000$, $F=54.05$, $df=1$), Ca ($p=0.000$, $F=126.01$, $df=1$), Mg ($p=0.000$, $F=111.10$, $df=1$), K ($p=0.000$, $F=44.56$, $df=1$), Fe ($p=0.000$, $F=14.62$, $df=1$) and Zn ($p=0.000$, $F=250.06$, $df=1$) of vine maple litterfall were greater than needle litterfall. However, the concentrations of Mn ($p=0.000$, $F=14.61$, $df=1$) and Al ($p=0.000$, $F=24.38$, $df=1$) of vine maple litterfall were lower than needle litterfall (Figures 4.5 to 4.6).

An indication of the influence of vine maple gaps on the nutrient concentrations available to trees immediately surrounding the gap may be obtained by comparing the nutrient concentrations of needle litterfall in gap plots to those in closed canopy plots; however, these readings may only be an indication of the retranslocation of nutrients before abscission. The mean concentration levels of N (1.05% gap - 0.93% closed canopy), Mn (0.09% gap - 0.07% closed canopy), and Al (0.026% gap - 0.023% closed canopy) in needle litterfall were higher (not significant) in the gap plots compared to those in the closed canopy plots; and, the concentration levels of Mg (0.082% gap - 0.089% closed canopy) and K (0.206% gap- 0.256% closed canopy) in needle litterfall were lower (not significant) in the gap plots compared to those in the closed canopy

Table 4.2

Nutrient concentrations of vine maple litterfall (g/kg). The individual plot means and standard deviations consist of three composite samples per plot in the two fall time collections (n=6). The overall means and standard deviations for the gap and closed canopy were calculated from the means of the individual plots (n=6).

Plot	N	P	Ca	Mg	K	Fe	Mn	Zn	Al
1g	14.35 ± 1.91	1.02 ± 0.31	21.03 ± 1.15	1.25 ± 0.28	9.05 ± 4.19	0.30 ± 0.19	0.53 ± 0.08	0.09 ± 0.01	0.29 ± 0.22
2g	10.87 ± 1.52	0.38 ± 0.07	13.19 ± 2.28	1.18 ± 0.20	7.01 ± 3.33	0.16 ± 0.05	0.39 ± 0.09	0.08 ± 0.00	0.10 ± 0.02
3g	11.37 ± 1.39	0.51 ± 0.09	13.11 ± 1.44	1.23 ± 0.14	5.22 ± 1.75	0.25 ± 0.03	0.49 ± 0.08	0.09 ± 0.02	0.15 ± 0.04
4g	9.93 ± 0.31	0.46 ± 0.07	15.80 ± 3.11	2.00 ± 0.39	4.62 ± 2.12	0.22 ± 0.04	0.47 ± 0.09	0.12 ± 0.03	0.13 ± 0.02
5g	11.09 ± 0.46	0.57 ± 0.13	12.90 ± 1.82	1.61 ± 0.47	6.14 ± 2.85	0.22 ± 0.09	0.92 ± 0.23	0.07 ± 0.02	0.16 ± 0.04
6g	10.81 ± 0.33	0.27 ± 0.09	14.97 ± 2.80	1.72 ± 0.21	5.45 ± 2.47	0.12 ± 0.03	0.56 ± 0.08	0.06 ± 0.01	0.09 ± 0.06
Gap	11.35 ± 1.41	0.54 ± 0.28	15.19 ± 3.17	1.50 ± 0.33	6.38 ± 1.89	0.20 ± 0.05	0.56 ± 0.19	0.09 ± 0.02	0.14 ± 0.05

Table 4.3

Nutrient concentrations of needle litterfall (g/kg). The individual plot means and standard deviations consist of three composite samples per plot in the two fall time collections (n=6). The overall means and standard deviations for the gap and closed canopy were calculated from the means of the individual plots (n=6).

Plot	N	P	Ca	Mg	K	Fe	Mn	Zn	Al
1g	9.11 ± 0.41	0.23 ± 0.02	8.82 ± 1.19	0.81 ± 0.13	' 72 ± 0.64	0.13 ± 0.09	0.81 ± 0.12	0.04 ± 0.01	0.31 ± 0.08
1c	9.28 ± 0.77	0.27 ± 0.04	10.94 ± 1.31	0.84 ± 0.14	2.16 ± 0.50	0.10 ± 0.02	0.68 ± 0.09	0.03 ± 0.00	0.18 ± 0.02
2g	12.13 ± 0.80	0.24 ± 0.02	8.18 ± 0.50	0.93 ± 0.11	2.30 ± 0.40	0.08 ± 0.01	1.32 ± 0.08	0.04 ± 0.01	0.35 ± 0.04
2c	8.31 ± 0.46	0.25 ± 0.03	7.93 ± 0.56	0.87 ± 0.09	1.82 ± 0.52	0.08 ± 0.01	0.64 ± 0.15	0.03 ± 0.00	0.27 ± 0.04
3g	10.71 ± 0.41	0.35 ± 0.02	11.53 ± 1.49	0.78 ± 0.07	2.03 ± 0.48	0.09 ± 0.02	0.54 ± 0.10	0.03 ± 0.00	0.19 ± 0.04
3c	9.93 ± 0.78	0.37 ± 0.02	10.75 ± 0.98	0.84 ± 0.04	2.38 ± 0.41	0.09 ± 0.01	0.56 ± 0.04	0.03 ± 0.00	0.14 ± 0.01
4g	10.63 ± 0.10	0.29 ± 0.02	9.91 ± 0.29	0.97 ± 0.19	2.07 ± 0.37	0.14 ± 0.11	1.20 ± 0.25	0.04 ± 0.01	0.32 ± 0.03
4c	12.10 ± 0.10	0.28 ± 0.02	7.52 ± 0.43	0.95 ± 0.11	2.49 ± 0.48	0.09 ± 0.04	1.07 ± 0.19	0.03 ± 0.00	0.04 ± 0.04
5g	8.42 ± 0.20	0.28 ± 0.03	9.55 ± 0.93	0.76 ± 0.06	2.16 ± 0.57	0.09 ± 0.07	0.53 ± 0.10	0.04 ± 0.01	0.16 ± 0.03
5c	8.35 ± 0.09	0.26 ± 0.05	10.47 ± 2.73	1.12 ± 0.61	4.21 ± 2.35	0.14 ± 0.18	0.52 ± 0.27	0.04 ± 0.02	0.19 ± 0.18
6g	11.80 ± 0.12	0.22 ± 0.02	8.10 ± 1.21	0.67 ± 0.13	2.06 ± 0.72	0.09 ± 0.03	0.91 ± 0.18	0.03 ± 0.00	0.21 ± 0.03
6c	7.61 ± 0.02	0.31 ± 0.04	8.51 ± 0.97	0.70 ± 0.13	2.33 ± 0.89	0.06 ± 0.05	0.63 ± 0.25	0.03 ± 0.01	0.22 ± 0.06
Gap	10.47 ± 1.46	0.27 ± 0.05	9.35 ± 1.29	0.82 ± 0.11	2.06 ± 0.19	0.10 ± 0.03	0.89 ± 0.33	0.04 ± 0.00	0.26 ± 0.08
CC	9.26 ± 1.61	0.29 ± 0.04	9.35 ± 1.54	0.89 ± 0.14	2.56 ± 0.84	0.09 ± 0.02	0.68 ± 0.02	0.03 ± 0.00	0.23 ± 0.09

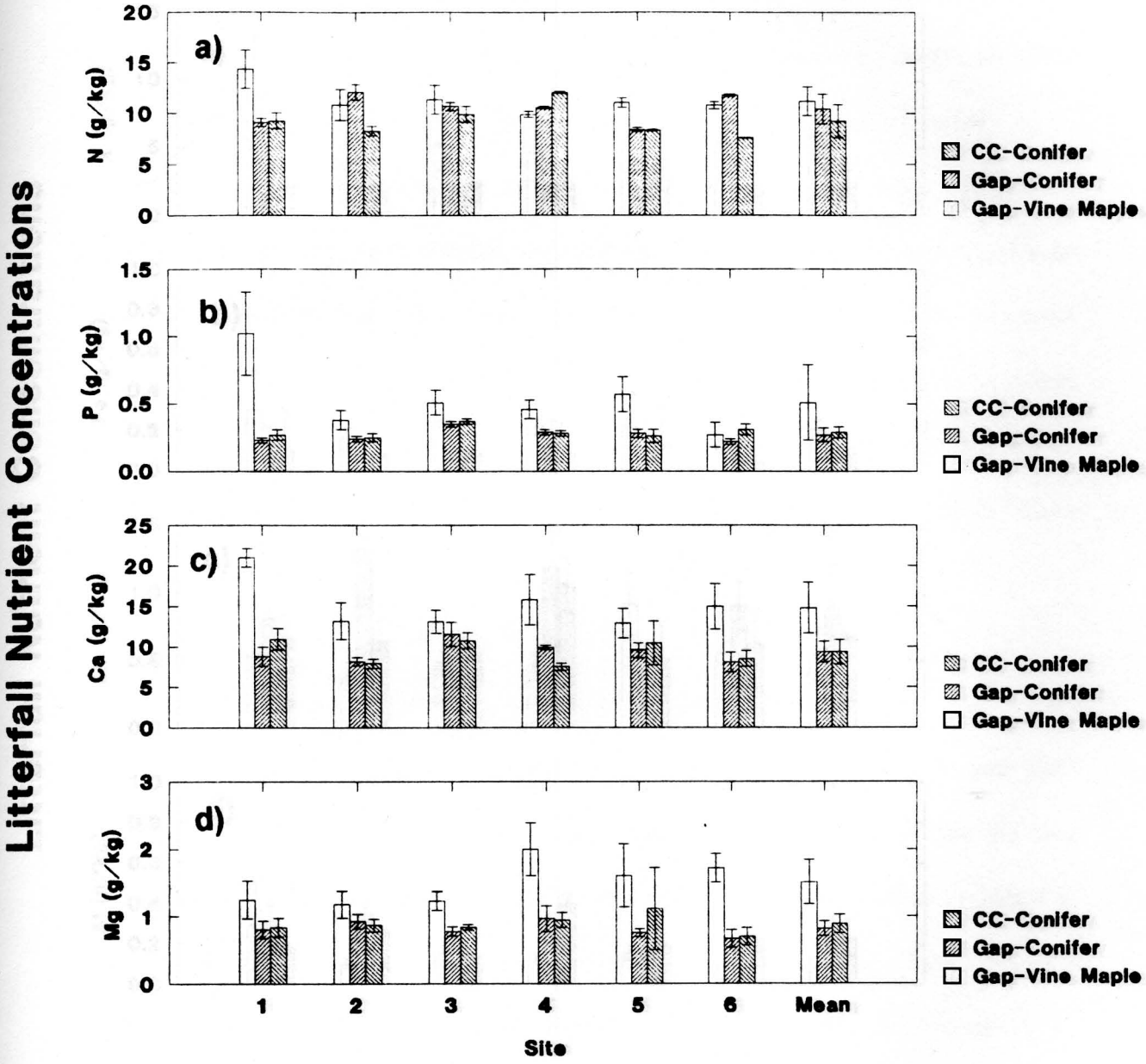

Figure 4.5 Mean a) N, b) P, c) Ca and d) Mg concentrations of litterfall during the fall time periods (%).

