ANALYTICAL STUDY OF PLANT/ENVIRONMENT INTERACTIONS IN THIMBLEBERRY AND DEVIL'S CLUB

By

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Abstract

The morphology, phenology and stem demography of devil's club and thimbleberry were examined to elucidate their niche utilization strategies. The study was conducted in the Kitimat River valley in west central B.C. during the 1986 and 1987 growing seasons. Thimbleberry was sampled in a girdled alder site and a nongirdled alder site, whereas devil's club was sampled in an old growth forest. The variation in the plant characters, as summarized by principal components axes, was apportioned within and among clones, between sites, years, and species. Except for the thimbleberry vegetative phenology, within-sites differences accounted for most variation and variation between-sites often exceeded that between years. Moreover, between-species differences accounted for less variation than within-species differences for morphology and phenology.

The variation in plant characters was also examined in relation to canopy cover, soils and adjacent vegetation using multivariate methods. The rate of vegetative development for devil's club in 1986 increased as canopy cover decreased; other environmental measures were uncorrelated with devil's club. Both vegetative and reproductive rates of development increased with disturbance due to girdling and increasing moisture for the combined girdled and ungirdled thimbleberry data set. Similarly, morphological size was greater for the combined thimbleberry data set with increasing moisture and disturbance. Environmental correlations were reflected differently within-sites, however, with rates of development, plant size and the number of flowers decreasing with increasing moisture at the nongirdled thimbleberry site.

The relationship between plant characters was also assessed. Phenology and morphology were correlated for both devil's club and thimbleberry; stem development began earlier and was more rapid with increasing stem size. Demography and phenology were unrelated.

Both species displayed different niche utilization strategies; thimbleberry being more flexible than devil's club. In contrast to devil's club, thimbleberry is morphologically and

phenologically responsive to disturbance and is rhizomatous rather than stoloniferous. Stems and lateral branches also had several phenological and developmental possibilities. This flexibility imparted an advantage to thimbleberry in the fluctuating conditions of its earlier successional niche.

The differing correlation structure between and within thimbleberry sites suggests that several scales of observation are necessary to clarify plant-environment relationships. Moreover, as environmental characters interact differently with plants from site to site, management must be site specific. Alder girdling may be a judicious management technique at drier sites, where thimbleberry is not as prolific under an open canopy.

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I. INTRODUCTION

Rubus parviflorus Nutt. (thimbleberry) and _Oplopanax horridus_ (Smith) Miq. (devil's club) are two clonal iteroparous shrubs which occur in different successional stages in B.C. forests. Thimbleberry is found in disturbed areas and early to mid-successional sites whereas devil's club is found in climax forests.

The differences observed between species, such as thimbleberry and devil's club, are often ascribed to different environmental conditions found in early and late successional seres along a successional gradient (Lee et al. 1986). Variation observed within and among populations and years within a species is linked to other factors. Variation between two genetically similar populations at different sites implies that there are environmental differences between sites which maintain this variation (Van Cauteren and Lefebvre 1986; Huenneke 1987; Matlock 1987; Maddox et al. 1989; Moot et al. 1989; Carlsson and Callaghan 1990). Variation within populations has been linked to genetic and environmental influences (Primack 1980, 1985; Huenneke 1987; Menges 1987; Schlichting 1989). Genetic variability can account for differences between clones of a single population living in a common environment (Huenneke 1987). Variation observed within individuals, which is manifested as plasticity, has been seen as evidence of a heterogeneous environment (Primack 1985; Kephart 1987; Schlichting 1989). Temporal variation, which may also be manifested as plasticity, has also been observed and is often explained by climatic heterogeneity (Kjellson 1985; Rathke 1988).

Observations of variability at these differing levels suggest a study quantifying the variation within and among populations and individuals. Investigating factors which maintain that variability may clarify genetic and environmental relationships (Koehl 1989).

In this thesis I examine relationships within and among individuals and populations of thimbleberry and devil's club to gain insight into the major factors shaping the development of these two species in the Kitimat valley. As ecologically different species, it was of interest to determine whether they responded differently to different environmental conditions. My study was also motivated by a need within the B.C. Forest Service for information about life histories of these two species which are important understory components. By comparing problem with

nonproblem species, the study will elucidate the method of niche utilization employed by each. I also had the personal goal to learn more about multivariate statistical techniques and plant ecology.

1.1 OBJECTIVES

The objectives of this study are:

1)   to document the morphology, phenology and demography of thimbleberry and devil's club in the Kitimat River valley in west central B.C. during the 1986 - 1987 growing seasons,

2)   to apportion variation in morphology, phenology and demography of devil's club and thimbleberry within and among clones, between sites, species and years and

3)   to ascertain to what extent canopy cover, soils and adjacent vegetation are correlated with phenology, demography and morphology at these different levels of organization.

1.2 PHENOLOGY, MORPHOLOGY AND DEMOGRAPHY

Phenology, morphology and demography were examined for both species in 1986 and 1987 at each level in the above hierarchy. Phenology is the study of periodic phenomena in an organism's life in response to environmental factors (Funk and Wagnalls 1978). As plants are sedentary organisms changes in timing of responses such as flowering and fruiting may be an effective strategy in a fluctuating environment and may be critical in a harsh environment (Gill and Mahall 1986). More information on phenology can be found in Rathcke and Lacey (1985).

Morphology is the study of the form and shape of plants and animals (Funk and Wagnalls 1978) and has also been related to function and strategy in differing environments (Barnes 1986; Lee et al. 1986; Hancock and Pritts 1987). Morphological relationships have been described with techniques such as plant growth analysis (Hunt 1982; Hardwick 1984; Hunt 1984; Jolliffe and Courtney 1984), morphometrics (Pimentel 1979) and allometry (White 1981; Joliffe and Courtney 1984; Weller 1987).

Plant demographic studies consist of actuarial measures. When correlated with biotic and abiotic factors these measures may explain community (Harper 1980; Crawley 1986; Moot et al. 1989) or population (Hutchings 1976, 1986; Harper and Bell 1979; Blom 1988) dynamics. Ecological demographers document the growth of genets or genetically distinct individuals (Harper and Bell 1979) by enumerating genets and their constituent parts, ramets or modules (Hutchings 1976). Modules which have been selected for study include leaves (Clark 1980; Lovett Doust 1981; Lovett Doust and Eaton 1982; White 1985; Garnier and Roy 1988), buds (Maillette 1982), rhizomes (Bell 1976), shoots (White 1980), branches (McGraw and Antonovics 1983) and flowers (Lovett Doust and Eaton 1982). Male and female plants within a population have also been counted (Alliende and Harper 1989). Commonly, stems are considered the most meaningful subunit for demographic analysis of clonal individuals (Sarukhán and Harper 1973; Hartnett and Bazzaz 1985). Reviews of demographic theory are provided by Harper and White (1974), White (1979), Harper (1980), Blom (1988) and Balogh and Grigal (1988). A comparative study of plant demography and plant growth analysis is described by Hunt (1978), Bazzaz and Harper (1979), Hunt and Bazzaz (1980) and Joliffe and Courtney (1984).

Differences within and among species, populations and individuals have often been described for phenology, morphology and demography. Recent studies attempt to link differing phenological, morphological and demographic patterns observed in various environments using life-history strategies though overall this approach has not proven conclusive (Stearns 1977; Grime 1979; Southwood 1988).

1.3   VARIATION IN MORPHOLOGY, PHENOLOGY AND DEMOGRAPHY

Variability or variation within- and among-groups has seldom been quantified. Scagel and Maze (1984) found that within individual variance exceeded the amount of between individual variance among two Stipa species and an intermediate when they apportioned morphological variation with ANOVA. Differences between the three groups accounted for the most variation (Scagel and Maze 1984). Other studies have described the morphological variation of individuals and clones in different populations (Aarssen and Turkington 1985; Barnes 1986; Herndon 1989; Maddox et al. 1989). Substantial variation was found for clonal structure both within and between populations (Maddox et al. 1989). Morphological measures of individual traits, such as leaf length or awn length, revealed variation within populations to be large (Aarssen and Turkington 1985; Barnes 1986; Herndon 1987). These studies support earlier research which also described large amounts of morphological variation among (Burdon 1980) and within (Fowler et al. 1983) populations. Reinartz and Popp (1987) reported that morphological variation may also be substantial within and between individuals. Clonal variation was large for shoot height, above and below ground biomass, and the pattern of root connections of northern prickly ash both within and among individuals (Reinartz and Popp 1987).

The extent of temporal and spatial variation has been quantified for demography. Demographic variation between years has been reported to be greater than variation occurring between populations in a single year (Weiss 1981; Mack and Pyke 1983; Waite 1984). Angevine (1983) found spatial demographic variation to be greater among populations within a species than between related species. At a finer scale of observation, greater demographic variation was found within a population than between populations at different sites (Huenneke 1987).

Spatial demographic variation has also been observed within and between individuals, with genetic (Burdon et al. 1983; Ennos 1985) and environmental (Werner 1985) influences invoked to account for the variation. Several studies have quantified the relative amounts of variation stemming from genetic and environmental effects (Sarukhán et al.1984; Blom and Lotz

1985; Cook 1985; Billington et al. 1990). In all cases cited environment accounted for most of the variation (Oka 1976; Sarukhán et al. 1984; Blom and Lotz 1985; Cook 1985). In a recent study, Billington et al. (1990) reported that environment accounted for up to 100 percent of the demographic variation in adjacent grass populations.

1.4   FACTORS CORRELATED WITH VARIATION

Factors which maintain variation have been measured at many different scales of observation. Phenological studies have compared similar communities, such as Asian rainforests (Newton 1988) or temperate bogs (Wieder et al. 1984), in widely divergent areas to seek common patterns. At this large scale of observation it is difficult to assess factors which control phenological differences, due to the interactive nature of biotic and abiotic influences, though climatic differences are often cited (Primack 1985).

Within-community studies comparing phenological development of differing strata have often been descriptive. Examples include phenological comparisons between the shrub layer and the canopy layer (Ralhan et al. 1985), between deciduous and evergreen trees (Gill and Mahall 1986) or the effects of canopy cover on understory plants (Nilson 1986).

Studies examining constancy or changes in phenological pattern between years have also been done (Helenurm and Barrett 1987). When several or all species in the community were observed, a sequential pattern of flowering or a divergence of flowering times has been reported (Pojar 1974; Heinrich 1976). Competition for pollinators seems to be the most widely accepted explanation for this asynchrony. Other studies have stated that nonrandom distributions of phenological data indicate that competition has occurred (Rathke 1984, 1988; Wieder et al. 1984; Kjellson 1985). Flowering phenology has also been viewed as a secondary trait related to fruit and seed production. According to this idea fruiting phenology is selected for times when seed dispersers are prevalent or seed predators are rare and flowering phenology is subject to these selection pressures (Stiles 1980; Primack 1985). Other explanations of flowering phenology have been purely physiological focussing on the availability of resources within the environment (Heinrich 1976; Kawano et al. 1982; Primack 1985).

Biotic and abiotic influences have been linked to demographic variation within communities or guilds though interpretations applied to these influences are often conflicting (Cook 1979; Bakker et al. 1980; Huenneke 1983; Beatty 1984; Verkaar and Shenkeveld 1984; Sakai and Sluak 1985; Dunn 1986; Huenneke and Sharitz 1986; Van der Toorn and Pons 1988; Balogh and Grigal 1988)

Demographic comparisons between species focus on early versus late seral species in an overall successional development (Bierzychudek 1982; Whitney 1986). Morphological comparisons between species are also made at different points along a successional gradient. Though morphological traits are correlated with environmental and ontogenetic differences between species (Antos and Zobel 1984; Barnes 1986; Lee et al. 1986), reproductive effort is most often quantified. Harper et al. (1970) argue that reproductive effort is expected to be maximized by annual species found early in succession, when competition is minimal, whereas perennial species, which predominate in later successional seres, minimize reproductive effort to devote higher proportions of energy to vegetative structures which may confer a competitive advantage (Harper et al. 1970). Since this idea was first espoused it has been elaborated by several others (Gadgil and Solbrig 1972; Abrahamson and Gadgil 1973). Although several studies have measured reproductive effort, few have accounted for below ground biomass. It is also unclear whether patterns in reproductive allocation are phenotypic or genotypic in origin (Hancock and Pritts 1987).

Demographic (Law et al. 1977; Whitney 1986; Fone 1989) and morphological (Garnier and Roy 1988) patterns were also compared within genera though in many cases no overriding trends were discernible and environmental factors accounting for the variation observed were not identifiable.

Environmental causes have been inferred for maintaining morphological, phenological and demographic variation among populations of a single species. Environmental influences were corroborated when different phenological races found in differing environments were examined in between population studies (Van Cauteren and Lefebvre 1986). Other studies have suggested environmental variables which maintain morphological variation among

populations though the relationships were not measured (Aarssen and Turkington 1985; Maddox et al. 1989). Environmental influences have also been suggested by adjacent dissimilar populations found at opposite ends of a gradient, such as moisture, that morphologically integrade where they overlap on the gradient (Barnes 1986). Finally, comparative studies between different populations have provided clues to the environmental correlates of demographic variation. In some cases, no differences in mortality were observed between sites (Garnier and Roy 1988), whereas in other cases soils properties (Sakai and Sluak 1985; Matlock 1987; Moot et al. 1989) and moisture (Sakai and Sluak 1985; Moot et al. 1989; Carlsson and Callaghan 1990) were found to affect longevity.

Phenological variation among individuals has been documented to examine the genetic component of phenological traits (Primack 1980; Primack 1985; Somers and Grant 1981; Kephart 1987). Successful selection of early and late developing subspecies in agriculture is evidence of the strong genetic component to phenology (Rathcke and Lacey 1985).

Morphological studies at the level of the individual or clone have frequently dealt with three ideas. First, morphological variation has been explained as an adaptation to differing environmental factors such as light or soil moisture (Pitelka et al. 1980; Gawler et al. 1987; Menges 1987). Secondly, the effects of physiological integration on the development of large long-lived clonal individuals has been examined (Hartnett and Bazazz 1983; Slade and Hutchings 1987a; Hutchings 1987b; Schmid and Bazazz 1987; Lau and Young 1988). Physiological integration implies that ramets in favorable areas may translocate resources to other ramets of the same clone in stressed areas and increase the longevity or growth of the recipient ramets. This physiological integration may buffer ramets within inclement areas and facilitate rapid growth of these ramets if conditions improve. Several studies have documented this translocation of resources and examined clonal architecture through a spatially heterogeneous area (Hartnett and Bazazz 1983; Slade and Hutchings 1987a; Slade and Hutchings 1987b; Lau and Young 1988). These studies found that rhizomes between stem ramets tended to be fewer and longer through areas of nutrient stress (Slade and Hutchings 1987a; Slade and Hutchings 1987b) and water stress (Hartnett and Bazazz 1983). Clumps of

stem ramets may therefore be widely separated or densely packed within a site. Architectural differences may affect competitiveness and/or cooperation between individuals (Hartnett and Bazazz 1985; Schmid and Bazazz 1987).

Thirdly relative resource allocations between sexual and vegetative reproductive have been documented (Pitelka et al. 1980; Eriksson 1985; Jurik 1985; Loehle 1987; Cid-Benevento 1987). Sexual and vegetative reproduction may maintain and spread a clonal individual under differing conditions. Abrahamson (1980) considered vegetative reproduction advantageous in early successional sites as it may more rapidly fill a site than sexual reproduction. In later successional sites, where density and competition are greater, sexual reproduction was thought to be a more effective method of clone maintenance (Abrahamson 1980). This idea has since been expanded to include other conditions than competitive intensity and density. Loehle (1987) predicts that

1) sexual reproduction will increase under conditions which the plant perceives as favorable to germination,

2) where nutrients are available sexual reproduction will be less costly and will increase,

3) vegetative reproduction will increase relative to sexual reproduction when the opportunities diminish for sexual progeny,

4) as the value of vegetative reproduction diminishes sexual reproduction will increase and

5) when both vegetative and sexual reproduction value decrease concurrently, the ratio of sexual to vegetative reproduction will increase.

Other researchers have examined the relationship between environment and reproductive allocation though patterns observed are not always consistent and predictable (Pitelka et al. 1980; Erikssen 1985; Jurik 1985; Cid-Benevento 1987). Under conditions of increasing density sexual reproduction may increase in relation to vegetative reproduction (Pitelka et al. 1980; Eriksson 1985). Other studies have found that sexual reproduction may increase with respect to vegetative reproduction under more favorable conditions such as

diminished density (Jurik 1985) or increased water, light or nutrient availability (Loehle 1987). Increased light was also found to increase the amount of sexual reproduction in comparison to vegetative reproduction by Cid-Benevento (1987), though vegetative reproduction was also found to increase.

Environmental heterogeneity has been inferred from variation within-individuals or plasticity (Primack 1985; Rathcke and Lacey 1985; Schlichting 1986; Kephart 1987). Morphological patterns within individuals have been linked with this environmental heterogeneity (Oberbauer and Strain 1986; Svenssen and Callaghan 1988; Schlichting 1989). Svennson and Callaghan (1988) found that small scale changes in vegetation and micro-environment were associated with small scale changes in the morphology of Lycopodium annotinum . Canopy position and light have also been correlated with leaf thickness and weight in Pentaclethra macroloba (Oberbauer and Strain 1986). Finally Schlichting (1989) demonstrated changes in the correlation structure of weight, number and sizes of leaf, flower, root and stem parts within Phlox individuals due to different nutrient, moisture and clipping treatments.

Demographic studies within-individual plants have focused on stem ramets within clones (Sakai and Sluak 1985). Earlier workers assumed that stem ramets experienced constant risks of mortality regardless of age or size (Harper 1978). More recent studies, however, have questioned this assumption and suggested that ramet mortality is altered by clonal integration (Cook 1979; Cook 1985; Eriksson 1988), positional effects (Eriksson 1988; Douglas 1989) and survival of sibling ramets on the same stolon (Eriksson 1988).

Environmental factors have frequently been cited as responsible for phenological, morphological and demographic variation at all spatial and temporal scales. Climate is considered to maintain phenological variation between years (Rathcke 1988) and within seasons (Kjellson 1985). Annual differences in climate also affect pollinator availability which impacts on flowering phenology, whereas seasonal patterns that affect germination determine optimum time of seed dispersal (Rathcke and Lacey 1985). Physiological studies have accentuated drought stress or water potentials as determinants of phenological strategy

(Jackson and Bliss 1984; Gill and Mahall 1986) though temperature is believed to be important for woody shrubs (Lieth 1974; Reader 1983). Interactions of photoperiod, temperature and moisture were also necessary to induce flowering (Rathcke and Lacey 1985).

Physiological studies have characterized the morphological responses to differing environmental conditions such as humidity, water stress and temperature (Mooney 1980; Roy and Mooney 1982,1989). Light, canopy cover, substrate, soil moisture and the dominant vegetation have also been correlated with size and number of leaves and the size and number of inflorescences in field studies (Pitelka et al. 1985; Gawler et al. 1987). Other studies (Givnish 1982; Menges 1987) predicted and subsequently corroborated morphological patterns in differing environmental conditions. Givnish (1982) predicted leaf height and the proportion of the total biomass devoted to leaves in differing light regimes and Menges (1987) constructed a model of leaf thickness, area and height and the percentage of biomass devoted to roots under differing regimes of canopy opening, drainage, soil texture and plant density.

Many studies have examined the environmental factors affecting demography though the large number of factors and their interactions do not form many consistent patterns. Descriptive studies have linked soils texture and moisture (Hobbs and Mooney 1987), disease (Cook 1979), environmental patchiness (Cook 1979), fire regime (Platt et al. 1988) and competition (Groves et al. 1990) with demography. Experimental studies involving manipulations have linked fire regime with demography (Hartnet 1987) as well as nutrient enrichment (Noble et al. 1979), predation (Noble et al. 1979; Bazely and Jefferies 1989) and trampling (Noble et al 1979). Other influences that have been identified include soil nutrients (Beatty 1984; Kelly 1989a), soil texture (Beatty 1984) and water level and sediment depth (Beatty 1984; Huenneke and Sharitz 1986). Cook (1979) also stated that herbivores, pathogens and drought stress are important causes of mortality in many communities.

Several studies have accentuated the effects of differing canopy cover or light conditions on demographic patterns (Huenneke 1983; Sakai and Sluak 1985; Dunn 1986; Balogh and Grigal 1988). In several shrub species abundance is controlled by regeneration which may differ under differing canopies (Balogh and Grigal 1988); under a closed coniferous canopy

regeneration was inversely related to site quality and moisture; under an aspen canopy regeneration was inversely related to soil nutrients. Canopy openings allowing greater light penetration into forest stands were also correlated with increased density and survival of Lonicera (Luken 1988). In another study increased survival during cold winters was reported for Plantago growing in the shelter of an overstory canopy (Moot et al. 1989). Kelly (1989b) showed that shading by taller neighbours and density of these neighbours affects recruitment of three annuals and two biennials in the grass chalklands of England. Kelly (1989a) also stated that daylength and temperature were also linked with variation in germination times. Low light and vegetation density were also linked to demography by Cook (1979), Verkaar and Shenkeveld (1984) and Van der Toorn and Pons (1988).

1.5   THIMBLEBERRY

Thimbleberry is a common shrub throughout B.C. Its range extends to 55° N latitude in the interior (Haeussler and Coates 1986), though it is found as far north as Alaska along the coast (Hultén 1968). The southern limit of its distribution is southern California (Hitchcock and Cronquist 1973).

Thimbleberry is morphologically quite variable and several subspecies have been described (Hultén 1968). The plant is composed of clumps of canes or stems which are connected by a network of rhizomes. Each stem lives from one to three years, bearing fruit and becoming lignified after the first year of growth. The deciduous stems are glandular and hairy before lignification occurs. Thimbleberry leaves are palmate, from 5 to 30 cm in length and feel soft like tissue paper. The showy, white flowers are borne in loose cymes (Hitchcock and Cronquist 1973). They produce a thimble-sized, soft, orange-red fruit which is an aggregation of drupes.

Thimbleberry is frequently found on sites following disturbances. It is especially successful at colonizing if present before disturbance (Eis 1981). Halpern (1989) found thimbleberry to be the dominant plant species approximately 10 years after logging and to have greater longevity than other early succession colonizers. Although not plentiful in later

successional seres, thimbleberry is present in natural gaps in the forest. In west central B.C., the plant is widespread, occurring in many forested ecosystems (Coupé et al. 1982).

Thimbleberry is perceived by foresters to be a serious competitor for light and nutrients, thus hindering the growth of young trees (Haeussler and Coates 1986). Many reports have focused on forest management of the species (Gratkowski 1971; Stewart 1973; Stewart 1974; Coates and Haeussler 1986). Biomass regression equations have also been prepared to provide inventory information (Alaback 1980; Alaback 1986).

Like many weedy species (Baker 1974; Holzner 1982), thimbleberry may be apomictic. Agamospermy is common in many Rubus species (Grant 1981; Richards 1984), though no information is available on the breeding system for thimbleberry. Richards (1984) states that few members of the genus are known to be fully sexually diploids. Of the thousands of Rubus species most are polyploid and apomictic (Nybom 1987).

A subject of other thimbleberry papers is plant/insect interactions, though these are primarily entomological (Briggs et al. 1982; Gilbert and Gutierez 1973; Jones 1983; McNicol et al. 1983). A comprehensive review of thimbleberry is found in Haeussler and Coates (1986).

1.6   DEVIL'S CLUB

In B.C., devil's club is distributed from Vancouver Island, north along the coast to Alaska and in the interior wet belt (Lyons 1976). Its range also extends into Oregon (Hitchcock and Cronquist 1973).