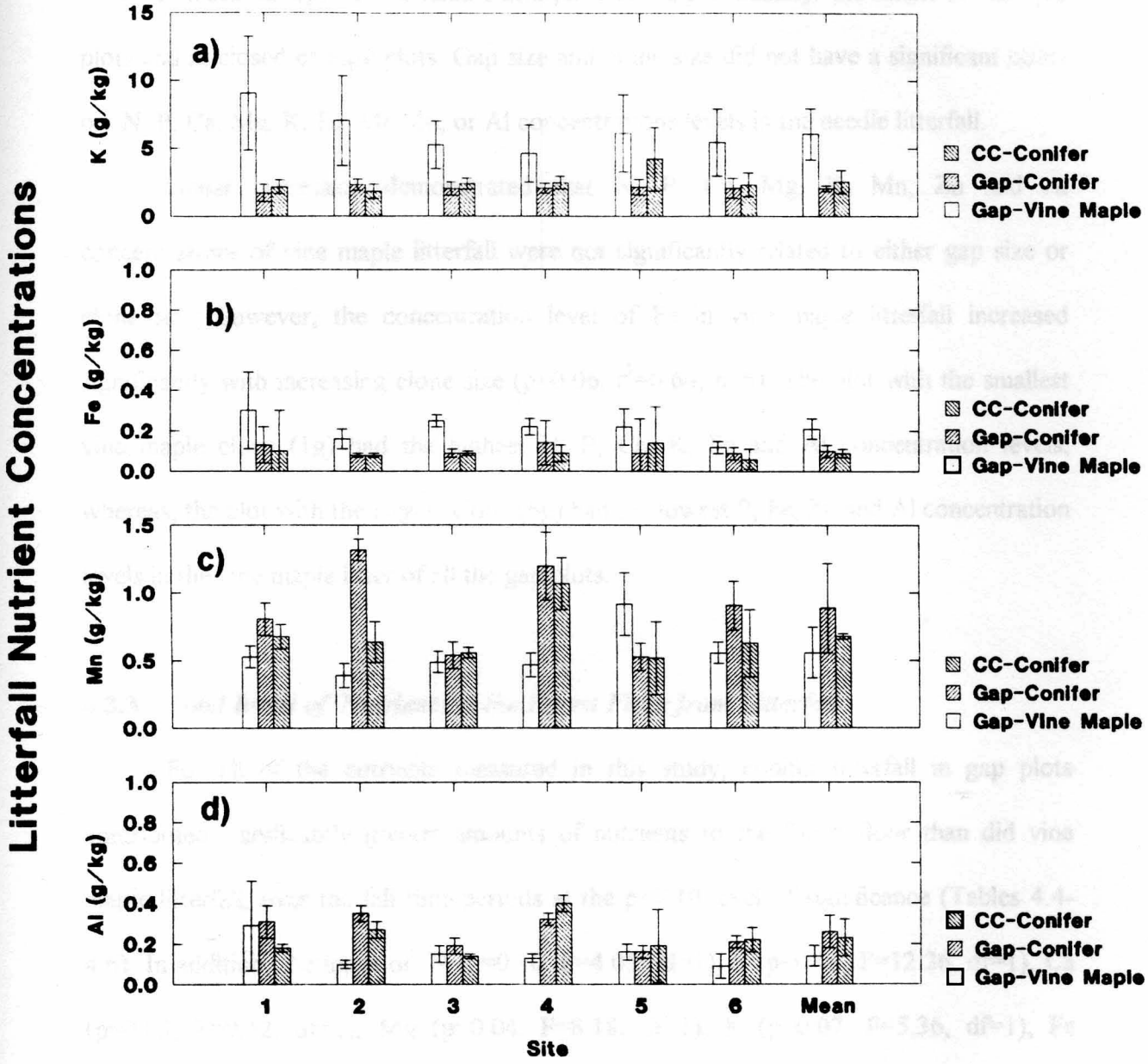

Figure 4.6 Mean a) K, b) Fe, c) Mn and d) Al concentrations of litterfall during the fall time periods (%).

plots. The concentration levels of P (0.03% gap - 0.03% closed canopy), Ca (0.94% gap - 0.94% closed canopy), Fe (0.01% gap - 0.01% closed canopy), and Zn (0.004% gap - 0.003% closed canopy) in the needle litterfall were approximately the same in the gap plots and in closed canopy plots. Gap size and clone size did not have a significant effect on N, P, Ca, Mg, K, Fe, Mn, Zn, or Al concentrations levels in the needle litterfall.

Linear regression demonstrated that N, P, Ca, Mg, K, Mn, Zn and Al concentrations of vine maple litterfall were not significantly related to either gap size or clone size; however, the concentration level of Fe in vine maple litterfall increased significantly with increasing clone size ($p=0.06$, $r^2=0.64$, $n=6$). The plot with the smallest vine maple clone (1g) had the highest N, P, Ca, K, Fe and Al concentration levels; whereas, the plot with the largest clone (6g) had the lowest P, Fe, Zn and Al concentration levels in the vine maple litter of all the gap plots.

4.3.3 *Total Input of Nutrients to the Forest Floor from Litterfall*

For all of the nutrients measured in this study, conifer litterfall in gap plots contributed significantly greater amounts of nutrients to the forest floor than did vine maple litterfall, over the fall time periods at the $p=0.10$ level of significance (Tables 4.4-4.6). In addition, the input of N ($p=0.10$, $F=4.05$, $df=1$), P ($p=0.02$, $F=12.26$, $df=1$), Ca ($p=0.03$, $F=9.42$, $df=1$), Mg ($p=0.04$, $F=8.18$, $df=1$), K ($p=0.07$, $F=5.36$, $df=1$), Fe ($p=0.09$, $F=4.58$, $df=1$), and Zn ($p=0.05$, $F=6.65$, $df=1$) from conifer litterfall was significantly lower in gap plots than that in closed canopy plots during the fall. However,

Table 4.4

Total input of nutrients to the forest floor from vine maple litterfall during the fall time periods (kg/ha). The individual plot means and standard deviations were calculated from total amount of needle litterfall during the fall collection multiplied by the mean nutrient concentration of the two collection periods for each composite sample (n=3). The overall means and standard deviations for the gap and closed canopy were calculated from the means of the individual plots (n=6).

Plot	N	P	Ca	Mg	K	Fe	Mn	Zn	Al
1g	0.49 ± 0.27	0.04 ± 0.02	0.71 ± 0.35	0.04 ± 0.03	0.32 ± 0.18	0.01 ± 0.01	0.02 ± 0.01	0.003 ± 0.00	0.009 ± 0.00
2g	1.41 ± 0.33	0.05 ± 0.01	1.70 ± 0.26	0.15 ± 0.04	0.91 ± 0.18	0.02 ± 0.01	0.05 ± 0.01	0.011 ± 0.00	0.013 ± 0.00
3g	0.58 ± 0.12	0.03 ± 0.02	0.66 ± 0.39	0.06 ± 0.04	0.27 ± 0.18	0.01 ± 0.01	0.02 ± 0.01	0.005 ± 0.00	0.007 ± 0.00
4g	0.83 ± 0.24	0.04 ± 0.01	1.29 ± 0.26	0.16 ± 0.04	0.40 ± 0.18	0.02 ± 0.01	0.04 ± 0.01	0.010 ± 0.00	0.010 ± 0.00
5g	1.67 ± 0.32	0.09 ± 0.01	1.93 ± 0.34	0.24 ± 0.01	0.91 ± 0.08	0.01 ± 0.03	0.07 ± 0.01	0.003 ± 0.00	0.008 ± 0.00
6g	2.14 ± 0.35	0.05 ± 0.01	2.95 ± 0.27	0.34 ± 0.01	1.07 ± 0.33	0.02 ± 0.03	0.11 ± 0.00	0.012 ± 0.00	0.019 ± 0.00
Gap	1.19 ± 0.66	0.05 ± 0.02	1.54 ± 0.86	0.17 ± 0.11	0.65 ± 0.35	0.02 ± 0.01	0.05 ± 0.04	0.007 ± 0.00	0.011 ± 0.00

Table 4.5

Total input of nutrients to the forest floor from needle litterfall during the fall time periods (kg/ha). The individual plot means and standard deviations were calculated from total amount of needle litterfall during the fall collection multiplied by the mean nutrient concentration of the two collection periods for each composite sample (n=3). The overall means and standard deviations for the gap and closed canopy were calculated from the means of the individual plots (n=6).

Plot	N	P	Ca	Mg	K	Fe	Mn	Zn	Al
1g	3.83 ± 2.32	0.10 ± 0.06	3.67 ± 2.14	0.34 ± 0.19	0.74 ± 0.49	0.05 ± 0.03	0.33 ± 0.16	0.02 ± 0.01	0.13 ± 0.06
1c	5.68 ± 0.68	0.17 ± 0.02	6.72 ± 1.13	0.52 ± 0.10	1.32 ± 0.13	0.06 ± 0.01	0.42 ± 0.08	0.02 ± 0.00	0.11 ± 0.02
2g	5.12 ± 0.34	0.10 ± 0.01	3.45 ± 0.22	0.39 ± 0.02	0.97 ± 0.06	0.03 ± 0.00	0.56 ± 0.04	0.02 ± 0.00	0.15 ± 0.01
2c	3.29 ± 0.15	0.10 ± 0.01	3.14 ± 0.15	0.34 ± 0.02	0.72 ± 0.05	0.03 ± 0.01	0.25 ± 0.02	0.01 ± 0.00	0.11 ± 0.02
3g	8.57 ± 0.81	0.28 ± 0.02	9.24 ± 1.22	0.62 ± 0.05	1.62 ± 0.05	0.07 ± 0.02	0.43 ± 0.05	0.03 ± 0.00	0.15 ± 0.03
3c	9.58 ± 0.31	0.36 ± 0.01	10.38 ± 0.94	0.81 ± 0.08	2.29 ± 0.21	0.09 ± 0.01	0.54 ± 0.03	0.03 ± 0.00	0.13 ± 0.01
4g	2.07 ± 0.07	0.06 ± 0.00	1.93 ± 0.09	0.19 ± 0.01	0.40 ± 0.02	0.03 ± 0.01	0.23 ± 0.00	0.01 ± 0.00	0.06 ± 0.01
4c	4.81 ± 0.23	0.11 ± 0.01	2.98 ± 0.04	0.38 ± 0.02	0.99 ± 0.09	0.03 ± 0.01	0.43 ± 0.02	0.01 ± 0.00	0.16 ± 0.01
5g	5.39 ± 0.94	0.18 ± 0.04	6.11 ± 0.54	0.48 ± 0.04	1.40 ± 0.35	0.06 ± 0.03	0.34 ± 0.01	0.02 ± 0.00	0.10 ± 0.00
5c	7.71 ± 0.31	0.24 ± 0.06	9.61 ± 0.25	1.03 ± 0.56	3.84 ± 1.90	0.12 ± 0.11	0.47 ± 0.19	0.04 ± 0.02	0.17 ± 0.07
6g	2.67 ± 0.24	0.05 ± 0.00	1.86 ± 0.43	0.16 ± 0.05	0.47 ± 0.01	0.02 ± 0.00	0.21 ± 0.04	0.01 ± 0.00	0.05 ± 0.00
6c	4.80 ± 0.55	0.20 ± 0.04	5.40 ± 0.98	0.44 ± 0.05	1.47 ± 0.05	0.05 ± 0.03	0.40 ± 0.05	0.02 ± 0.00	0.14 ± 0.04
Gap	4.61 ± 2.34	0.13 ± 0.09	4.38 ± 2.84	0.36 ± 0.17	0.93 ± 0.50	0.04 ± 0.02	0.35 ± 0.13	0.02 ± 0.01	0.11 ± 0.04
CC	5.98 ± 2.28	0.20 ± 0.10	6.38 ± 3.15	0.59 ± 0.27	1.77 ± 1.15	0.06 ± 0.04	0.42 ± 0.10	0.02 ± 0.01	0.14 ± 0.03

Table 4.6

Total input of nutrients to the forest floor from litterfall during the fall time periods (kg/ha). The individual plot means and standard deviations were calculated from the sum of the total input of nutrients to the site from vine maple litterfall and needle litterfall (n=3). The overall means and standard deviations for the gap and closed canopy were calculated from the means of the individual plots (n=6).