The stems and the underside of the large leaves have many thorns. This large plant is often up to 3 meters high and 5 meter long decumbent stems are common. Leaves are large, up to 35 cm wide, maplelike in shape and 7 - 9 lobed. The white flowers are produced on an elongate raceme and yield showy scarlet berries.

Devil's club is found in old growth forests and does not persist in logged areas. Klinka et al. (1989) state that it commonly occurs in very moist, water receiving sites with nitrogen rich soils.

No information on reproductive biology is available though most members of the Araliaceae are known to be outcrossing and fully sexual and some are dioecious (Flanagan and Moser 1985). Devil's club flowers are hermaphroditic (Hitchcock and Cronquist 1973).

Little research has been done on devil's club except for ethnobotanical studies (Turner 1982) and a pharmacological report (Smith 1983). Biomass regression equations, which predict above-ground biomass from stem basal diameter, were calculated by Alaback (1980, 1986) and Yarie and Mead (1989) to assist in field inventories.

II. STUDY AREAS

2.1 DESCRIPTION OF STUDY AREA

2.1.1 GEOGRAPHIC LOCATION

The three study sites are located in west central British Columbia about 8 kilometers east of the townsite of Kitimat along Highway 25. This area is 54°10' latitude and 128° 35' longitude. All three sites are close to the Kitimat River or its estuary. The devil's club site, referred to as DC throughout this document, is located within a B.C. Forest Service reserve on the east bank of the river in an area of old growth forest designated as L6201 and L6202 by the Ministry of Forests (Figure 1). One thimbleberry site, designated as WED throughout this thesis, is situated between the Wedeene and the Little Wedeene rivers close to their confluence with the Kitimat River at L6144 and L6141 (Figure 1). The other thimbleberry site, KIT, abuts a small arm of the Kitimat River at L6235 and L6235 (Figure 1). KIT and WED will be collectively referred to as TB.

The study sites were chosen because of the abundance of the study species, their close proximity and the differing canopy cover at each thimbleberry site.

2.1.2 EDAPHIC ENVIRONMENT

Much of the bedrock within the area is composed of crystalline rocks. Throughout the valley large deposits of unconsolidated glacial material formed from the breakdown of these hard rocks are common. Along the river and its tributaries glaciofluvial and fluvial materials form floodplains and terraces made up of sequential deposition of these materials (Haeussler et al. 1984). The study sites were formed by this sequential deposition and may still experience flooding. Channels of water and standing pools are common throughout the sites. All three sites are edaphically similar.

Soils are generally Orthic Humo-Ferric Podzols with thick Ae horizons. Due to the heavy rainfall and the coarse nature of these soils the Ae horizons lose aluminum and iron to deeper reddish brown Bf horizons. Decaying wood and other organic materials, impregnated with fungal hyphae, blanket the ground forming a surface LFH layer often greater than 10 cm thick (Valentine et al. 1978; Haeussler et al. 1984).

Figure 1. Map of the study area showing the location of each site in relation to the river system and each other.
(- - - = gravel logging roads)
KIT = girdled alder thimbleberry site,
WED = nongirdled alder thimbleberry site,
DC = devil's club site
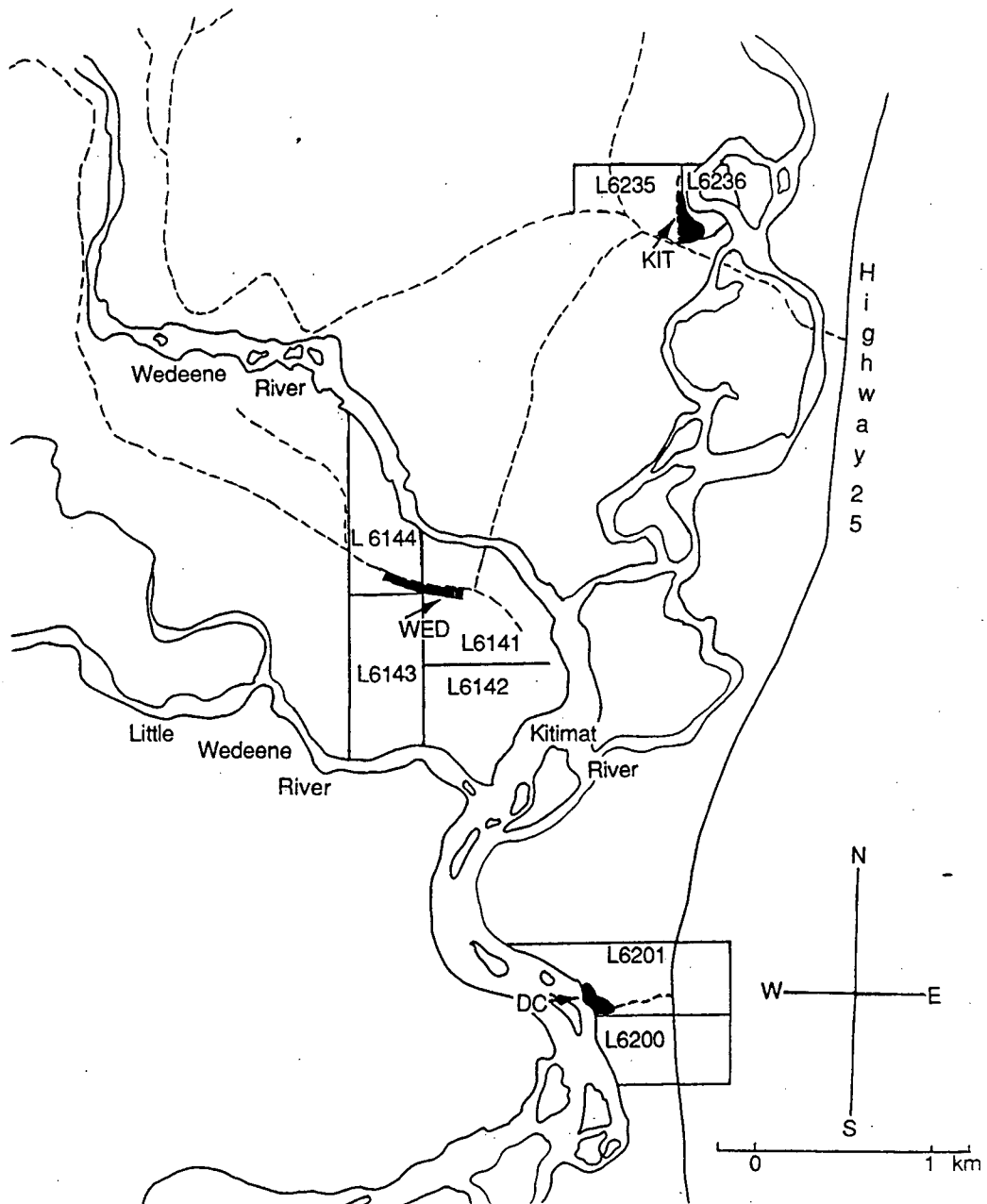
2.1.3 DISTURBANCE HISTORY

Although one or two trees adjacent to the river were felled, the devil's club site remains relatively undisturbed. The only other signs of human disturbance include a large hole in one of the oldest cedars and a fishermen's path which follows the river at the edge of the site. An area adjacent to the DC site is presently used by the townspeople as a source for firewood and occasionally trees were felled onto the B.C. Forest Service reserve. Within the reserve the DC site encompasses an area of about 80 square meters.

Disturbance is more noticeable in the the thimbleberry sites. The KIT thimbleberry site was logged in 1969 and subsequently burned. The WED thimbleberry site was logged in 1969, burned and planted with spruce in 1975. Regeneration of Alnus rubra (alder) proceeded naturally on both sites and a dense canopy of this species rapidly filled in both areas. In 1985 alder were girdled leaving the trees standing but effectively dead at the KIT site.

2.2   CLIMATE

The study area, which is characterized as sub-oceanic or coastal transitional, is located in the Northern Drier Maritime Subzone of the Coastal Hemlock Biogeoclimatic Zone (CWHf1) (Krajina 1965,1969; Haeussler et al. 1984). This zone has wet and mild weather compared to other areas at similar latitudes. This climate is predominantly coastal but is influenced by continental factors.

Warm maritime winds deposit rain onto the westward facing slopes of the Coast Mountains and by the time they reach the CWHf zone have lost much of their moisture. As a result this area is drier than the outer coast and may have long dry spells during which fire hazards are common (Haeussler et al. 1984).

In the winter the ground is covered by a thick layer of snow and does not usually freeze. When cold spells due to the influx of continental air do occur their duration is short (Haeussler et al. 1984).

Weather patterns for precipitation, hours of sunshine and number of degree days from January to August of 1986 and 1987 are displayed in Figure 2. This number of degree days greater than 0° C for each time period is calculated as:

$$\sum_{i=1}^{i=n} (\text{mean } T_i > 0°C)$$

where n is the number of days in the time period, i is the day number and mean T is the average temperature for day i greater than 0° C. The summer rainfall was high in both years and there was no two week period without rain. Although spring temperatures differed little between years, 1987 had more rain than 1986 from March to mid-June, whereas from mid-June to August 1987, was more sunny, warmer and had less rain than 1986.

Figure 2.   Weather in the study areas from January to August 31, 1986 and 1987
(Environment Canada, 1986 & 7).