Plot	N	P	Ca	Mg	K	Fe	Mn	Zn	Al
1g	4.32 ± 2.44	0.13 ± 0.06	4.39 ± 2.26	0.38 ± 0.20	1.06 ± 0.47	0.06 ± 0.17	0.34 ± 0.17	0.02 ± 0.01	0.14 ±0.07
1c	5.68 ± 0.68	0.17 ± 0.02	6.72 ± 1.13	0.52 ± 0.10	0.32 ± 0.13	0.06 ± 0.08	0.42 ± 0.08	0.02 ± 0.00	0.11 ±0.02
2g	6.53 ± 0.67	0.15 ± 0.01	5.15 ± 0.43	0.55 ± 0.05	0.88 ± 0.24	0.05 ± 0.05	0.61 ± 0.05	0.03 ± 0.00	0.16 ±0.04
2c	3.29 ± 0.15	0.10 ± 0.01	3.14 ± 0.15	0.34 ± 0.02	0.72 ± 0.05	0.03 ± 0.02	0.25 ± 0.02	0.01 ± 0.00	0.11 ±0.02
3g	9.15 ± 0.95	0.31 ± 0.04	9.90 ± 1.37	0.69 ± 0.07	1.89 ± 0.25	0.08 ± 0.05	0.46 ± 0.05	0.03 ± 0.00	0.16 ±0.03
3c	9.58 ± 0.61	0.36 ± 0.01	10.38 ± 0.94	0.81 ± 0.08	2.29 ± 0.21	0.09 ± 0.03	0.54 ± 0.03	0.03 ± 0.00	0.13 ±0.01
4g	2.90 ± 0.31	0.09 ± 0.01	3.21 ± 0.28	0.35 ± 0.05	0.80 ± 0.19	0.05 ± 0.01	0.28 ± 0.01	0.02 ± 0.00	0.07 ±0.01
4c	4.81 ± 0.23	0.11 ± 0.01	2.98 ± 0.04	0.38 ± 0.02	0.99 ± 0.09	0.03 ± 0.02	0.43 ± 0.02	0.01 ± 0.00	0.16 ±0.01
5g	7.06 ± 1.22	0.27 ± 0.04	8.04 ± 0.16	0.72 ± 0.04	2.31 ± 0.10	0.09 ± 0.04	0.48 ± 0.04	0.03 ± 0.00	0.12 ±0.01
5c	7.71 ± 0.31	0.24 ± 0.06	9.61 ± 2.48	1.03 ± 0.56	3.83 ± 1.90	0.12 ± 0.19	0.47 ± 0.19	0.04 ± 0.02	0.17 ±0.07
6g	4.80 ± 0.11	0.10 ± 0.01	4.81 ± 0.18	0.49 ± 0.05	1.53 ± 0.33	0.05 ± 0.04	0.32 ± 0.04	0.02 ± 0.00	0.07 ±0.01
6c	4.80 ± 0.55	0.20 ± 0.04	5.40 ± 0.98	0.44 ± 0.05	1.47 ± 0.17	0.05 ± 0.05	0.40 ± 0.05	0.02 ± 0.00	0.14 ±0.04
Gap	5.79 ± 2.23	0.17 ± 0.09	5.92 ± 2.52	0.53 ± 0.15	1.58 ± 0.57	0.06 ± 0.02	0.40 ± 0.11	0.03 ± 0.01	0.12 ± 0.04
CC	5.98 ± 2.28	0.20 ± 0.10	6.37 ± 3.15	0.59 ± 0.27	1.77 ± 1.15	0.06 ± 0.04	0.42 ± 0.10	0.02 ± 0.01	0.14 ± 0.03

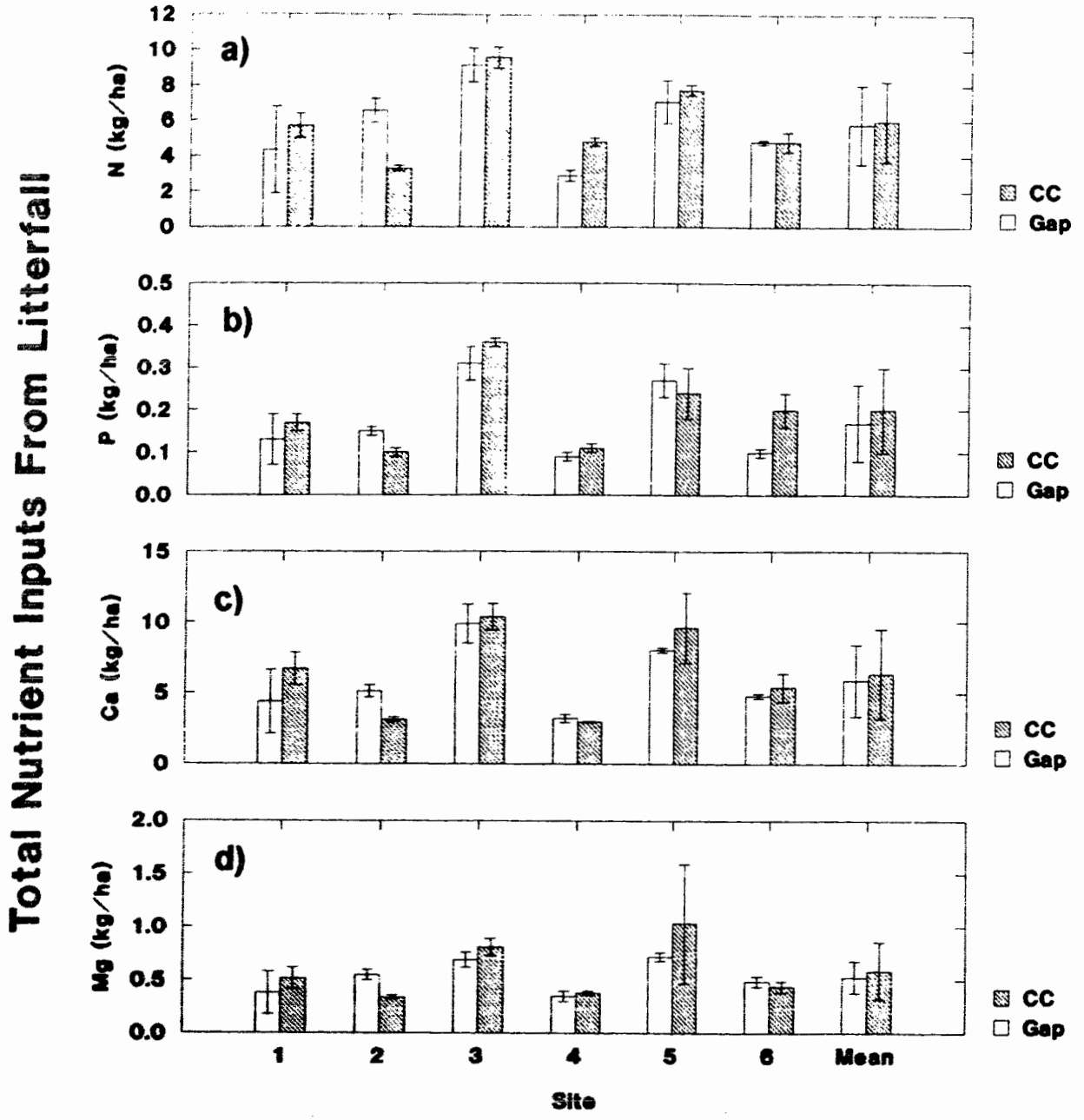

Figure 4.7 Total input of a) N, b) P, c) Ca and d) Mg to the forest floor from litterfall during the fall time periods (kg/ha).

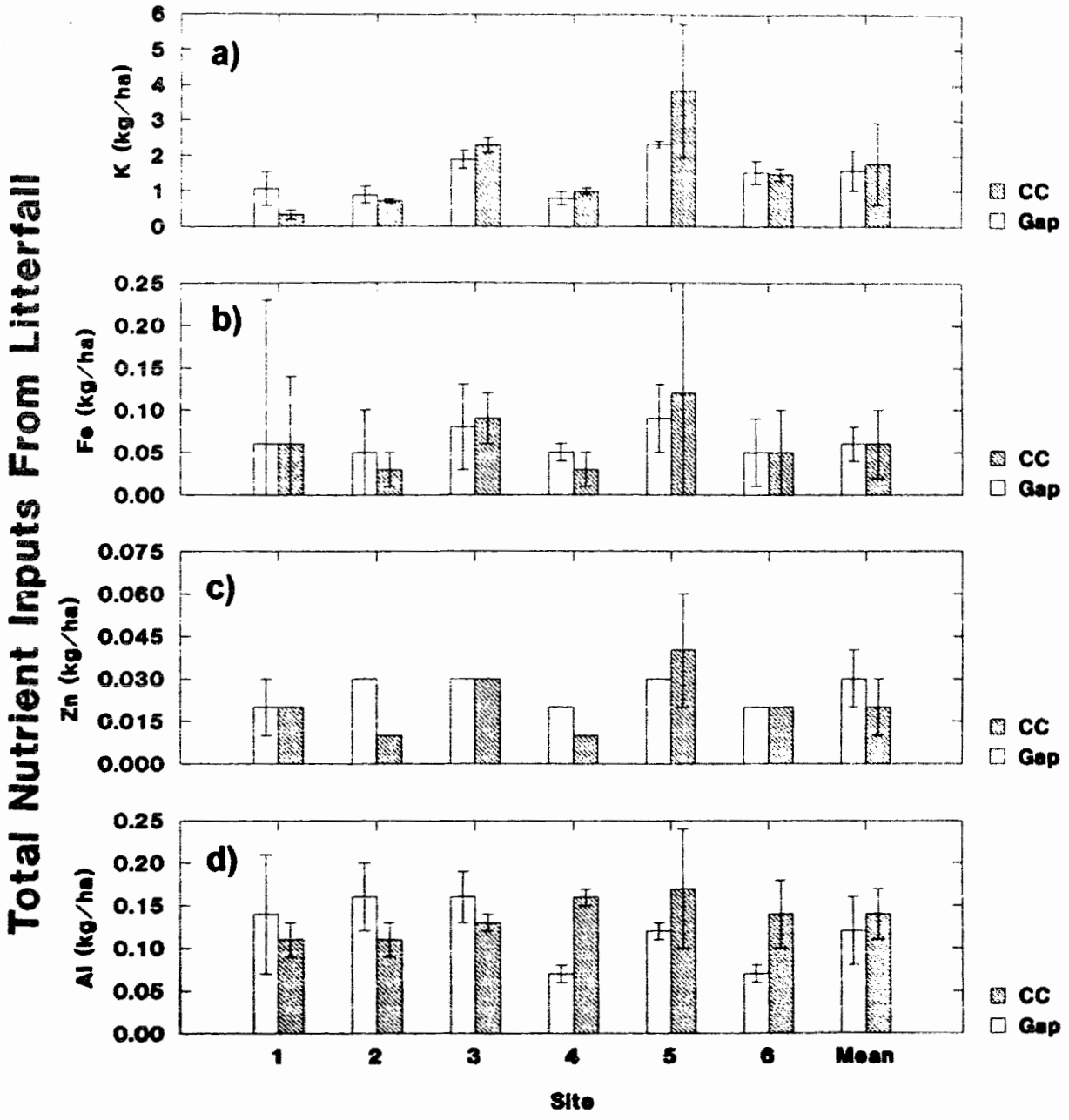

Figure 4.8 Total input of a) K, b) Fe, c) Mn and d) Al to the forest floor from litterfall during the fall time periods (kg/ha).

the total input of the nutrients N, P, Ca, Mg, K, Fe, Mn, Zn, and Al from vine maple and needle litterfall on gap plots did not differ significantly from the input of these nutrients from needle litterfall on closed canopy plots during the fall (Figures 4.7 to 4.8). During the fall, canopy gap area and vine maple clone size did not have a significant effect on the total amount of nutrient inputs to the forest floor from litterfall in vine maple gaps.

4.3.4 *Litter Decomposition*

After intervals of decomposition of six months and one year respectively, the mass loss of vine maple litter compared to needle litter was significantly greater on both the gap plots ($p=0.001$, $F=50.54$, $df=1$ and $p=0.003$, $F=31.14$, $df=1$; respectively) and closed canopy plots ($p=0.001$, $F=48.18$, $df=1$ and $p=0.007$, $F=18.814$, $df=1$; respectively); a similar result was obtained for the closed canopy plots after two years of decomposition ($p=0.09$, $F=4.32$, $df=1$) (Table 4.7 and Figures 4.9-4.10). After two years on the gap plots, however, the mass loss of vine maple litter compared to needle litter due to decomposition was approximately the same.

After six months of decomposition, the percentage mass loss for vine maple litter ranged from 34 to 53%; and, for the needle litter, the percentage value ranged from 23 to 38%. After one year, the percentage mass loss of the vine maple litter ranged from 37 to 68%; whereas, for the needle litter, the percentage mass loss ranged from 32 to 42%. After two years, the percentage spread of mass loss of the vine maple litter was 34 to 64%, which was approximately the same as the percentage spread in the mass loss of the needle litter (39-57%).

Table 4.7

Percentage mass loss due to decomposition. The individual plot means and standard deviations consist of three samples per plot. The overall means and standard deviations for the gap and closed canopy were calculated from the means of the individual plots.

Plot	Vine Maple Litter - Six Months	Vine Maple Litter - One Year	Vine Maple Litter - Two Years	Needle Litter - Six Months	Needle Litter - One Year	Needle Litter - Two Years
1g	52.8 ± 4.5	51.9 ± 7.1	41.0 ± 15.5	30.8 ± 0.8	38.0 ± 7.1	45.0 ± 5.0
1c	49.4 ± 2.2	61.6 ± 5.1	59.7 ± 3.7	37.4 ± 4.2	39.3 ± 2.0	41.2 ± 8.1
2g	42.8 ± 1.5	55.2 ± 2.2	51.5 ± 3.0	32.7 ± 0.3	41.2 ± 1.3	54.0 ± 6.1
2c	34.3 ± 6.9	39.0 ± 3.1	28.5 ± 13.7	30.5 ± 1.3	36.8 ± 1.0	39.3 ± 8.0
3g	42.2 ± 3.7	49.4 ± 3.0	51.4 ± 3.0	30.0 ± 0.9	37.5 ± 1.3	39.2 ± 8.1
3c	42.9 ± 2.1	53.0 ± 5.2	57.3 ± 2.0	31.5 ± 1.3	38.0 ± 1.7	43.8 ± 3.9
4g	50.1 ± 4.3	59.1 ± 2.1	56.0 ± 5.5	31.8 ± 0.8	42.3 ± 2.1	57.0 ± 3.9
4c	41.7 ± 1.4	54.3 ± 4.6	56.6 ± 0.9	30.2 ± 0.3	41.8 ± 1.2	40.3 ± 3.8
5g	37.9 ± 1.2	37.8 ± 1.0	34.7 ± 16.8	28.8 ± 2.3	34.2 ± 1.8	43.2 ± 3.8
5c	43.1 ± 3.0	51.2 ± 0.9	63.6 ± 27.8	28.3 ± 1.0	37.8 ± 0.8	39.8 ± 7.6
6g	38.2 ± 5.5	51.6 ± 3.6	54.2 ± 5.4	23.2 ± 1.4	32.3 ± 4.9	40.3 ± 2.4
6c	43.8 ± 4.0	67.8 ± 5.0	58.2 [a]	29.8 ± 3.0	43.2 ± 0.6	51.3 ± 8.1
Gap	44.0 ± 6.2	50.8 ± 7.2	48.1 ± 8.4	29.6 ± 3.4	37.8 ± 3.7	46.4 ± 3.0
CC	42.5 ± 4.8	54.5 ± 9.8	53.8 ± 12.6	31.3 ± 3.2	39.5 ± 2.5	42.6 ± 4.5

[a] Based on one sample only

The greatest percentage of mass loss for both litter types occurred within the first six months of decomposition. After two years of decomposition, there was no sizable increase in mass loss of either litter type, compared to the mass loss values obtained for each litter type after one year of decomposition. For the vine maple litter, an average mass loss of 44% occurred within the first six months, with an additional 7% occurring in the second six months, and no additional loss occurring within the second year. For the needle litter, an average mass loss of 30% occurred within the first six months, with an

additional 8% occurring in the second six months, and an additional 3% occurring in the second year.

Mass losses of vine maple litter at the end of six months of decomposition were higher (not significantly) beneath the vine maple gap plots than beneath the closed canopy plots. However, at the end of both one year and two years of decomposition, mass losses of vine maple litter were higher (not significantly) beneath the closed canopy plots than beneath the vine maple gap plots. At the end of each decomposition time period of six months and one year, the mass losses for the needle mix were higher (not significantly) beneath the closed canopy plots than that beneath the vine maple gap plots. At the end of two years of decomposition, mass losses beneath the gap plots, though higher than that beneath the closed canopy plots, were not significantly different. Consequently, at the p=0.10 level, no significant differences in decomposition rates were found between vine maple litter on gap plots and vine maple litter on closed canopy plots, and conifer litter on gap plots and conifer litter on closed canopy plots.

Vine maple litter decomposition rates in vine maple gap plots were significantly related to clone size, aspect and percentage of open sky. Vine maple litter decomposition rates at the end of six months had a significant inverse relationship to the size of the vine maple clone: the larger the clone, the slower the rate of decomposition ($p=0.10$, $r^2=0.55$, $n=6$) (Figure 4.11a). Vine maple litter decomposition rates at the end of one year were significantly related to aspect: the more south-facing, the higher rates of decomposition ($p=0.05$, $r^2=0.65$, $n=6$) (Figure 4.11b). Decomposition rates of vine maple litter in vine maple gaps were also significantly related to the amount of incoming light in the summer

months, in terms of percentage of open sky and total direct and diffuse light. At the end of one year, the decomposition rates were significantly lower the greater the percentage of open sky ($p=0.01$, $r^2=0.86$, $n=6$), and the greater the amount of direct and diffuse light ($p=0.02$, $r^2=0.77$, $n=6$). Similarly, at the end of two years, the decomposition rates were significantly lower the greater the percentage of open sky ($p=0.08$, $r^2=0.57$, $n=6$) and the greater the amount of direct and diffuse light ($p=0.033$, $r^2=0.72$, $n=6$) (Figures 4.11c-4.12c).

Similarities were found in the factors influencing the rates of conifer litter decomposition to those influencing vine maple litter decomposition. At the end of six months, decomposition rates of needles were significantly related to canopy gap area and the size of the vine maple clone: the larger the gap area, the slower the rate of decomposition ($p=0.06$, $r^2=0.61$, $n=6$); and the larger the clone, the slower the rate of decomposition ($p=0.01$, $r^2=0.83$, $n=6$) (Figures 4.13a and 4.13b). At the end of one year, the rate of mass loss of needle litter was significantly related to aspect, and to clone size: the more south facing in aspect, the higher the rates of decomposition ($p=0.01$, $r^2=0.88$, $n=6$); and the smaller the clone, the higher the rate of decomposition ($p=0.09$, $r^2=0.56$, $n=6$) (Figure 4.13c and 4.14a). At the end of one year, the rate of mass loss of needle litter was also related to percent open sky in the vine maple gaps ($p=0.08$, $r^2=0.57$, $n=6$); the greater the percentage of open sky, the slower the rate of decomposition (Figure 4.15b). After two years of decomposition, the rate of mass loss of needle litter in vine maple gaps was significantly related to aspect ($p=0.06$, $r^2=0.64$, $n=6$); the more south-facing, the higher the rates of decomposition (Figure 4.15c).

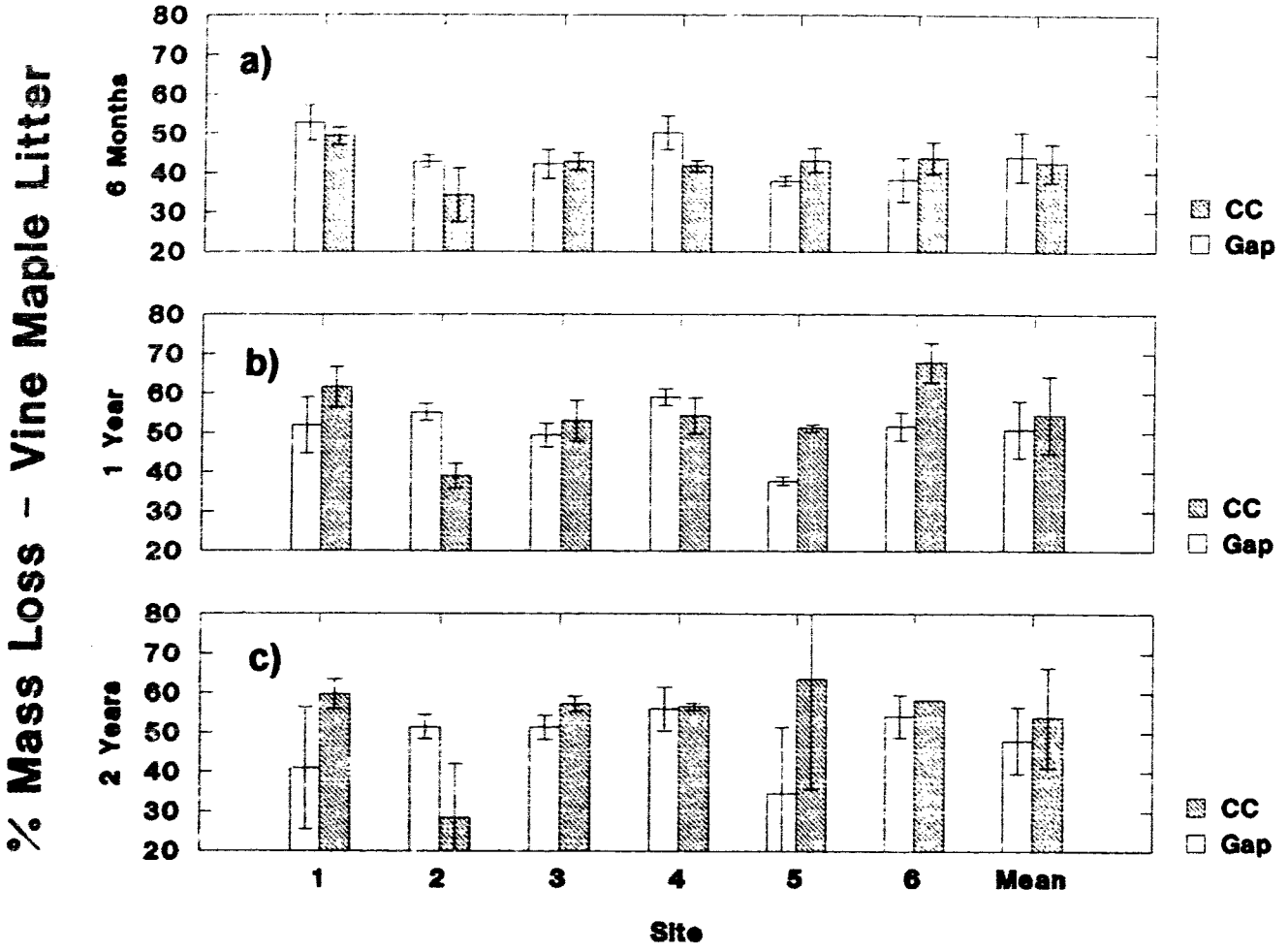

Figure 4.9 Percent mass loss of vine maple litter after a) six months, b) one year, and c) two years of decomposition.

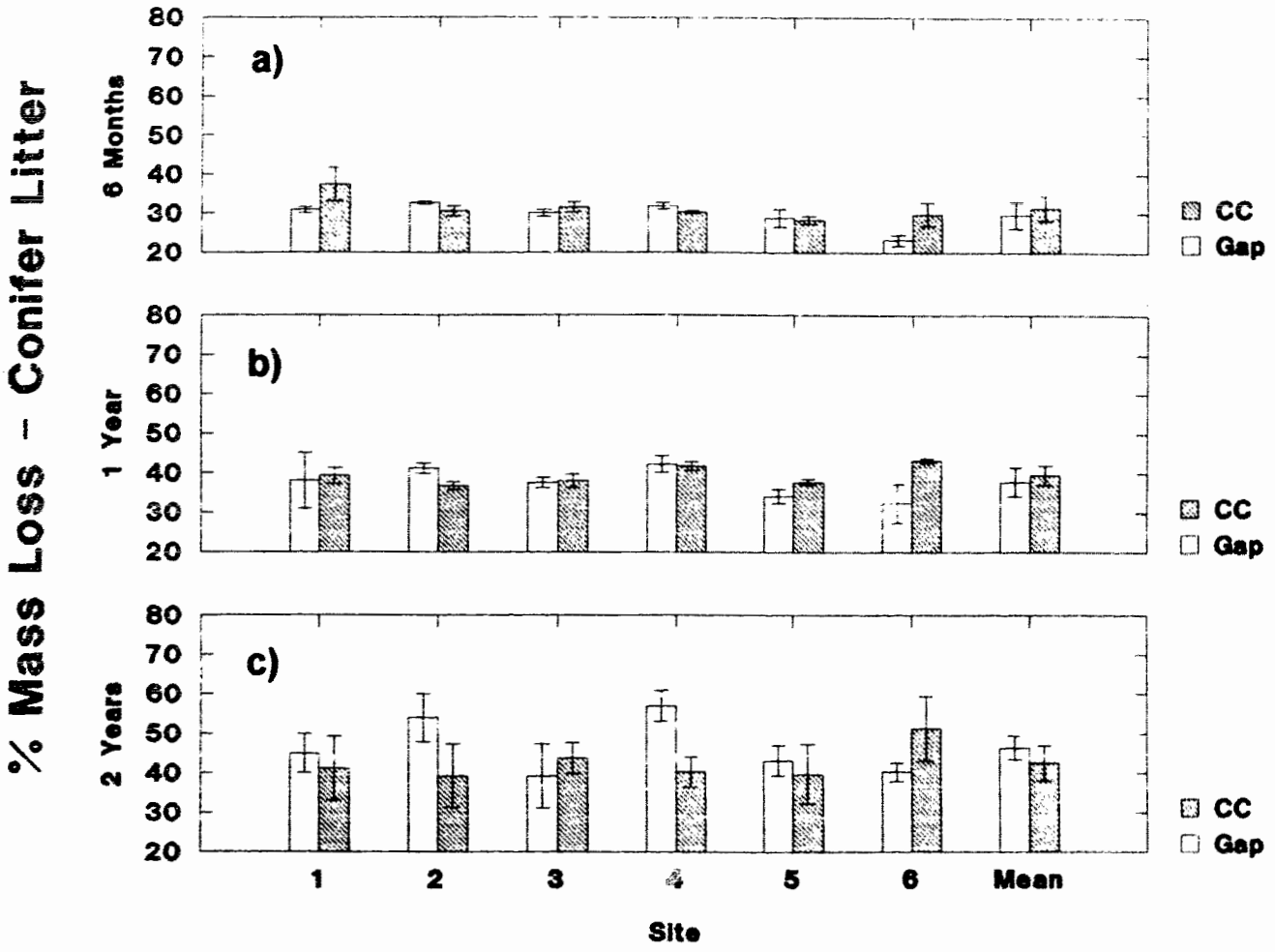

Figure 4.10 Percent mass loss of conifer litter after a) six months, b) one year, and c) two years of decomposition.