a) number of degree days
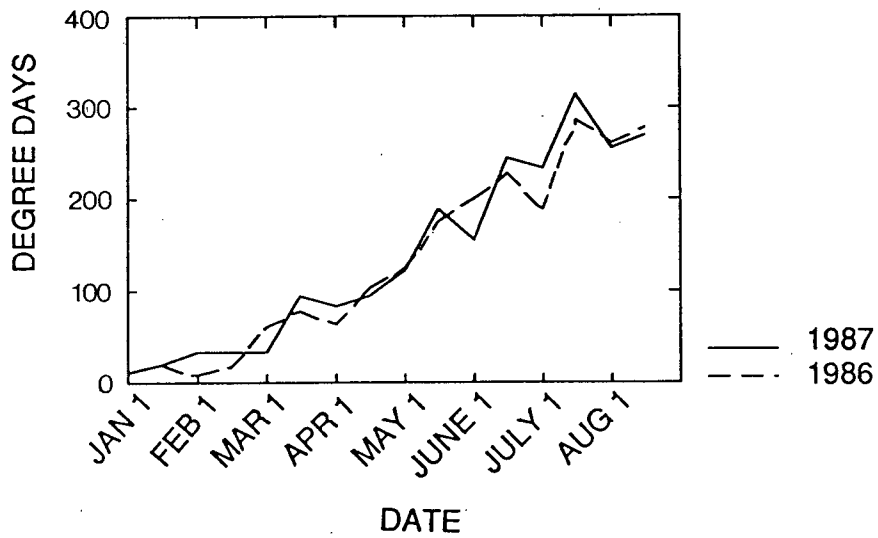
DATE

b) number of hours of sunshine
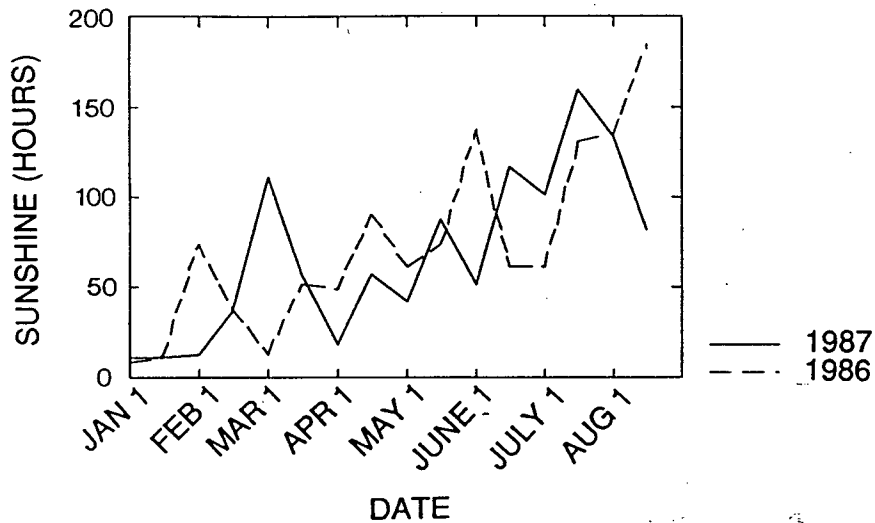
DATE

c) rainfall (mm)
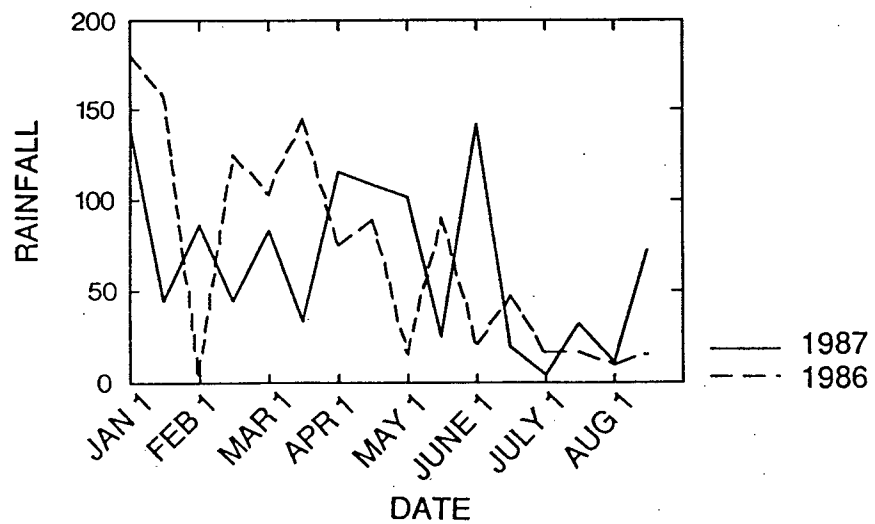
DATE

III SAMPLING METHOD & DATA COLLECTION

3.1   DESIGN

Transects were established at each site in early May 1986. In the KIT thimbleberry site, transect lines were established perpendicular to an old logging road. The length of each transect line varied to ensure that each line went through standing girdled alder only (Figure 3a). At the WED site (Figure 3b) parallel transects were also positioned at right angles to an old road though these crossed areas of standing live alder . Transect lines were at least 50 meters apart at the KIT site and 75 meters apart at the WED site to minimize the chance of sampling the same genet twice. WED is a larger site than KIT so transects were more widely spaced. Two transects, one on either side of a gully which traversed the site, were laid out in the DC site (Figure 3c).

Twenty-one sampling quadrats were systematically positioned along the transects at each site. The distance between quadrats was selected to minimize intra-individual effects on the data; however, this could not be assured as genets could not be individually delineated. Thimbleberry quadrats were separated by at least 10 m whereas devil's club quadrats were spaced greater than 15 m apart to accommodate this larger plant. As the study is descriptive and estimates of the standard error of the mean were not required, stringent random sampling was not adhered to. In addition Pimentel (1979, p. 59) states that as biological systems are nonrandom and measures are usually repeatable, it is safe to assume that nonrandom samples do not differ from those that would be generated by random sampling.

Quadrat size was set to encompass at least five stems of each sampled plant. These circular quadrats had a diameter of 1 m for thimbleberry and 1.5 m for devil's club. Each quadrat was within a larger 3 m diameter plot in which soil samples and species presence/absence and frequency data were collected.

Figure 3.   Map of quadrats and transects in each study site.
(Open circles indicate quadrats which were morphologically sampled in 1986 and 1987. Solid circles indicate quadrats which were morphologically sampled in 1987 only).

a) KIT - girdled alder thimbleberry site

▨▨▨ nongirdled alder - closed canopy
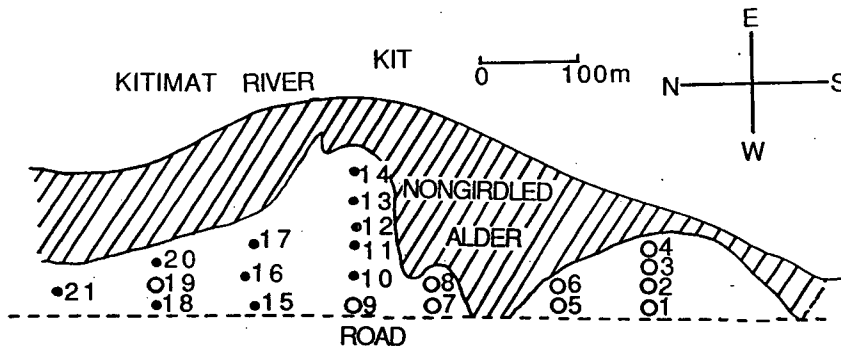
b) WED - nongirdled alder thimbleberry site

███ standing water   ▨▨▨ no canopy cover
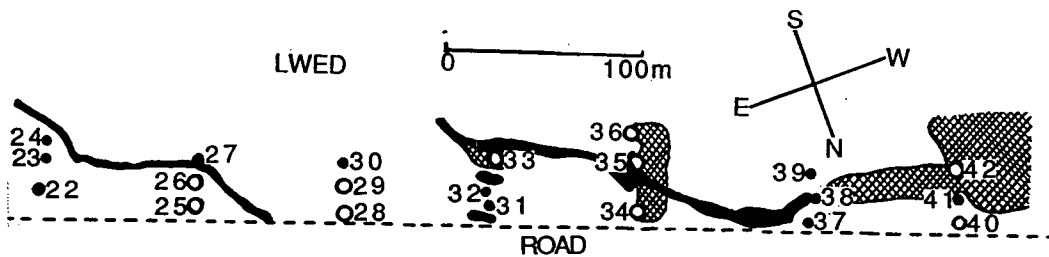
c) DC - devil's club site

███ standing water   ▨▨▨ no canopy cover - gap in forest
[⋯⋯] path
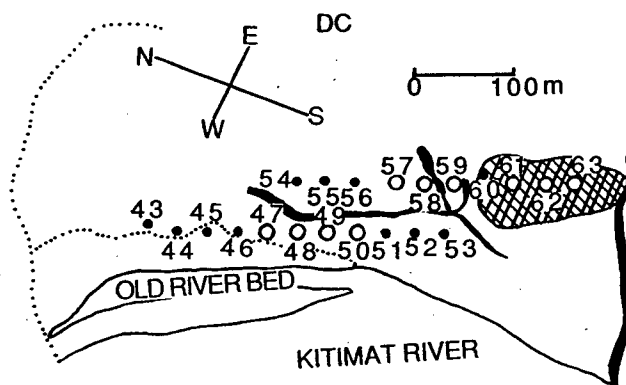
3.2   CANOPY COVER

To estimate canopy cover high contrast black and white negatives of the canopy over each quadrat were taken with a 28mm lens during the second week of July in both years. The lens chosen showed a field of view wide enough to estimate light effects on the sample plants at all times of day. A smaller field of view would only measure effects due to cover at midday, when the sun is overhead, and a larger field would overestimate the effects of neighbours of the same height as the sample plants. The camera base was aligned in a N-S direction with a compass and the camera was always placed on the eastern side of the tripod. The base of the camera was 1.5 meters over the quadrat centre and was levelled with a small bubble level.

Each negative was read through a video camera into the Kontron Image Processing System at the University of British Columbia, wherein the analyzer calculated the percent cover of the total area in each picture. This value provides an estimate of the amount of light reaching any one quadrat. The program to run the Kontron was written by Mike Weiss of the Department of Botany at the University of British Columbia.

The method of cover estimation by analysis of photographs is described by Anderson (1964), Pope and Lloyd (1975), Chan et al. (1986) and Chazdon and Field (1987).

3.3   SOILS

All soil sampling was done outside of the inner quadrat but within the larger surrounding three meter diameter quadrat to minimize disturbance on sample plants. The thickness of the LFH horizon was measured and approximately 250 ml of the mineral soil directly underneath the LFH was collected.   As soil properties vary both laterally and vertically (Mader 1963; Beckett & Webster 1971; Coutin et al. 1983; Carter and Lowe 1986), no distinction was made between soil horizons for collecting purposes. Within quadrat variability was not quantified in this study, rather the sampling method was assumed to represent the average condition found in each quadrat.

The percentage of coarse fragments, pH, the percentages of sand, silt and clay, total nitrogen, the depth to mineral soil and the percentage organic matter within the mineral soil

were measured. The variables were chosen to characterize the soil's nutrient availability, structure or texture, biological activity, drainage or water holding properties and buffering ability thereby reflecting the differing environmental character among quadrats (Singer & Munns 1989).

All soils were analyzed using the methods described by Lavkulich (1981) except for the fine fraction component. The pH was measured by the water measurement method with 50 ml of distilled water added to 20 g of soil as the only change in the method. Total nitrogen was colourmetrically determined with the autoanalyzer. The leco analyzer was used to measure total carbon or the percentage of organic matter.

Particle size of the fine fragment was determined by the hydrometer method (Bouyoucos 1962).

3.4   PLANT NEIGHBOURS

In 1986 all plants within the three m diameter quadrat were identified. Nomenclature follows Coupé et al. (1982). In 1987 each 3 m quadrat was divided into quarters and each plant species within the quadrat was identified and was assigned a score from 1 to 4 depending on the number of quadrat quarters in which it was present. This provided a simple measure of local frequency.

Vegetation is frequently examined to estimate competitive interactions and although surrounding vegetation was considered to potentially impact on plant characters, it was primarily of interest as a summary of the environmental conditions within each quadrat (Watkinson 1985; White 1985; Tilman 1986; Tilman 1988; Austin 1990). Vegetation pattern is commonly correlated with environmental factors in community ecological studies (Greig-Smith 1983; Kershaw & Looney 1985; Chang & Gauch 1986; Bradfield & Campbell 1986; Menges 1986; Austin 1987).

3.5   MORPHOLOGY

In 1986 morphological measures were made during the weeks of May 25, July 6 and August 3 (Table 1). Where possible six stems, which were also phenologically sampled, were sampled in each quadrat. Ten quadrats were sampled in each of the three sites (Figure 3). Only devil's club stems originating within the quadrat were measured and the widest range of devil's club stem sizes and ages were represented in the sample at each quadrat. At the thimbleberry sites, four stems produced in the current year and two produced in 1985 were sampled. Measurements on each stem for both species included the following:

a)   number, length, basal diameter of all branches and their position along the main stem,

b)   length and basal diameter of all stems,

c)   number, length, width and position of all leaves,

d)   number and position of devil's club inflorescences and

e)   number of flowers per stem and number of flowers per inflorescence for thimbleberry.

Basal diameter was measured at 1 cm above the ground or immediately above the basal swelling for each stem. Position of stem leaves and branches referred to their distance up the stem from the basal diameter measurement. Branch basal diameter was measured at the closest possible point along the branch to the stem and this was also the reference point for leaf branch position. The position of devil's club inflorescences referred to the particular stem or stem branch terminated by that inflorescence. Leaf length is the distance from the attachment to the stem to the opposite point of the palmate leaf blade. Leaf width is the maximum distance across the leaf blade from point to point.

In 1987 all measurements, except for leaf measurements, were repeated at all 21 quadrats at weekly to biweekly intervals (Table 1). Records of the number of flowers per stem and per inflorescence at these same sampling times were also made for thimbleberry. The number of leaves per stem were counted once during the week of July 5, but measures of leaf length or width were not recorded.

Table 1. Phenological, morphological and demographic sampling in 1986 and 1987. The circles indicate the phenological sampling dates in 1986 and 1987. The squares indicate the morphological and demographic sampling dates in 1986 and 1987.