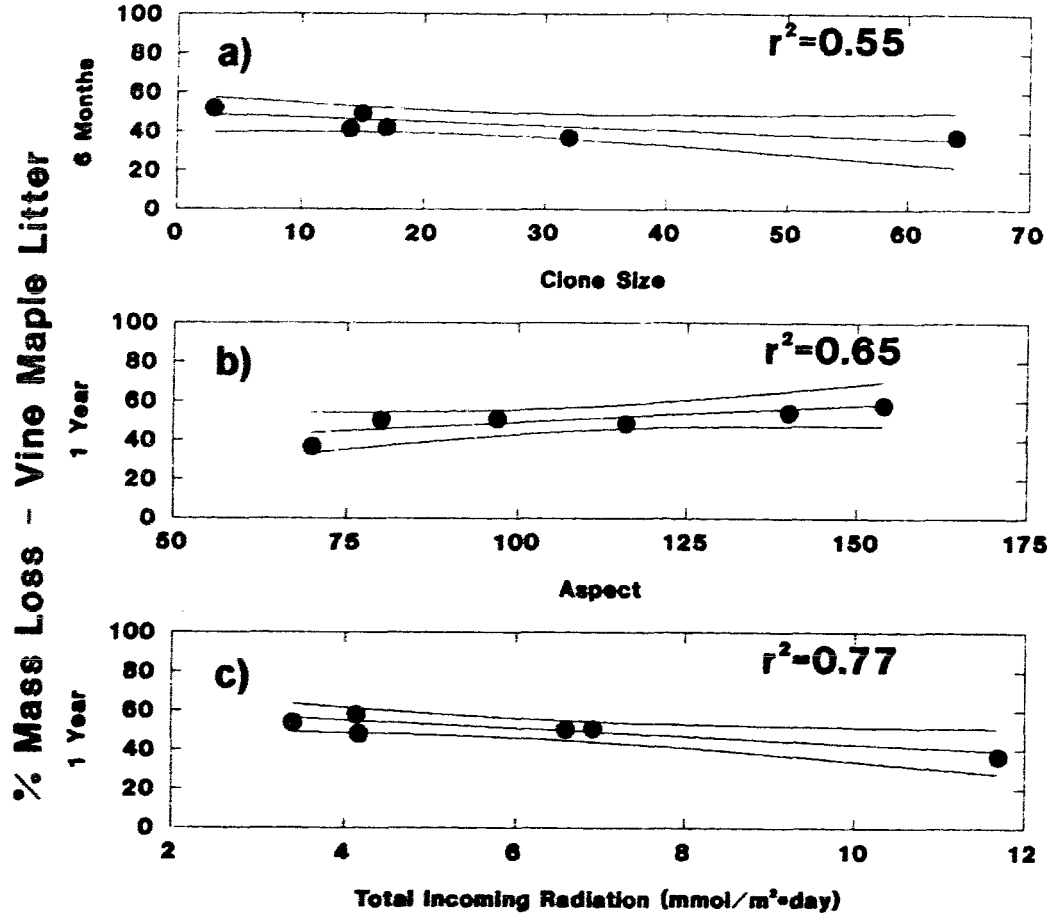

Figure 4.11 a) A regression of vine maple litter decomposition rates in vine maple gaps after six months of decomposition to the size of the vine maple clone. A regression of vine maple litter decomposition rates after one year of decomposition in vine maple gaps to b) aspect and c) total direct and diffuse incoming radiation in the summer months.

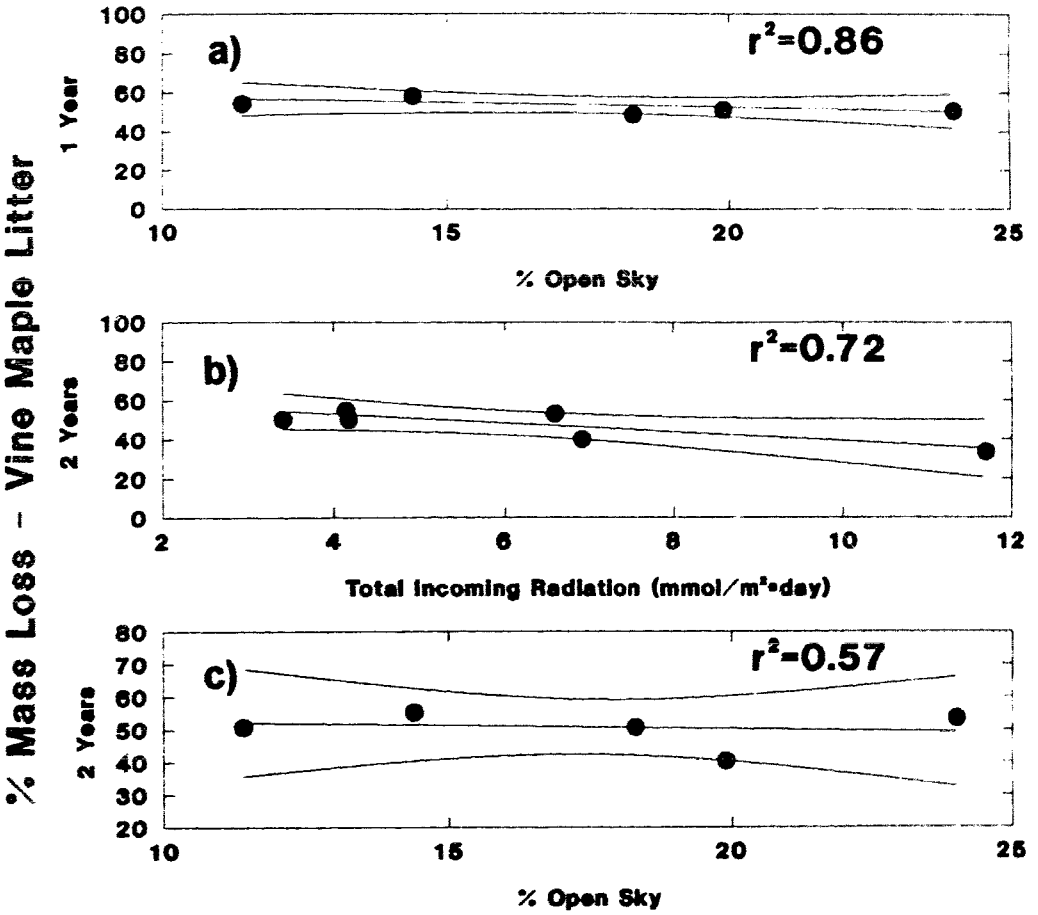

Figure 4.12 a) A regression of vine maple litter decomposition rates in vine maple gaps after one year of decomposition to % open sky in the summer months. A regression of vine maple litter decomposition rates in vine maple gaps after two years of decomposition to b) total direct and diffuse incoming radiation in the summer months and c) % open sky in the summer months.

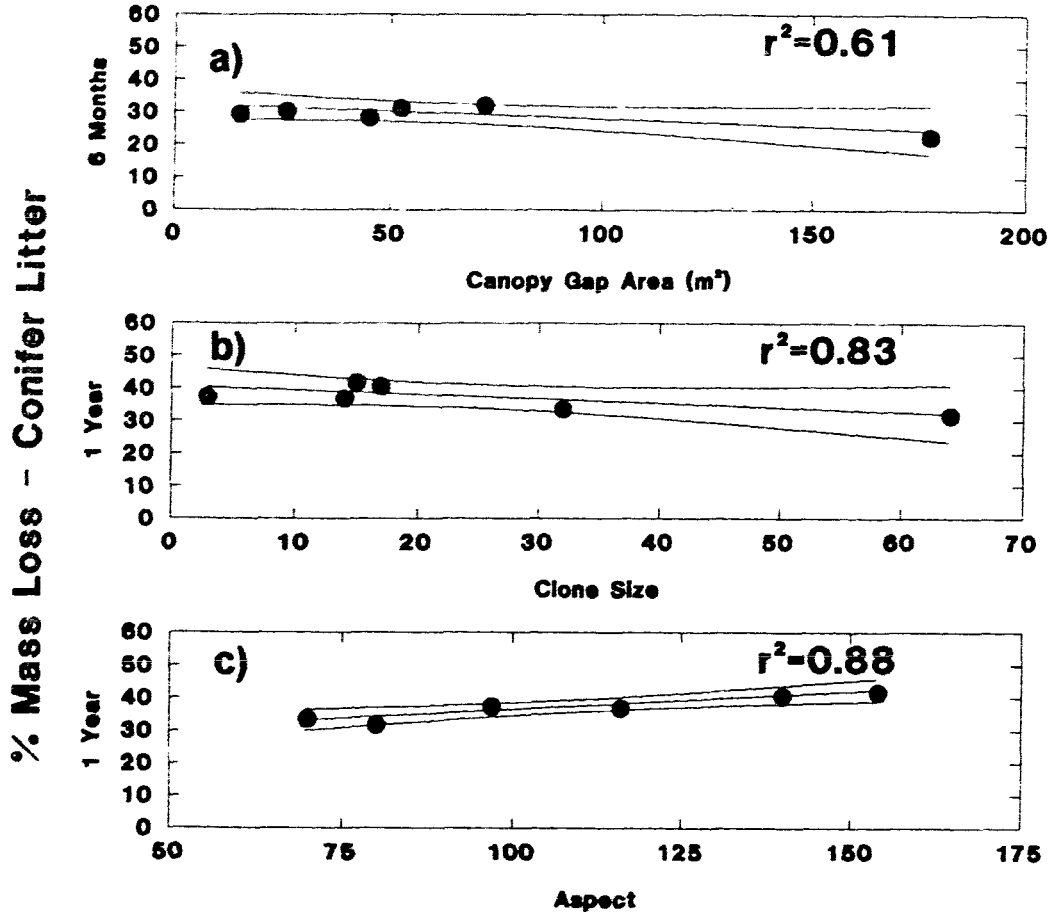

Figure 4.13 A regression of conifer litter decomposition rates in vine maple gaps after six months of decomposition to a) canopy gap area and b) the size of the vine maple clone. c) A regression of conifer litter decomposition rates in vine maple gaps after one year of decomposition to aspect.

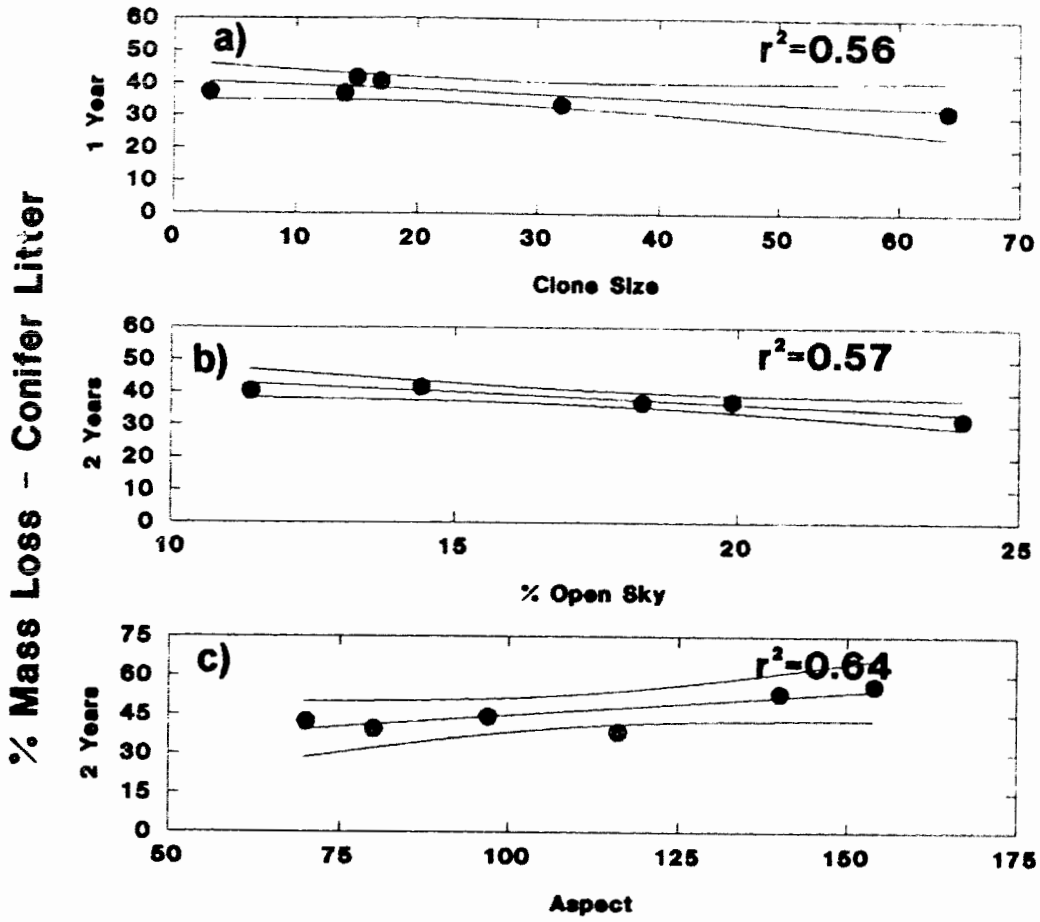

Figure 4.14 A regression of conifer litter decomposition rates in vine maple gaps after one year of decomposition to a) the size of the vine maple clone and b) % open sky in the summer months. c) A regression of conifer litter decomposition rates in vine maple gaps after two years of decomposition to aspect.

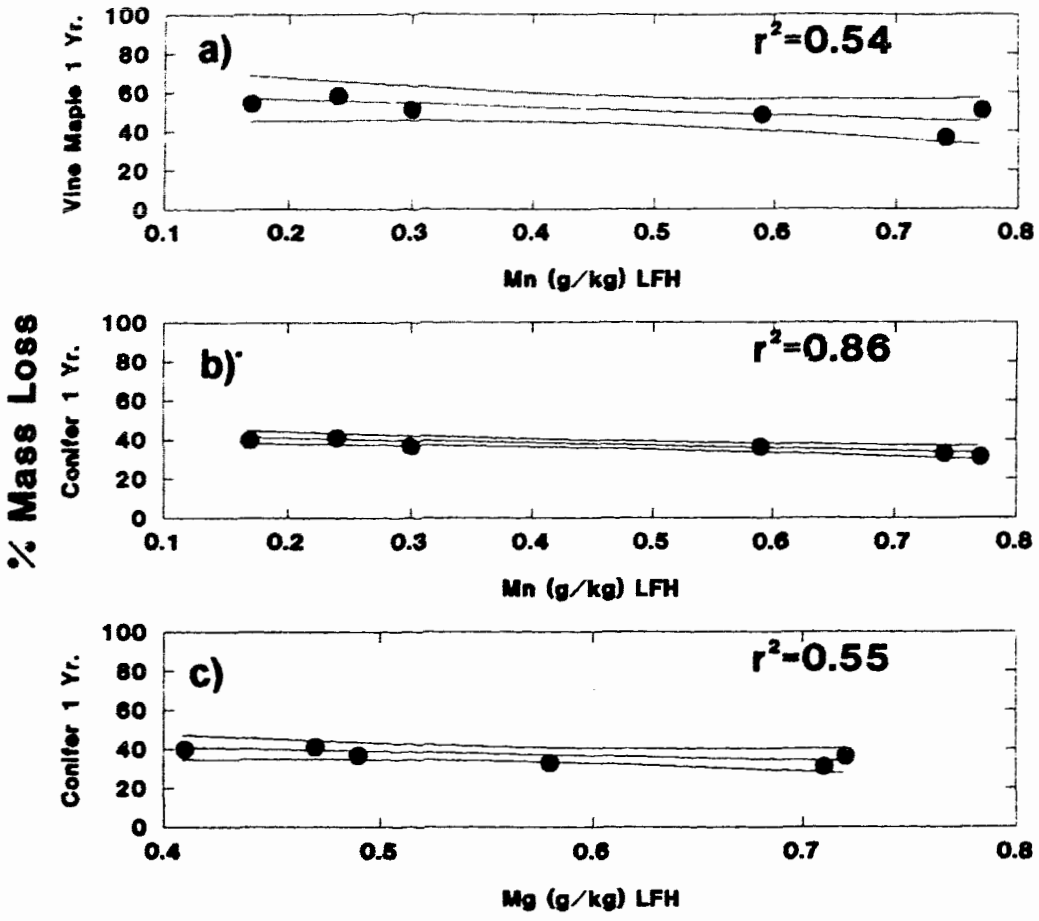

Figure 4.15 a) A regression of vine maple litter decomposition rates in vine maple gaps after one year of decomposition to Mn concentrations in the LFH. b) A regression of conifer litter decomposition rates in vine maple gaps after one year to b) Mn and c) Mg concentrations in the LFH.

At the end of one year in gap plots, nutrient concentration levels of Mn in the forest floor were significantly related to the rates of decomposition of both vine maple litter and conifer litter: the higher the concentration level of Mn in the forest floor, the lower the rate of decomposition of vine maple litter ($p=0.10$, $r^2=0.54$, $n=6$) and conifer litter ($p=0.01$, $r^2=0.86$, $n=6$). Similarly, at the end of one year in gap plots, the rate of decomposition of conifer litter was significantly related to the concentration levels of Mg in the forest floor: the higher the concentration level of Mg in the forest floor, the lower the rate of decomposition ($p=0.09$, $r^2=0.55$, $n=6$) (Figures 4.15a to 4.15c).

4.4 Discussion

The results of this component of the study indicate that soil properties in vine maple gaps may be influenced by several characteristics of litterfall and litter decomposition that differ from those of the surrounding forest. It was predicted that vine maple gaps experience faster decomposition rates, lower rates of litterfall, and higher litterfall nutrient concentration levels than those beneath the surrounding closed canopy. In the literature, vine maples are generally associated with rapid rates of litter decomposition and nutrient cycling, and vine maple litter supplies a rich source of nutrients to the forest floor (Haeussler et al. 1990; Krajina et al. 1982). In this study, needle litterfall was significantly greater in closed canopy plots than that in the gap plots in the fall; however, there was no difference in total annual litterfall between gap and closed canopy plots. The N, P, Ca, Mg, K, Fe and Zn concentration levels were significantly higher in vine maple litterfall than those in conifer litterfall; however,

concentrations of Mn and Al were significantly lower in vine maple litterfall than those in conifer litterfall. In addition, there was no significant difference in the total input of nutrients from litterfall during the fall to gap plots compared to closed canopy plots. Vine maple litter decomposed faster than conifer litter; however, the conifer litter on gap plots decomposed at the same rate as the conifer litter on closed canopy plots.

The power of the statistical tests in this study was likely quite low, due to the small sample size, small effect size and the high within-plot sample variability (Toft and Shea 1983). Furthermore, some of the properties of litterfall accumulation and litter decomposition, that were not significantly different between the gap and closed canopy, were found to be influenced by the size of the vine maple clone and the size of the canopy gap in vine maple gap plots. Some of the differences between gap and closed canopy plots which were not found to be statistically significant may be significant, however, with a larger sample size. Consequently, many of the trends found in this study, though statistically insignificant, are worth noting as they indicate possible areas for further research.

4.4.1 *Litterfall*

With respect to the rate of litterfall as measured by the amount of litter accumulation by weight, the hypothesis tested was that the rates are lower in vine maple gaps than in closed canopy plots. As predicted, the amount of conifer litterfall beneath closed canopy plots was significantly greater than that beneath vine maple gaps (by 50%) during the fall. Furthermore, in gaps during the fall, the total amount of vine maple

litterfall was four times less than the total amount of needle litterfall. That there was less leaf biomass in the vine maple gaps is likely the reason for their lower amounts of litterfall during the fall.

The total annual litterfall, though greater beneath the closed canopy plots than that beneath the vine maple gap plots, was not significantly different. In contrast, Fried et al. (1990) found that the total annual litterfall was substantially greater on bigleaf maple sites than on Douglas-fir sites in Oregon, probably due to the greater leaf biomass of bigleaf maples. Several reasons may account for the similarity in the amounts of annual litterfall beneath vine maple gaps and the surrounding closed canopy forest. Firstly, the large proportion, by weight, of needles in the litterfall beneath vine maple gaps made the total weight of litterfall not significantly different from the weights of needle litterfall in the closed canopy plots. Russel (1973) noted that although vine maple makes an important relative contribution to the total understory biomass, the relative biomass contribution of vine maple is slight when all forest vegetation layers are considered. In the winter, Fried et al. (1990) measured considerable amounts of Douglas-fir litterfall beneath bigleaf maple, attributing the high litterfall to winter storms. Secondly, vine maple gaps may be too small to have a significant effect on annual litterfall input. The low D/H ratios of the vine maple gaps (Table 1.2) indicates that they would likely receive considerable windblown litter from the surrounding conifer forest. The non-significant difference in litterfall beneath vine maple gaps and the surrounding forest is consistent with findings of Chapter 2, where temperature and moisture regimes were not found to significantly differ; and with the findings of McGhee (1996) that light regimes were not significantly different.

Thus, it appears that vine maple gaps may behave as though they were not gaps at all at the forest floor.

Linear regression indicated that the rate of vine maple litterfall was significantly related to clone size: the larger the clone, the higher the rate of vine maple litterfall. The rate of vine maple litterfall reaching the forest floor also significantly increased the concentration levels of Ca in the LFH. This result may be explained by the fact that Ca concentrations of vine maple litterfall are significantly higher than those of conifer litterfall. The rate of needlefall reaching the forest floor in vine maple gaps was not significantly related to canopy gap size, nor was the rate of needlefall significantly related to nutrient concentrations in the LFH of gap plots. This result may be explained by wind effects distributing conifer litterfall relatively uniformly among vine maple gaps regardless of their size.

4.4.2 *Nutrient Concentrations in Litterfall*

Vine maple litter is believed to provide a rich supply of nutrients to the site (Haeussler et al. 1990), and is associated with high rates of nutrient cycling (Krajina et al. 1982). Compared to Douglas-fir litter, vine maple litter has a higher concentration of N (Triska and Sedell 1976). In this study, the hypothesis tested was that the concentrations of nutrients in the litterfall of vine maple gaps are higher than those of the closed canopy. Consistent with the findings of Russell (1973) that vine maple leaves are rich in nutrients, the results of this study indicated that the concentration levels of N, P, Ca, Mg, K, Fe, and Zn, in vine maple litter were significantly higher than those of conifer litter.

Therefore, the hypothesis was supported, suggesting that over time, vine maple may improve the nutritional status of soils within the study area. This finding correlates with that of Chapter 3 where it was found that concentrations of Ca, Mg, K, and Al are significantly higher in the LFH beneath vine maple gaps than those beneath the closed canopy.

4.4.3 *Input of Nutrients to Forest Floor From Litterfall*

Vine maple litterfall provides a rich supply of nutrients to the site, and is associated with high levels of nutrient cycling (Krajina et al. 1982). In this study, the hypothesis tested was that the concentrations of nutrients in the litterfall of vine maple gap plots are higher than those of the closed canopy plots. Over the fall time periods, the total amount of the nutrients N, P, Ca, Mg, K, Fe, Mn, Zn, and Al from vine maple litterfall and needle litterfall on gap plots did not differ significantly from the total input of these nutrients from needle litterfall on closed canopy plots. Although the nutrient content of vine maple litterfall was significantly greater than that of conifer litterfall for all of the nutrients measured in this study, conifer litterfall in gap plots over the fall time periods contributed significantly greater amounts of nutrients to the forest floor than did vine maple litterfall. This is consistent with the finding of Russel (1973) that although vine maple makes an important relative contribution to the total understory biomass, the relative biomass contribution of vine maple is slight when all forest vegetation layers are considered. Neither vine maple gap area, nor the size of the vine maple clone significantly influenced the total input of nutrients to the forest floor from litterfall in gap plots. As noted above,

these results may be explained by wind effects distributing litterfall from all sources relatively uniformly among vine maple gaps regardless of their size.