1986
MAY

S	M	T	W	T	F	S
				1	2	3
4	5	6	7	8	9	10
11	12	13	14	15	16	17
18	19	20	㉑	㉒	㉓	24
[25]	[26]	[27]	[28]	[29]	[30]	31

JUNE

S	M	T	W	T	F	S
1	②	③	④	⑤	6	7
8	9	10	11	12	13	14
15	16	⑰	⑱	⑲	20	21
22	23	24	25	26	27	28
29	㉚					

JULY

S	M	T	W	T	F	S
		①	②	3	4	5
[6]	[7]	[8]	[9]	[10]	11	12
⑬	⑭	⑮	16	17	18	19
20	21	22	23	24	25	26
27	㉘	㉙	㉚	31		

AUGUST

S	M	T	W	T	F	S
③	④	⑤	[6]	[7]	[8]	⑨
10	11	12	13	14	15	16
17	18	⑲	⑳	㉑	22	23
24	25	26	27	28	29	30
31						

1987
MAY

S	M	T	W	T	F	S
					1	2
3	4	5	6	7	8	9
10	11	12	[13]	[14]	[15]	[16]
[17]	18	19	20	21	22	23
24	25	[26]	[27]	[28]	[29]	[30]
31						

JUNE

S	M	T	W	T	F	S
	1	2	[3]	[4]	[5]	6
7	8	[9]	[10]	[11]	12	13
14	15	[16]	[17]	[18]	19	20
21	[22]	[23]	[24]	25	26	27
28	29	30				

JULY

S	M	T	W	T	F	S
			1	2	3	4
[5]	[6]	[7]	[8]	[9]	10	11
12	13	14	15	16	17	18
19	20	[21]	[22]	[23]	[24]	25
26	[27]	[28]	[29]	[30]	31	

AUGUST

S	M	T	W	T	F	S
						1
2	3	4	5	[6]	[7]	8
9	10	11	12	[13]	[14]	[15]
16	17	[18]	[19]	20	[21]	22
23	[24]	[25]	[26]	27	[28]	29
30	31					

3.6   PHENOLOGY

In 1986 phenology was observed biweekly or once every two weeks at each quadrat (Table 1). The observations were recorded using the phenological codes of Dierschke (1972) (Table 2). Vegetative and generative development was coded for each species.

In 1987 phenological codes were assigned to both species in the same manner as 1986 though sampling was done at weekly to biweekly intervals (Table 1) to more closely monitor changes in growth state. Where possible six individual stems and their branches were also assigned codes at each observation time to ascertain within quadrat variation for both species and phenological differences between branches and one- and two-year-old stems for thimbleberry.

Table 2.   Phenological codes (Dierschke 1972).

Vegetative		Generative	
0	Closed bud	0	with blossom buds
1	buds green tips	1	blossom bud recognizable
1a	germination		
2	green leaf out but not unfolded	2	blossom buds strongly swollen
3	leaf unfolding up to 25%	3	shortly before flowering
4	leaf unfolding up to 50%	4	beginning flowering
5	leaf unfolding up to 75%	5	in bloom up to 25%
6	full leaf unfolding	6	in bloom up to 50%
7	shoot elongation ceases	7	full bloom
8	first leaves turned yellow	8	fading
9	leaf yellowing up to 50%	9	completely faded
10	leaf yellowing over 50%	10	bearing fruit
11	bare	11	seed/fruit dispersal

3.7   DEMOGRAPHY

Demographic records of all stems within the 1 m diameter quadrats for thimbleberry and the 1.5 m diameter quadrats for devil's club were recorded in 1986, 1987 and in July 1988 (Figure 2). Demographic records consisted of the following:

a) identifying and counting all stems,

b) recording stem births and deaths and

c) aging all stems.

As thimbleberry stems live only two or three years, become lignified at the end of the first year and branch in the second year, it was possible to determine the age of each stem. Devil's club stems, however, are extremely long lived and age estimations were based on counts of annual terminal bud scale scars.

IV ANALYTICAL TECHNIQUES

4.1 TECHNIQUES

The primary techniques used in this study were multivariate in nature though univariate techniques such as analysis of variance (ANOVA) and the Mann-Whitney test were also used. The Mann-Whitney test is comparable to a nonparametric two-sample t-test (Zar 1974). Relationships within each matrix of environmental or plant characters were initially examined with principal components analysis (PCA). PCA also generated summary axis variables which were used in subsequent analyses such as ANOVA and canonical correlation analysis (CANCORR). The latter describes relationships between environmental variables and plant characters whereas the former was used to apportion variation. Weighted multidimensional scaling (WMDS) provided a nonparametric corroboration of the relationships suggested by CANCORR.

4.1.1 PRINCIPAL COMPONENT ANALYSIS (PCA)

Principal component analysis (PCA) is an ordination technique that yields a set of axes which effectively summarize the variation in a data matrix (Pimentel 1979; Greig-Smith 1983). The analysis may proceed via a correlation matrix, thereby removing the effect of differing measurement scales on the analysis, or via a covariance matrix which is used when a single measurement scale is represented in the data. In this study, unless measurement scales differed for the initial variables, the covariance matrix was used.

PCA is a useful technique and has several advantages. All axes are orthogonal or uncorrelated and the primary axes represent most of the variation in the original data set. As a result the dimensionality of the data is reduced. Eigenvectors may also represent more inclusive summaries of biological processes than raw data. Each axis may, therefore, be ascribed with a biological interpretation as a unique response to a set of conditions and further analyzed as a new summary variable. As the sum of the variation expressed by the eigenvectors equals 100% and axes are orthogonal they can also be further repartitioned into component parts and the component parts summed over all the axes (Pimentel 1979; Scagel

and Maze 1984). Finally as axes scores approximate multivariate normality, they more closely fulfill the assumptions of parametric analysis (Pimentel 1979).

PCA has few assumptions. First it is based on variables which are real numbers. Ideally the sample should be random and variables should vary monotonically in relation to each other or be linearly related (Pimentel 1979; Greig-Smith 1983). If this latter condition is not fulfilled infolding of the data or convolution occurs (Greig-Smith 1983). Although nonlinearity is a common problem with biological data, environmental characters usually fulfill this criterion (Greig-Smith 1983). Regardless the technique is not invalidated by some divergence from these conditions (Pimentel 1979).

The primary disadvantage of the technique is the difficulty of ascribing biologically meaningful interpretations to the results. If the initial characters measured do not adequately reflect biological phenomena a meaningful pattern may not emerge. Secondly deciding which axes to interpret and how important those axes are can be quite subjective (Pimentel 1979). Although the first axis will represent more of the total variation of the original data than the second axis, it may not have more biological significance.

4.1.2 ANOVA

While analysis of variance (ANOVA) is mostly used to test for differences between group means only, it was only used to partition variance. No hypothesis testing was performed.

As sums of square are additive and independently derived (Sokal and Rohlf 1969), they can be divided into those components of the total variation due to between groups and within groups. Using PCA axis scores variation between and within groups was calculated for the whole data set in the following manner:

$$\text{Variation}_A = \sum_{i=1}^{i=n} (SS_A \backslash SS_{tot})(\lambda_i)$$

where SS equals the sums of squares due to the ANOVA term A and (λ_i) is the percent of variation of the total data set accounted for by eigenvector i of the total n eigenvectors (Scagel and Maze 1984).

4.1.3 CANONICAL CORRELATION (CANCORR)

Canonical correlation analysis seeks linear relationships between matrices by ordinating each matrix while simultaneously maximizing the correlation coefficients between each pair of canonical variates axes (Gittins 1985). In this study, CANCORR was used to seek relationships between plant characters and environmental variables and between pairs of plant characters.

CANCORR has many similarities to PCA. Most of the variation of the original data is accounted for by the first few axes so the technique effectively reduces the dimensionality of the data (Gittins 1985). The canonical axes are also uncorrelated except for consecutive pairs from each matrix for which correlation is maximized (Gittins 1985). CANCORR generates new axes of canonical variates by multipling vectors of original variables by canonical weights.

CANCORR is a metric ordination technique implying that some assumptions must be met to achieve accurate results from the data. The sample size must be larger than the sum of the number of variables from each matrix (Pimentel 1979; Gittins 1985). As sample size decreases in relation to the number of variables spurious results are generated and removing or adding samples may substantially alter results (Pimentel 1979). To meet all conditions the data must also be linear and continuous though this assumption can be waived for descriptive analyses (Gittins 1985). Assumptions of multivariate normality can be met by using PCA axes scores of raw data as input data (Pimentel 1979; Gittins 1985).

CANCORR has received much criticism as an unwieldy and unreliable technique (Pimentel 1979; Gittins 1985). Spurious correlations may result especially if collinearity exists between variables of either matrix. Commonly raw data is orthogonally transformed via PCA or some other ordination technique to overcome these problems; however transformation may confound and complicate deciphering of the results. In addition to spurious results, it is possible for the canonical correlation to be high while the canonical variates are not strongly correlated with the original data or all multiple correlations are low (SAS Technical Report P-161 1985). Other tools such as redundancy analysis or communalities, used with canonical coefficients, may alleviate these shortcomings (Gittins 1985). Perhaps the most difficult problem to overcome

is making biological sense of mathematical relationships. Numerical relationships do not necessarily yield real biological relationships.

Another means of seeking relationships between two matrices, whether raw data matrices or axes scores from an ordination, may simply be to correlate axes from each matrix (Jeffers 1978). CANCORR has the advantage of expressing these relationships while also seeking major linear trends in all the axes concurrently. Like other multidimensional techniques, it manipulates all data thereby overcoming the oversimplification of univariate analyses which examine only one variable at a time. The complexity of the analyses may also be an advantage if it forces the user to more closely examine and justify the results than other more straightforward methods.

4.1.4   WEIGHTED MULTIDIMENSIONAL SCALING (WMDS)

Weighted multidimensional scaling (WMDS) is an ordination technique which seeks to maximize the mathematical relationship between similarities (proximities) in symmetric matrices and Euclidean distances between points (Kruskal and Wish 1978). Unlike PCA it does not assume a linear relationship between the variables and is based on distances between points rather than angles between vectors (Schiffman et al. 1981).

WMDS can be used to reduce dimensionality and analyze relationships within one matrix or between several matrices using either metric or nonmetric models. Metric models relate proximities directly to distances whereas nonmetric models merely retain the rank order between proximities and distances (Kruskal and Wish 1978). Both models require input data be in the form of symmetric matrices. No other limitations are imposed.

INDSCAL or Individual Distances Scaling of Proximity Data is a metric version of WMDS which seeks relationships between several similarities matrices (Carroll 1987). It has two underlying assumptions. First, INDSCAL assumes that a set of dimensions (axes) exist which account for all the meaningful variation (except for error) between all similarities between quadrats (Carroll 1987); secondly it assumes that the distances between all quadrats can be simply related to proximities by a unique subject weight for each matrix (Carroll 1987).

Two dimensional WMDS or WMDS of one matrix attempts to maximize the relationship between distances and proximities data so that

$$d^2_{ij} = f (x_{ir} - x_{jr})^2$$

where d_{ij} is the Euclidean distance between points i and j and x_{ir} and x_{jr} is the similarity or proximity between quadrats x_i and x_j on axis r. Multiway WMDS or WMDS between more than one matrix , such as INDSCAL, stretches or shrinks each axis by a weight factor for each matrix so that

$$d^2_{i,j,k} = w_{kr}(x_{ir} - x_{jr})^2$$

where $d_{i,j,k}$ is the distance between points i and j for sample k and w_{kr} is the weighting of each sample k on axis r (Kruskal and Wish 1978). The goodness of fit is assessed by one of many stress measures which assess the dispersion between distances and proximities (Kruskal and Wish 1978). The objective of the procedure is therefore to minimize stress over all values (Kruskal and Wish 1978). Computationally the procedure iterates until the reduction in stress is minimized (Kruskal and Wish 1978).

Interpretation is based on graphs which show the linear separation of each quadrat for each matrix and graphs of subject weights. The weight space displays a point for each matrix. The length of the vector from the origin to this point represents the amount of variation of each matrix which is accounted for by the model while the angle between the two vectors is inversely proportional to the relationship between the two original matrices (Young and Lewyckyj 1979; Schiffman et al.1981).

As each dimension or axis generated is considered to be a response to a stimulus, the number of axes or dimensions chosen can be critical. More axes diminish stress. However not all dimensions can be meaningfully interpreted. There is also no stringent mathematical criterion for judging dimensionality though the number of quadrats must be almost four times the number of dimensions (#dimensions < 4 (#quadrats - 1)). A line graph of the number of dimensions versus the amount of stress for each dimension is used as a subjective aid for deciding dimensionality (Kruskal and Wish 1978).

As previously stated the objective is to minimize stress. However stress can be affected by several factors including a nonsymmetric matrix, replication at each variable, ties in the data or missing values. The most serious produce local minima for stress. As the iterative nature of the process terminates when stress reduction ceases it is possible that a global minimum for the whole data set will not be reached (Kruskal and Wish 1978; Shiffman et al. 1981).

In this study WMDS was used to provide a nonparametric check on CANCORR. More information on WMDS may be obtained from Kruskal (1964a, 1964b) and Carroll and Chang (1970).

V DATA ANALYSIS

5.1 GRAPHICAL ANALYSES

Initial exploration of the data used graphs. Canopy cover was graphed to illustrate changing light conditions over the quadrats at each site. Scatters of phenological codes against time also showed how developmental rates differed between sites, species and years and the extent of the variation at each level in this nested hierarchy. Finally graphs of the thimbleberry demographic data were drawn to illustrate the general demographic trends over the three year period of the study. As devil's club population did not change substantially during the study, graphs of the age distribution on July 30, 1987 only were drawn.

5.2 ENVIRONMENT

Table 3 displays the analytical methods for environmental variables other than canopy cover. PCA axes of soils variables, frequency and presence/absence of plant neighbours were generated to produce input data for subsequent CANCORR and to show correlations between raw variables. As PCA requires that samples exceed variables (Pimentel 1979), species lists used as input data to PCA were modified prior to ordination. All species in greater than 17 quadrats and less than 5 quadrats were removed from the KIT, WED and DC species lists and species in greater than 38 quadrats and less than 4 quadrats were removed from the TB species lists. This modification diminished the effects of rare or abundant species on the analyses (Greig-Smith 1983). Distance matrices of these same raw variables were used in WMDS though soils variables were first standardized to zero mean and equal variance. Separate Euclidean distance matrices and matrices of PCA axes scores were produced for KIT, WED, TB and DC yielding 4 matrices for soil variables and 8 matrices for presence/absence and frequency of plant neighbours.

Table 3.   Analytical methods for environmental data. Arrows indicate the sequence of
analyses from raw variables through summary variables used as input data to
CANCORR and WMDS.
(When KIT, WED, TB or DC are listed, a separate analysis is
performed for each)
KIT = girdled alder thimbleberry site, N = 21
WED = nongirdled alder thimbleberry site, N = 21
TB = KIT and WED thimbleberry data, N = 42
DC = devil's club site, N = 21

Soils

| variables include:
pH, % coarse fragments,
%sand, % silt, % clay,
%organic matter, depth to
mineral soil, total N | PCA
- correlation matrix among
  variables
- KIT, WED, TB, DC → CANCORR

Euclidean distance matrix
among quadrats
- KIT, WED, TB, DC → WMDS |
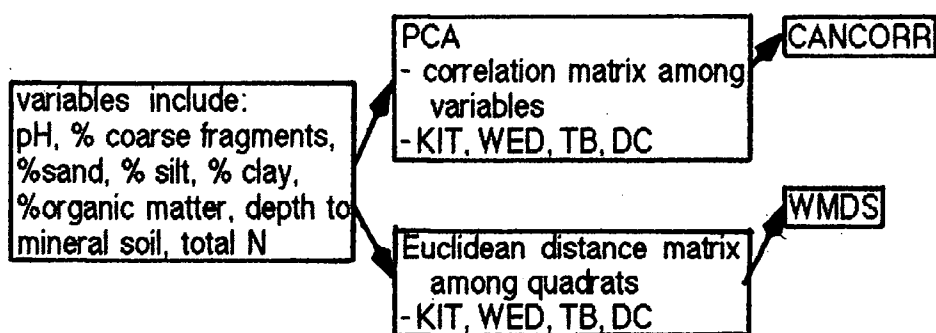
Species Neighbors - 1987

All species in > 17 quadrats and <5 quadrats removed from KIT, WED, DC raw data
       matrices
All species in > 38 quadrats and <4 quadrats removed from TB raw data matrix

Frequency

| variables include lists of all
species in quadrats coded
from 0 - 4 based on
number of quadrat quarters
in | PCA
- covariance matrix among
  variables
- KIT, WED, TB, DC → CANCORR

Euclidean distance matrix
among quadrats
-KIT, WED, TB, DC → WMDS |

Presence/Absence

| variables include lists of all
species coded 0 or 1 based
on presence/absence | PCA
- covariance matrix among
  variables
- KIT, WED, TB, DC → CANCORR

Euclidean distance matrix
among quadrats
- KIT, WED, TB, DC → WMDS |

The influence of plant neighbors was examined at different scales as different environmental attributes may be reflected at each scale. As presence/absence data of plant neighbors represents a coarser scale of measurement than cover or frequency of vegetation, more coarse grained environmental gradients may be reflected at this scale (Allen and Wyleto 1983). Allan and Starr (1982) also indicate that coarse grained presence/absence data may reflect influences due to time scales which are not apparent in finer-scaled frequency data.

5.3   MORPHOLOGY

The morphological variables and analyses are displayed in Table 4.   Data were divided into groups for analysis. Except for the ANOVA between species, devil's club and thimbleberry were analyzed separately. The two species were sufficiently different that morphological descriptions of each one required different variables. These divisions also reflect differences in annual sample sizes . In 1986, 10 quadrats only were sampled whereas 21 were sampled in 1987. Except for the ANOVAs which apportioned variation among quadrats and years, data from 1987 were used.

Input variables used in simple correlation, ANOVA and CANCORR were generated by PCA. All PCAs were performed on correlation matrices as measurement scales differed between variables. Correlations were calculated between PCA scores and the 1986 and 1987 canopy cover data for DC, KIT, WED and TB. ANOVA was used to partition PCA scores among years, sites, species and quadrats. Variation in thimbleberry data was partitioned using a nested ANOVA as years, sites and quadrats could be simultaneously considered. Devil's club was not included in the nested ANOVA as only differences between thimbleberry sites were of interest. ANOVA was also used to partition variation among quadrats for the number of stem leaves in 1987, the stem lengths in 1987 and leaf length and width in 1986. Most quadrats contained at least 5 replicates of these variables whereas other morphological traits were not as numerous within quadrats. As sample sizes within quadrats were unequal these variables were

not summarized with PCA but were analyzed individually. Finally Euclidean distance matrices among quadrats were calculated from the standardized morphological data and analyzed using WMDS. Matrices of PCA axes scores and Euclidean distance matrices were produced for the KIT, WED, DC and TB data sets.

Table 4. Analytical methods for morphological data. Arrows indicate the sequence of analyses from raw variables through summary variables to ANOVA, WMDS, CANCORR or simple correlation. Sampling time is the second week of July unless otherwise indicated. (When KIT, WED, TB or DC are listed, a separate analysis is performed for each)
KIT = girdled alder thimbleberry site, N = 21 in 1987, 10 in 1986
WED = nongirdled alder thimbleberry site, N = 21 in 1987, 10 in 198
DC = devil's club site, N = 21 in 1987, 10 in 1986
TB = KIT and WED thimbleberry data, N = 42 in 1987, 20 in 1986

| 1986 & 1987 TB variables include: # flowers per branch @ Aug.8, #flowering stems @ Aug. 8,# 2-year-old stems @ June 30,# 1-year-old stems @ June 30, # leaves/1-year-old stems, # leaves/2-year-old stems,1-year-old stem length, 2-year-old stem length,1-year-old stem basal diameter, 2-year-old stem basal diameter, branch length, branch basal diameter | → | PCA -correlation matrix among variables | → | ANOVA - to apportion TB variation among years and sites -Y = A + B(A) + E where A = years, B = sites, E = error or within sites & Y = PCA axis scores |

| 1986 & 1987 DC variables include: # stems @ June 30,# branches/stem, # leaves/stem, stem length, stem diameter, branch length, branch basal diameter | → | PCA - correlation matrix among variables | → | ANOVA - to apportion DC variation among years -Y = A + E where A = years, E = error or within years & Y = PCA axis scores |

| 1987 TB & DC - variables include: # branches per stem, # flowers/stem (TB) or bunches (DC),# stems, # leaves/branch, # leaves, stem length, stem diameter, branch diameter, branch length | → | PCA - correlation matrix among variables | → | ANOVA - to apportion variation among species - Y = A + E where A = species, E = error & Y = PCA axis scores |

Table 4 continued

DC & TB		ANOVA
1987 #stem leaves	→	- to apportion DC & TB
1987 stem length		variation among quadrats
1986 leaf length		Y = A + E where
1986 leaf width		A = quadrats, E = error &
		Y = raw data

1987 TB, KIT, WED variables include: # branches/stem @ 30/6, # flower/ inflorescence @ 8/7, # flowering stems @ 8/7, # flowers/stem @ 8/7, # 2-year-old stems @ 30/6, # 1-year-old stems @ 30/6, # leaves, # branch leaves, # leaves/1-year-old stem, # leaves/ 2-year-old stem, 1-year-old stem length, 2-year-old stem length, 1-year-old stem diameter, 2-year-old stem diameter, branch length, branch diameter	PCA - correlation matrix among variables -KIT, WED, TB	correlation with canopy cover from 1986 & 1987 -KIT, WED, TB
		CANCORR
	Euclidean distance matrix among quadrats KIT, WED, TB	WMDS