4.4.4 *Litter Decomposition*

Due to its higher nutrient content, lower lignin content, and higher proportion of surface area to mass, hardwood litter generally decomposes more rapidly than conifer litter; and is believed to enhance the productivity of conifer stands (Assman 1970; Perry 1970; Fried et al. 1990). According to a general observation made by Haeussler et al. (1990), vine maple litterfall decomposes faster than conifer litterfall. In this study, the hypotheses tested were that decomposition rates in vine maple gaps are higher than those in closed canopy plots, and that vine maple litter decomposes faster than conifer litter. While the hypothesis that vine maple litter decomposes faster than conifer litter was supported, the hypothesis that the decomposition rates in vine maple gaps are faster than those in closed canopy plots was not supported.

Vine maple litter is believed to decompose more rapidly than Douglas-fir litter due to a lower lignin content and higher level of nitrogen concentration (Haeussler et al. 1990). In addition, the thin leaves of vine maple contribute to their faster decomposition rates (Haeussler et al. 1990). Consistent with findings from other studies on hardwood-conifer comparisons (Chalinor 1968; Gessel and Turner 1974; Tappeiner and Alm 1975; Fried et al. 1989), this study found that vine maple litter decomposes faster than conifer litter. The rapid decomposition of vine maple litter -- as postulated for bigleaf maple litter (Fried 1989) -- could benefit both maple and the surrounding conifers because nutrients

rapidly become available to tree roots rather than being sequestered in the forest floor, as is the case under conifers.

While the mass loss of vine maple litter was found to be significantly greater than conifer litter at the end of the six-month and one-year decomposition periods on both the gap and closed canopy plots, and at the end of the two-year decomposition period on the closed canopy plots; the mass loss was approximately the same for vine maple litter and conifer litter at the end of the two year decomposition period on the gap plots. This result agrees with that in a study in a forest in western Washington where significant differences in weight loss were observed at the end of one year, but no significant differences were evident at the end of two years of decomposition among different species (Edmonds 1980). For both litter types in this study and in the study by Edmonds (1980), it is likely that only the very slowly decomposable material such as lignin remains after two years of decomposition.

For both litter types, the greatest percentage of mass loss occurred within the first six-month period. After two years of decomposition, there was no sizable increase in mass loss in either litter type compared to the mass loss values reached after one year of decomposition. Two factors can explain these results. Firstly, litter typically has an initial rapid phase of decomposition followed by a slower phase, due to the faster decomposing component breaking down first leaving behind the more slowly decomposing component such as lignin (Harmon et al. 1990). Harmon et al. (1990) found that vine maple leaf litter has a much larger amount of this 'fast' component (29-40%) than Douglas-fir litter (7-13%). Secondly, the first six-month period coincided with the winter months

(characterized by an abundance of moisture and mean monthly temperatures above freezing), resulting in continued decomposition activity and large losses due to leaching; whereas, the second six months coincided with the summer months (characterized by a moisture deficit especially in late summer), resulting in lower decomposition rates. However, in the summer of 1994 when measurements were made, there did not appear to be a moisture deficit in the study area (see Chapter 2).

Differences in rates of decomposition of vine maple litter on gap plots and vine maple litter on closed canopy plots were not statistically significant. Similarly, differences in decomposition rates between conifer litter on gap plots, and conifer litter on closed canopy plots, were not significant. Rates of decomposition are dependent on a number of factors including the availability of nutrients, moisture, energy, and the type of soil organisms involved in decomposition (Pritchett and Fisher 1987). According to Krajina et al. (1982), Moder humus tends to form beneath vine maple (which generally has a higher biological activity than Mor humus forms associated with conifer litter); however, this could not be confirmed as humus forms were not measured in this study. The results of Chapter 2 on temperature and moisture regimes showed that there were no significant differences in the amounts of precipitation reaching the forest floor throughout the year in gaps and closed canopy plots, and that there was no significant difference in soil temperature or soil moisture in gap and closed canopy plots throughout the year. In addition, McGhee (1996) found no difference in the amount of solar radiation reaching the forest floor in vine maple gaps compared to that in closed canopy plots. Therefore, the lack of differences in decomposition rates between vine maple gaps and closed canopy

may be explained by the lack differences in environmental conditions influencing decomposition rates on the sites.

Depending on the litter type, rates of mass loss within gap plots were also related to gap size and clone size characteristics. The rate of vine maple litter and needle litter decomposition in vine maple gaps within the first six months was significantly related to the size of the vine maple clone: the larger the clone the slower the rate of decomposition. This result may be explained by the finding that larger gaps (which support larger clones) had significantly cooler mid-day air temperatures than smaller gaps in the summer and fall and had significantly lower soil moisture content throughout the year, both of which may hinder decomposition rates. A similar result was obtained in a study in a mixed montane forest in China. This study, on the effects of gap size on litter decomposition rates, also found that smaller developmental gaps (5 m diameter) had faster rates of decomposition than larger developmental gaps (30 m diameter or larger) (Zhang and Liang 1995). Zhang and Liang (1995) observed that larger gaps received greater amounts of precipitation and solar radiation at the forest floor than smaller gaps, and concluded that larger gaps allow soil moisture to evaporate more quickly because of the reduced influence of the surrounding trees. The combination of higher and more stable moisture and temperature regimes in small gaps (and under the canopy) resulted in higher microbial activities and higher decomposition rates in small gaps.

At the end of the one year period, the concentration levels of Mn in the forest floor were significantly related to the rates of decomposition of both vine maple litter and conifer litter in gap plots: the higher the concentration of Mn in the forest floor, the lower

the rates of decomposition. These results suggest that higher Mn levels may adversely affect the activity of soil decomposers. As noted in the previous chapter, Mn concentrations in the LFH were found to be significantly higher beneath larger gaps than beneath smaller gaps; and larger gaps were found to have slower rates of decomposition than those of smaller gaps.

Chapter 5

Conclusions

Chapter 5
Conclusions

5.1 Introduction

A concern over the maintenance of long-term forest site productivity in coastal British Columbia warrants a close examination of the roles of hardwoods in these conifer-dominated forest ecosystems. The overall goal of the research presented in this thesis was to determine if significant differences in soil properties exist between the forest soils of vine maple canopy gaps as compared to those of the surrounding closed canopy western hemlock forest. The two research objectives addressed were :

1. To examine selected inherent soil properties within persistent vine maple gaps in a coastal western hemlock forest to determine if the gaps are edaphic or priority in origin.

2. To examine soil properties influenced by the forest canopy to determine the effects of persistent vine maple gaps on forest soils.

To determine if vine maple gaps are *edaphic* gaps (characterized by a difference in the inherent edaphic conditions of the site), or *priority gaps* (characterized by no differences in the inherent edaphic conditions of the site) in origin, selected inherent soil properties of six persistent vine maple gaps were compared to those of six closed canopy plots. The paired plots had similar aspect and relief (including slope and slope position). To determine the effects of persistent vine maple gaps on the physical and chemical properties of the forest floor and surface mineral soil horizons, soil properties in the vine maple gaps were compared to those in the adjacent western hemlock forest. Litterfall accumulation, litter decomposition, temperature regimes, and moisture regimes were

examined to gain insights into why soil properties did or did not differ between vine maple gaps and the surrounding forest.

5.2 Origin of Persistent Vine Maple Gaps

The first objective of this study was to determine if persistent vine maple gaps are edaphic or priority in origin. In conifer forests of coastal B.C. and the Pacific Northwest, hardwood species, while pioneer species, rarely persist into late stages of stand development. However, in the Oregon Coast Range, Russel (1973) found that vine maple abundance follows a bi-modal distribution during the successional time frame (early abundance after clearcutting, followed by near extinction under conifers at the age of 40 years, and increasing in abundance again as openings in the forest canopy occur); while, in coastal B.C. forests, McGhee (1996) observed that vine maple occupies some canopy openings (not created by tree mortality) throughout stand development. Other studies have observed that vine maple is able to persist through the stem exclusion phase of stand development, and well-established patches have been found in old growth Douglas-fir forests (O'Dea et al. 1995; Spies et al. 1990).

The reason that vine maple has the ability to resist the regeneration of taller canopy dominants and subsequent canopy closure can be explained by the determination of the origin of vine maple gaps. For vine maple gaps to be priority in origin, vine maple must establish a dense mat of stems early in stand development that is large enough to prevent invasion of the site by conifers and the subsequent overtopping of the site as the stand grows up around them (McGhee 1996). Vine maple has been observed to have an initial growth rate that is much faster than that of most conifers, quickly allowing it to establish a

position in a stand following disturbance that seriously interferes with the growth of Douglas-fir and western hemlock (Krajina et al. 1982; McGhee 1996) -- as do many other hardwoods and shrubs on conifers (Tappeiner and Zasada 1993). For vine maple gaps to be edaphic in origin, inherent soil properties or site characteristics must give vine maple a competitive advantage over other species. Previous studies have shown that small-scale edaphic differences can strongly influence species composition, forest structure, and ecosystem function (Lertzman et al. 1996); and, that species with a competitive advantage on specific inherent conditions can exclude other species from growing on these sites.

Since the inherent soil properties of the vine maple sites are characteristics not expected to have been altered since the time of stand establishment, a finding of differences in inherent soil characteristics of vine maple gaps compared to those in the surrounding forest would support the hypothesis that persistent vine maple gaps are edaphic in origin; whereas, a finding of no differences in inherent soil characteristics would support the hypothesis that persistent vine maple gaps are priority in origin. Indirect evidence that vine maple gaps may be priority gaps comes from an observation of McGhee (1996) that there are an equivalent number of large stumps in vine maple gaps compared to the surrounding forest, indicating that the vine maple sites are equally suitable for the growth of conifers.

The inherent soil properties of vine maple gaps examined in Chapter 2 did not differ from those in the surrounding forest. In the vine maple gap plots, soil moisture readings below the rooting zone and groundwater table levels were not significantly different from those in the adjacent forest. There was an indication that soil moisture

regimes may possibly differ between vine maple gaps and the surrounding forest since (throughout the year) soil moisture values at the 80 cm level, and groundwater table levels readings were both higher in the vine maple gap plots compared to those in the surrounding forest. The small sample size, however, and the high within-plot sample variability may account for these differences not being statistically significant. The possibility exists therefore, that these differences may become significant with a larger sample size.

The results presented in Chapter 3 of this study relate to the relationship between vine maple gaps and physical and chemical properties of the forest floor and the mineral soil. Inherent soil property comparisons between the vine maple gaps and the surrounding closed canopy forest were made for soil texture, gravel content, and the pH level of the parent materials. The gravel content (measured at 5, 20, 50 and 100 cm) and the pH level of the parent materials (measured at 50 and 100 cm depths) did not differ significantly between vine maple gaps and the surrounding closed canopy forest. Likewise, no significant differences were found in soil texture (percentages of sand, silt and clay); and almost all of the samples collected from the study area fell within the loamy sand textural class.

Since the results from the comparison of selected inherent soil properties between persistent vine maple gaps and those of the surrounding closed canopy forest did not show any significant differences, the hypothesis of McGhee (1996) that persistent vine maple gaps are edaphic in origin is rejected. Consequently, the hypothesis of McGhee (1996) that persistent vine maple gaps are priority in origin is supported. The origin of persistent vine

maple gaps therefore, appears to be due to vine maple colonizing a site first, and establishing a dense mat of stems early in stand development that is large enough to prevent the subsequent regeneration of these sites by conifers. As the stand develops around these vine maple patches, a canopy gap appears in the mid to late successional stages.