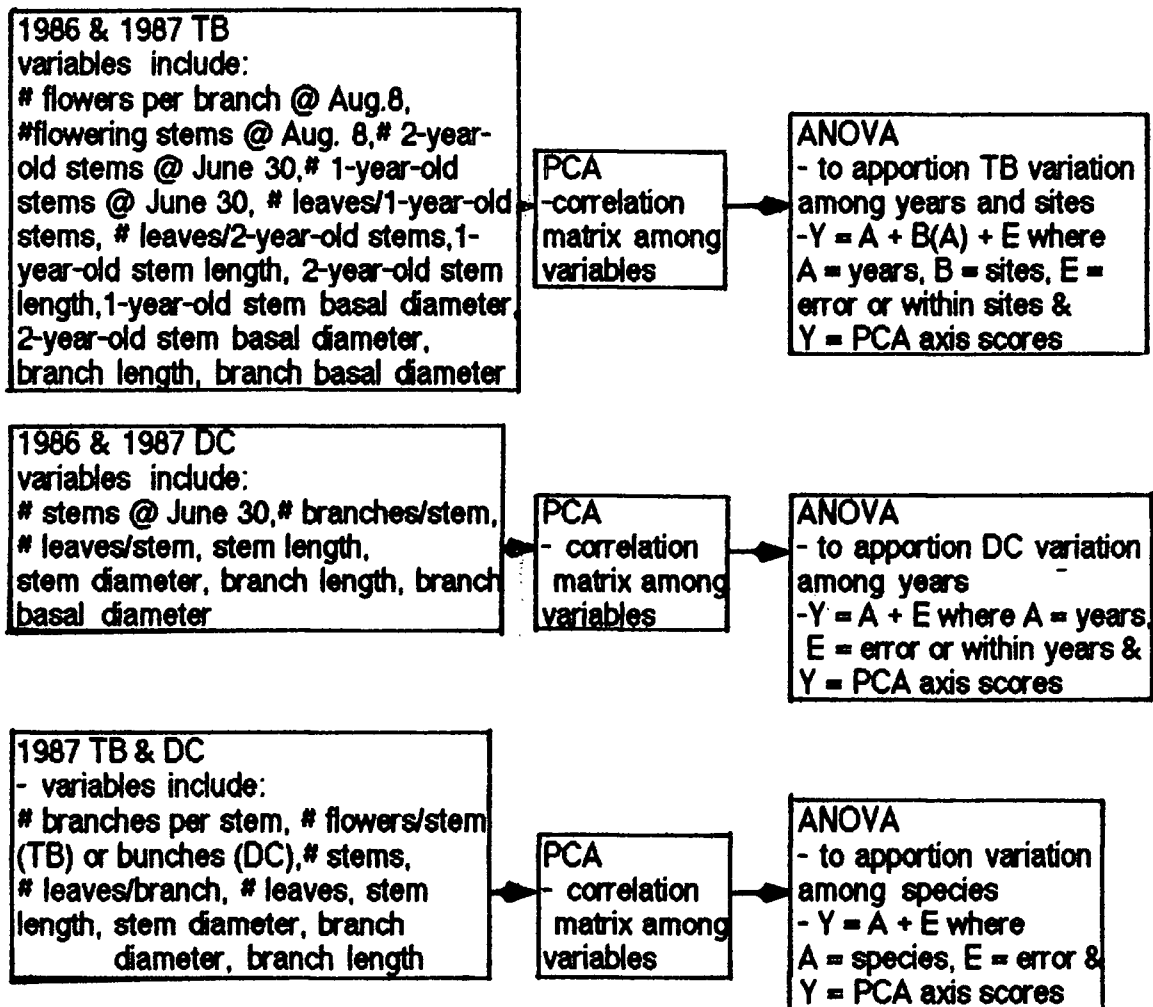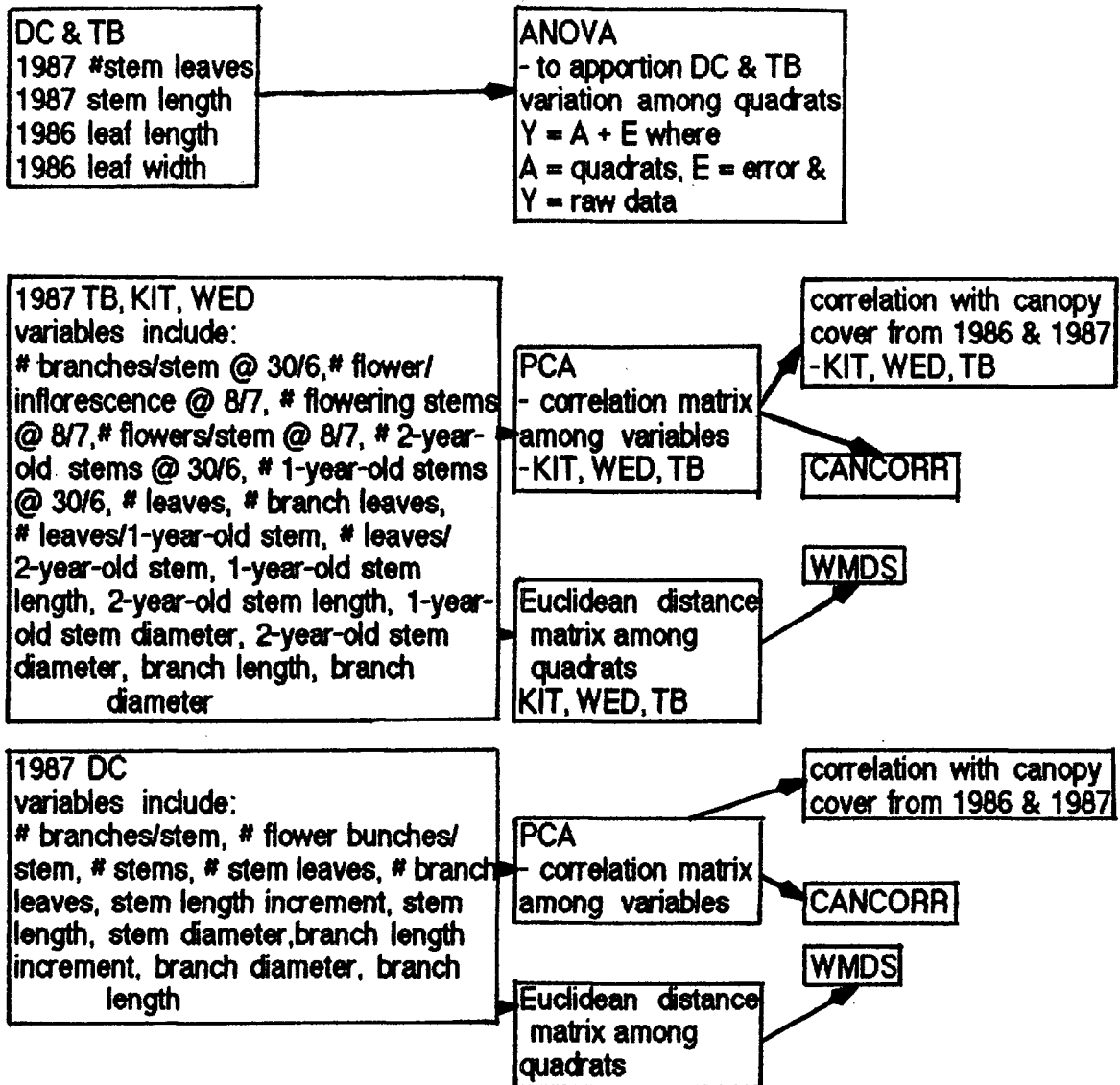| 1987 DC variables include: # branches/stem, # flower bunches/ stem, # stems, # stem leaves, # branch leaves, stem length increment, stem length, stem diameter, branch length increment, branch diameter, branch length | PCA - correlation matrix among variables | correlation with canopy cover from 1986 & 1987 |
| | | CANCORR |
| | Euclidean distance matrix among quadrats | WMDS |

5.4   PHENOLOGY

The sequence of phenological analysis is displayed in Table 5. The slope of a linear regression line was calculated as input data to all subsequent analyses. The slope of the line was an effective summary variable as it gave an estimate of the rate of change of phenological development with time. Simple linear regression was found to yield higher r^2 values than log-

log or log-normal relationships in all cases. Slopes were calculated for each year and for both vegetative and generative data at each quadrat for 1986 and 1987 and for stems within each quadrat in 1987. PCA axes scores of covariance matrices and Euclidean distance matrices of slopes of regression lines were used in subsequent CANCORR and WMDS. The slopes of regression lines were also correlated with canopy cover in 1986 and 1987. Finally ANOVA was used to partition generative and vegetative slopes of regression lines between years, sites, species, quadrats and stems within quadrats.

Nested ANOVA was used to partition variation among years and sites for thimbleberry as this model allowed simultaneous comparisons between different levels in the hierarchy. Devil's club was not included in the nested analysis as site differences for thimbleberry only were of interest. Separate ANOVAs were used to partition variation for both generative and vegetative data. Generative data may be less plastic than vegetative data and both vegetative and generative were considered functionally separate. ANOVA was also used to apportion variation among quadrats using both stem and branch phenologies. Variation within quadrats was apportioned separately from other strata as the number of stems and branches within quadrats were not equal.

5.5 DEMOGRAPHY

The effect of density on thimbleberry longevity and the rate of stem production was examined with regression analysis of the number of stems in a quadrat and the percentage of the total number of stems in a quadrat surviving to each time period. The time periods were those used in PCA analysis (Table 6). The sequence of all further analyses is displayed in Table 6. PCA axes scores of covariance matrices were used as input data in ANOVA and CANCORR; whereas Euclidean distance matrices were used in WMDS. ANOVA was used to partition variation between years and sites for thimbleberry and within and between quadrats for both thimbleberry and devil's club PCA axes scores. Comparisons between the two species were not possible as devil's club numbers did not fluctuate significantly during the course of the study.

Table 5.   Analytical methods for phenological data. Arrows indicate the sequence of
           analyses from raw data through summary variables to CANCORR, ANOVA and
           WMDS.
           (When KIT, WED, TB or DC are listed, a separate analysis is
           performed for each)
           KIT = girdled alder thimbleberry site, N = 21
           WED = nongirdled alder thimbleberry site, N = 21
           TB = KIT and WED thimbleberry data, N = 42
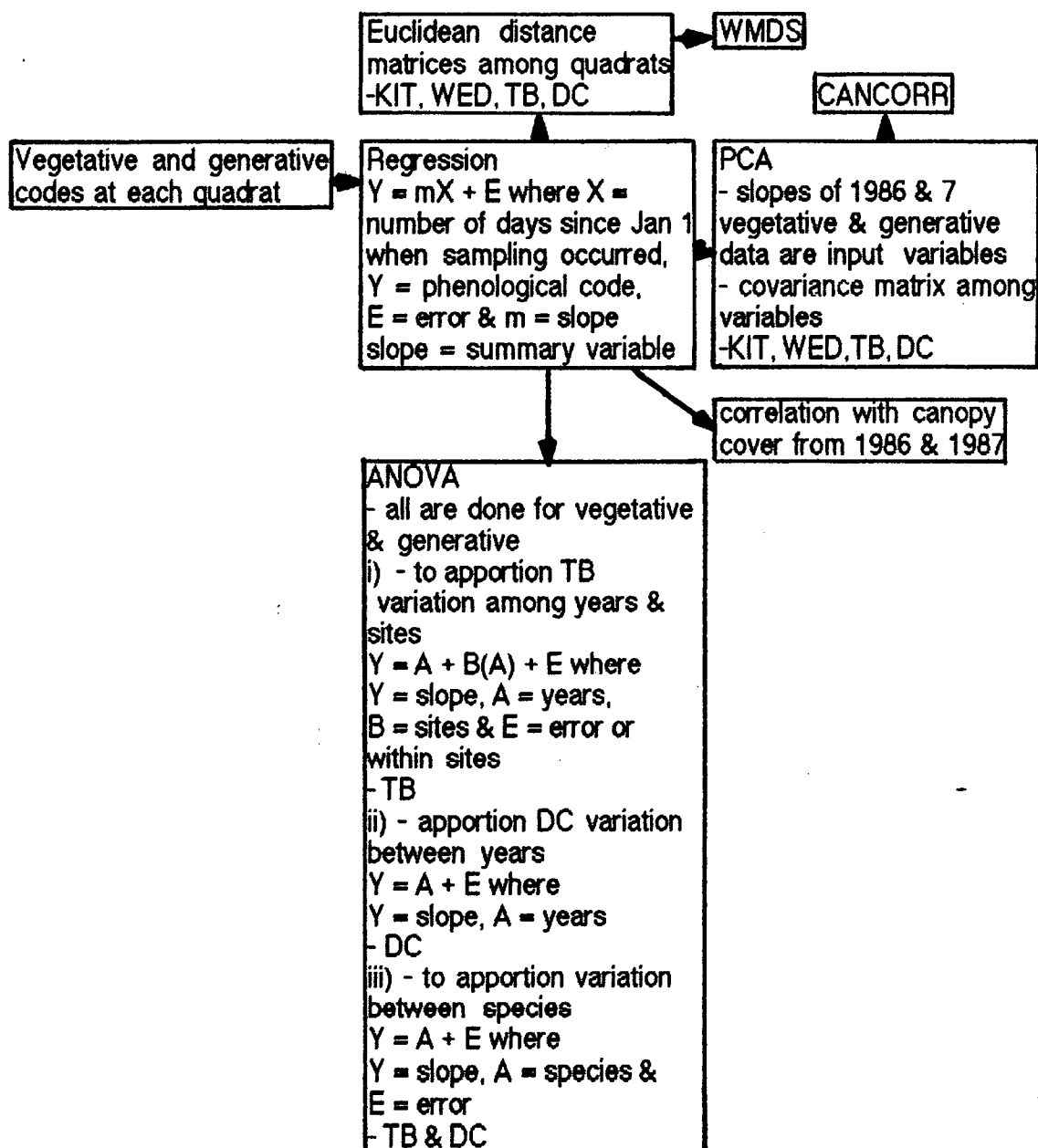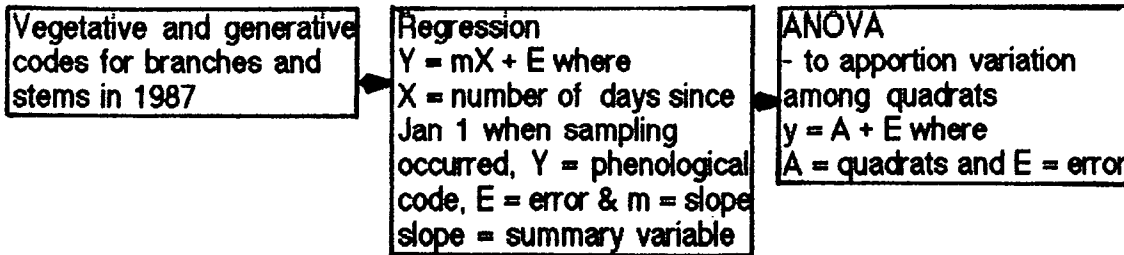   DC = devil's club site, N = 21