5.3 Influence of Persistent Vine Maple Gaps on Forest Soil Properties

A number of researchers have identified the effects of vegetation on soil properties. For example, differences in soil properties have been observed due to different tree and understory species (Alban 1969, Challinor 1969, Fried et al. 1989, Lutz and Chandler 1946, Tappeiner and Alm 1975, Tarrant and Miller 1963); while other studies have focused on differences in chemical properties of litter and forest floors under different species (Fried et al. 1989, Gessel and Balci 1965, Gessel and Turner 1974, Grier and McColl 1971, MacLean and Wein 1978, Tarrant et al. 1951). The second objective of this study was to examine the physical and chemical soil properties influenced by the forest canopy to determine the effects of persistent vine maple gaps on forest soils. Mineral soil properties (including bulk density, organic matter concentration, pH, C/N ratio, total N concentration, and soil moisture) and forest floor properties (including depth, weight, and nutrient concentrations) of adjacent vine maple gaps and western hemlock forest were compared. To gain insights into why soil properties did or did not differ, litterfall accumulation, litter decomposition, temperature regimes, and moisture regimes, were compared on the paired plots.

A few studies have noted the influence on soil properties of canopy openings created by tree mortality (Mladenoff 1987, Vitousek and Denslow 1986). Such developmental gaps are characterized by a temporary release of resources at the forest floor (due to an increase in available energy and moisture), and a subsequent increase in nutrient availability (due to an increase in decomposition rates) (Pickett and White 1985). Over time, developmental gaps become absorbed into the surrounding closed canopy by the release of previously suppressed saplings, germination of dormant seeds in the soil seed bank, layering or sprouting of pre-disturbance plants, or germination of seeds brought into the gap by wind or animal transport (Feinsinger 1989). In contrast to developmental gaps, persistent vine maple gaps maintain their position in the stand throughout stand development; and several soil and microclimate properties typically associated with developmental gaps were not characteristic of vine maple gaps.

Unlike developmental gaps, vine maple gaps have remarkably similar temperature regimes to those in the adjacent forest. While air temperatures were significantly cooler in gap plots compared to the surrounding closed canopy forest in the spring and summer (likely due to the high evapotranspirational demands of vine maple), air temperatures in vine maple gaps were the same as those in the closed canopy forest in the fall and winter. Vine maple gaps did not significantly influence surface soil temperatures at any time of the year. These results support the finding of McGhee (1996) that there is no difference in light regimes between vine maple gaps and those of the surrounding forest. Since temperature affects decomposition rates, the results also show that temperature regimes

did not contribute to differences in soil properties under persistent vine maple gaps compared to the surrounding forest.

Vine maple gaps did not have a significant influence on moisture regimes, which is also unlike developmental gaps. The amount of precipitation reaching the forest floor was not significantly different in gap plots compared to closed canopy plots; although, gap plots did receive greater amounts of precipitation throughout the year. According to Denslow (1987), moisture levels in the upper soil horizons are consistently and significantly higher in gaps than in the adjacent forest understory in small and large gaps and in both rainy and dry seasons; however, in this study soil moisture content values (while lower at 30 cm and 50 cm in vine maple gaps than in the closed canopy throughout the year) were not significantly different between vine maple gaps and the surrounding forest. The slightly lower readings may be attributed to the high transpirational demands associated with vine maple, as evidenced by the relationship between vine maple clone size and soil moisture -- the greater the number of stems on the clone, the lower the soil moisture content within the upper 30 cm rooting zone. As soil moisture affects rates of leaching and decomposition, the results show that moisture regimes did not contribute to differences in soil properties under persistent vine maple gaps compared to the surrounding forest

While Fried et al. (1990) obtained inconsistent results for forest floor weight differences between bigleaf maple sites and Douglas-fir sites, in this study the weight of the forest floor -- though lower beneath vine maple gaps compared to the closed canopy -- were not significantly different. Since there were no differences in the total annual

accumulation and decomposition rates of litterfall, if follows that there would be no difference in forest floor weights. Only the depth of the forest floor was significantly different between vine maple gaps and the adjacent forest -- the forest floor was thinner in the gap plots compared to the closed canopy plots. This finding may be accounted for by the fact that vine maple litter (a component of the forest floor found only in gap plots) decomposes more quickly than conifer litter and therefore is incorporated more rapidly into the mineral soil. Further evidence of this is the shallower depth of the F horizon beneath vine maple gaps than beneath the closed canopy. Larger vine maple had significantly thicker forest floors than smaller vine maple gaps. This result may be accounted for by the finding that larger vine maple gaps had significantly larger rates of vine maple litterfall than smaller vine maple gaps.

In the mineral soils, no significant differences were found in physical soil properties influenced by the forest canopy between persistent vine maple gap plots and closed canopy plots. The bulk density of the surface mineral soil was not significantly different in vine maple gaps than those in the surrounding forest. This finding contrasts with that of Fried et al. (1990) who found the bulk densities of the surface mineral soil under some bigleaf maple sites to be significantly lower than those under Douglas-fir. The similarity in bulk density measurements in this study between vine maple gaps and the surrounding forest may be accounted for by the finding that there were no differences in rates of litterfall accumulation and litterfall decomposition. Larger vine maple gaps had a greater influence on physical properties than smaller vine maple gaps -- larger vine maple gaps had significantly lower bulk densities in the upper mineral soil than smaller vine maple gaps.

As noted above, this result may be accounted for by the finding that larger vine maple gaps had significantly larger rates of vine maple litterfall than smaller vine maple gaps.

With respect to the chemical soil properties of the mineral soil that may be influenced by the forest canopy, this study observed no significant differences between vine maple gaps and the adjacent forest. While higher, the pH levels were not significantly different in the upper mineral soils between vine maple gap plots and closed canopy plots. Organic matter concentration and total N content values of the upper mineral soils were similar between vine maple gaps and closed canopy plots; however, total N content values of the upper mineral soils were significantly higher beneath larger clones than beneath smaller clones. The latter result may be explained by the larger amount of vine maple litterfall beneath larger clones than smaller clones. Throughout the study area, the organic matter concentration (10 to 20%) and the total N concentration (0.21 to 0.50%) in the upper layers of the mineral soil indicated that the soils were relatively rich in organic matter and unlikely to be deficient in N (Watts 1983). In his study, Fried et al. (1990) found the organic C concentration and the total N content of the upper 10 cm of the mineral soil beneath bigleaf maple to be significantly higher that those of the surrounding conifer forest; however, he also found that bigleaf maple contributes significantly larger amounts of total annual litterfall than conifers, which was not the case for vine maple in this study. The C/N ratios, while lower in gap plots (24) at 10 cm than closed canopy plots (28), were not significantly different; however, a larger sample size may have produced significantly different C/N ratios. This finding is similar to that of Fried et al. (1990) for bigleaf maple. The possibly lower C/N ratios in the vine maple gaps may be

biologically important, since values above 25 suggest low N availability due to immobilization (Watts 1983).

With respect to the chemical soil properties of the forest floor that are influenced by the forest canopy, the study showed significant differences between vine maple gaps and the adjacent forest that were consistent with previous observations on soil properties beneath vine maple (Haeussler et al. 1990; UBC Bot. Garden 1976; Krajina et al. 1982). Meidinger and Pojar (1991) have noted that the storage of nutrients in vegetation and forest floor is extremely important in the maintenance of ecosystem productivity in soils in the Coastal Western Hemlock biogeoclimatic zone in which the study area is located. Results of this study showed that the LFH beneath gap plots had significantly higher total Ca, Mg, K, and Al concentrations than the LFH beneath the closed canopy plots; however, the total amounts (weight) of N, P, K, Ca, Mg, Mn, Fe, Zn, and Al stored in the LFH of both gaps and closed canopy plots were not significantly different. In his study, Fried et al. (1990) also found that the forest floor beneath bigleaf maple had higher concentrations of Ca and Mg, but no difference was observed in the weight of nutrients in the forest floor beneath bigleaf maple and Douglas-fir. The pH level of the LFH was significantly higher in the gap plots than in the closed canopy plots, further indicating that vine maple returns a higher amount of bases to the forest floor from litterfall.

In the fall, litterfall accumulations were significantly greater in closed canopy plots than in vine maple gap plots; however, no significant differences in total annual litterfall accumulations were found between gaps and closed canopy plots. Larger vine maple clones had significantly higher rates of litterfall accumulation than smaller vine maple

clones. The litterfall accumulation beneath vine maple gaps compared to conifers were different from those of bigleaf maple; bigleaf maple has significantly higher amounts of total annual litterfall than Douglas-fir (Fried 1989). Compared to conifer litterfall, the concentrations of N , P, Ca, Mg, K, Fe ,and Zn, in vine maple litterfall were significantly higher; and the concentrations of Mn and Al were significantly lower. However, there were no significant differences in the total input of nutrients to gaps and closed canopy plots from litterfall during the fall. For bigleaf maple, Fried et al. (1990) found that the concentrations of most nutrients were significantly higher in bigleaf maple litter than in Douglas-fir litter, and (unlike this study) bigleaf maple contributed a greater mass of nutrients to the forest floor through litterfall than Douglas-fir.

Vine maple litter decomposed faster than conifer litter; however, litter on gap plots decomposed at the same rate as litter on clo ed canopy plots. Since vine maple gaps did not have significantly greater amounts of energy and moisture at the forest floor compared to that beneath the closed canopy, the similarity in decomposition rates between gap and closed canopy plots is not surprising. In gap plots, however, decomposition rates were significantly influenced by clone size and gap size: larger gaps and larger clones had slower rates of decomposition. The lower soil moisture content of the surface soils beneath larger vine maple gaps than beneath smaller vine maple gaps may account for the lower decomposition rate beneath larger vine maple gaps.

In summary, unlike developmental gaps, vine maple gaps do not appear to significantly influence temperature and moisture regimes or rates of litter decomposition. Compared to conifer litter, vine maple litter had higher concentrations of N , P, Ca, Mg,

K, Fe and Zn, which resulted in higher pH levels in the forest floor and higher concentrations of bases (Ca, Mg, K) in the forest floor in persistent vine maple gaps. This suggests that vine maple gaps may improve the nutritional status of soils within the study area. The slight differences in organic matter concentration, total N, C/N ratio and pH of the upper mineral soil between the vine maple gaps and the adjacent western hemlock sites were not significant. Larger vine maple gaps had significantly higher rates of litterfall, slower rates of decomposition, higher bulk densities and total N contents in the upper mineral soil, and thicker forest floors, than smaller vine maple gaps. This study is consistent with the findings of a recent review by Binkley (1995) who found that soils can dramatically differ under different species of trees; however, he observed that no study has shown that any species uniformly pushes all soil variables in unfavourable (or favourable) directions.

Many soil and site properties do not significantly differ between vine maple gaps and the surrounding conifer forest for several possible reasons. Firstly, the similarities in temperature and moisture regimes and rates of litter decomposition between vine maple gaps and the surrounding closed canopy forest are consistent with the low D/H ratios of vine maple gaps (Table 1.2) since the microclimate of gaps with low D/H ratios is moderated by the shade of surrounding trees (Canham et al. 1990; Smith 1986). Secondly, vine maple foliage may have a significant moderating effect on temperature and moisture regimes at the forest floor. Thirdly, the small contribution of vine maple litter compared to the total amount of litterfall, relative to most other hardwood species, suggests that vine maple may require a greater length of time to have a significant

influence on chemical soil properties than other hardwoods. Lastly, there may be significant differences between vine maple gaps and the surrounding conifer forest however, they may not have been detected because the power of the statistical tests in this study were quite low -- because of the small sample size, small effect size, and the high within-plot sample variability (Toft and Shea 1983). Further research, therefore, with a larger sample size would be helpful in clarifying the role of vine maple gaps in the ecology of coastal conifer forests of southwestern British Columbia.

5.4 Significance of Research

Persistent vine maple gaps are priority in origin and since they differ greatly from developmental gaps, the results of this study are important to the understanding of the role of vine maple in the Coastal Western Hemlock biogeoclimatic zone. The results also contribute to the information base from which forest managers and conservation officers manage ecosystems. Traditionally, vine maple is considered to be a competitive species that should be removed from coniferous forest management areas. Over the course of several rotations -- as suggested by Fried et al. (1990) for bigleaf maples -- vine maple is likely to have beneficial influences on soil properties, offsetting its impact as a competitor and justifying its role on commercial sites. Since the conservation of vine maple gaps contributes to the maintenance of biodiversity and structural diversity in our forests, its removal may have ecological consequences. As noted by Fried et al. (1990), the current productive capability of the forest soils in coastal British Columbia and the American Pacific Northwest result from thousands of years of shifting mosaics of conifers and

hardwoods; therefore, concern for maintaining long term soil productivity warrants a close examination of the influence of hardwood species on soil properties and the implication of removing hardwoods from commercial conifer forests.

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