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                              ┌─────────────────────────┐    ┌──────┐
                              │ Euclidean  distance     │◄──►│ WMDS │
                              │ matrices among quadrats │    └──────┘
                              │ -KIT, WED, TB, DC       │        ┌──────────┐
                              └─────────────────────────┘        │ CANCORR  │
                                                                 └──────────┘
┌───────────────────────────┐ ┌─────────────────────────┐ ┌─────────────────────────┐
│ Vegetative and generative │ │ Regression              │ │ PCA                     │
│ codes at each quadrat     │ │ Y = mX + E where X =    │ │ - slopes of 1986 & 7    │
└───────────────────────────┘ │ number of days since Jan 1│ │ vegetative & generative │
                              │ when sampling occurred, │ │ data are input  variables│
                              │ Y = phenological code,  │ │ - covariance matrix among│
                              │ E = error & m = slope   │ │ variables               │
                              │ slope = summary variable│ │ -KIT, WED, TB, DC       │
                              └─────────────────────────┘ └─────────────────────────┘
                                                            ┌─────────────────────────┐
                                                            │ correlation with canopy │
                                                            │ cover from 1986 & 1987  │
                                                            └─────────────────────────┘
                   ┌─────────────────────────────┐
                   │ ANOVA                       │
                   │ - all are done for vegetative│
                   │ & generative                │
                   │ i) - to apportion TB        │
                   │  variation among years &    │
                   │ sites                       │
                   │ Y = A + B(A) + E where      │
                   │ Y = slope, A = years,       │
                   │ B = sites & E = error or    │
                   │ within sites                │
                   │ - TB                        │
                   │ ii) - apportion DC variation │
                   │ between years               │
                   │ Y = A + E where             │
                   │ Y = slope, A = years        │
                   │ - DC                        │
                   │ iii) - to apportion variation│
                   │ between species             │
                   │ Y = A + E where             │
                   │ Y = slope, A = species &    │
                   │ E = error                   │
                   │ - TB & DC                   │
                   └─────────────────────────────┘
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Table 5 continued

Vegetative and generative codes for branches and stems in 1987	Regression Y = mX + E where X = number of days since Jan 1 when sampling occurred, Y = phenological code, E = error & m = slope slope = summary variable	ANOVA - to apportion variation among quadrats y = A + E where A = quadrats and E = error

The number of stems living to each age class from cohorts produced in May 1986 and 1987 were used as input data to ANOVAs which apportioned thimbleberry variation between years and sites. This measure incorporates both density effects and life expectancy between quadrats through time. Age distributions were partitioned among quadrats for both species. Age distributions represented the variation at one time only and allow comparison between devil's club and thimbleberry. The age distributions did not, however, have equal sample sizes within quadrats so devil's club age data were grouped to satisfy PCA requirements.

Table 6.   Analytical methods for demographic data. Arrows indicate the sequence from raw data through summary variables to ANOVA, CANCORR and WMDS. (When KIT, WED, TB or DC are listed, a separate analysis is performed for each)
KIT = girdled alder thimbleberry site, N = 21
WED = nongirdled alder thimbleberry site, N = 21
TB = KIT and WED thimbleberry data, N = 42
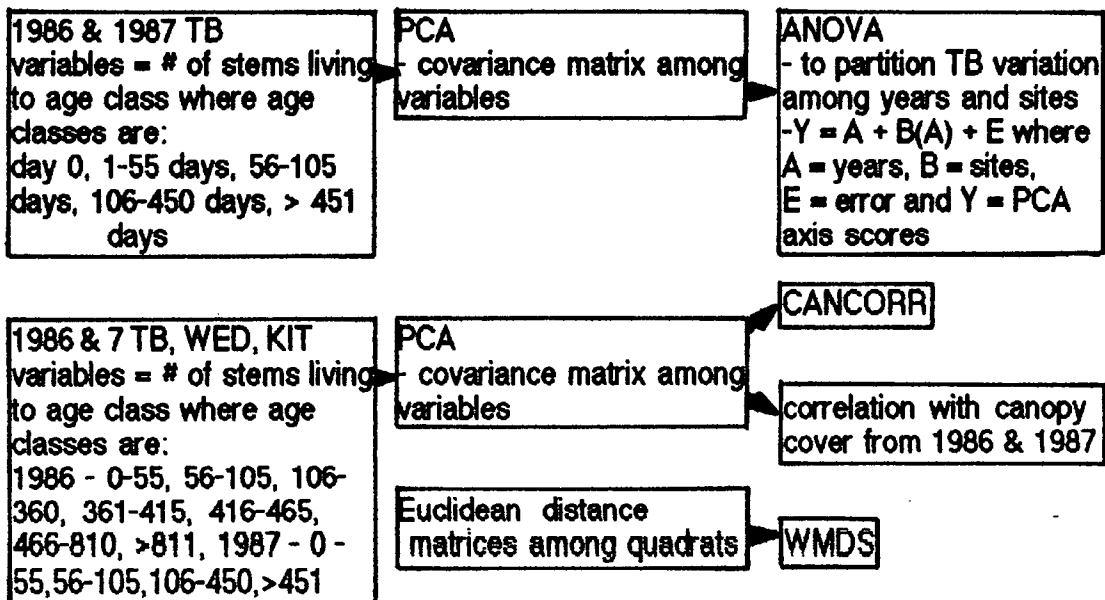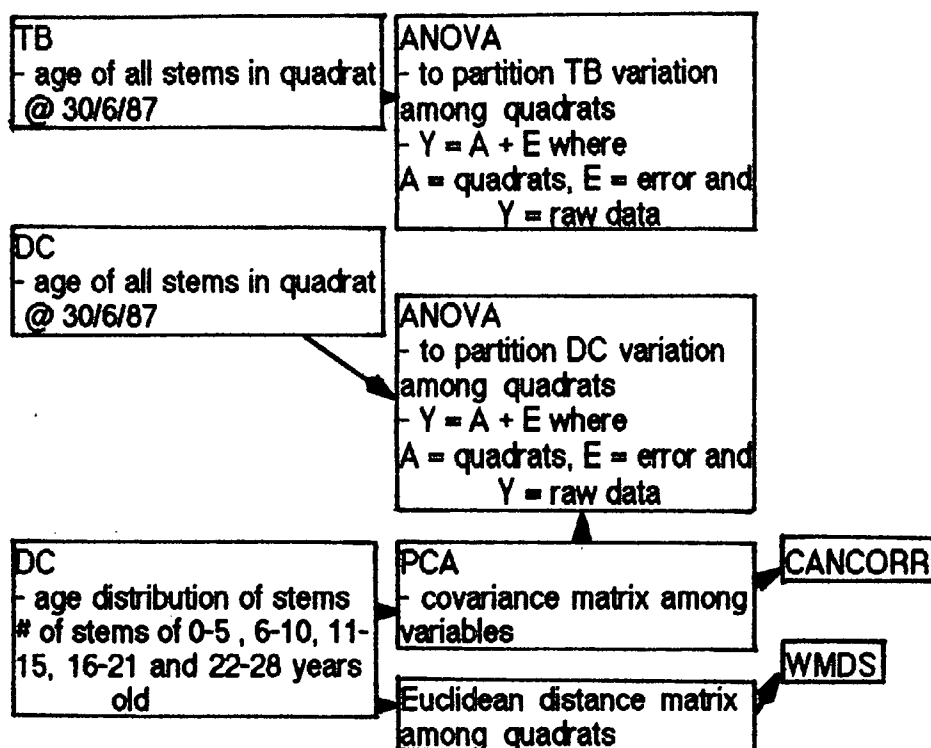DC = devil's club site, N = 21

1986 & 1987 TB variables = # of stems living to age class where age classes are: day 0, 1-55 days, 56-105 days, 106-450 days, > 451 days	PCA - covariance matrix among variables	ANOVA - to partition TB variation among years and sites -Y = A + B(A) + E where A = years, B = sites, E = error and Y = PCA axis scores

CANCORR

1986 & 7 TB, WED, KIT variables = # of stems living to age class where age classes are: 1986 - 0-55, 56-105, 106-360, 361-415, 416-465, 466-810, >811, 1987 - 0 - 55,56-105,106-450,>451	PCA - covariance matrix among variables	correlation with canopy cover from 1986 & 1987

	Euclidean distance matrices among quadrats	WMDS

Table 6 continued

TB - age of all stems in quadrat @ 30/6/87	ANOVA - to partition TB variation among quadrats - Y = A + E where A = quadrats, E = error and Y = raw data
DC - age of all stems in quadrat @ 30/6/87	ANOVA - to partition DC variation among quadrats - Y = A + E where A = quadrats, E = error and Y = raw data

CANCORR

DC - age distribution of stems # of stems of 0-5, 6-10, 11-15, 16-21 and 22-28 years old	PCA - covariance matrix among variables Euclidean distance matrix among quadrats

WMDS

5.6 CANCORR AND WMDS

Relationships between all environmental variables and plant characters and between the matrices of plant characters were examined with WMDS and CANCORR (Figure 4). PCA axes scores were used as input data to CANCORR and WMDS was performed on pairs of Euclidean distance matrices (Tables 3 - 6). The first 10 axes generated by PCAs were used in CANCORR, though interpretation was based on the first three only. Canonical axes were only interpreted when canonical correlation coefficients were greater than .75 and the redundancy value for each matrix was greater than 1 divided by the number of variables in that matrix. All correlations of less than .50 were not considered large enough, either between PCA axes and raw data or canonical axes and PCA axes, to warrant interpretation. The analyses outlined in Figure 4 were performed for KIT, WED, DC and TB. WMDS is used to corroborate CANCORR and WMDS results are reported only where they clarify discrepancies in the CANCORR results.

5.7 COMPUTATION

All analyses were done using the computing facilities at the University of British Columbia. The computing packages used included UBC ANOVAR (Greig and Osterlin 1978) for analysis of variance, MIDAS (Fox and Guire 1976) for all simple correlation analyses and some PCA analyses, SYSTAT (Wilkinson 1988) and SYGRAPH (Wilkinson 1988) for all graphical presentation of the data and SAS (SAS Users Guide 1986) for all WMDS and CANCORR. The ALSCAL procedure which is incorporated into SAS was used for all WMDS (Young and Lewyckyj 1979). Some PCA analyses were also performed using a program written by Gary Bradfield of the Botany Department. All packages, except SYSTAT and SYGRAPH were available on the mainframe. SYSTAT and SYGRAPH were used on the Macintosh Plus personal computer in the Botany department. Other packages and subroutines developed at the University of British Columbia were also used.

Figure 4.   WMDS and CANCORR analyses. Arrows indicate all pairwise comparisons analyzed with WMDS and CANCORR. Analyses were performed using WED, KIT, TB and DC data sets.
KIT = girdled alder thimbleberry site, N = 21
WED = nongirdled alder thimbleberry site, N = 21
TB = KIT and WED thimbleberry data, N = 42
DC = devil's club site, N = 21
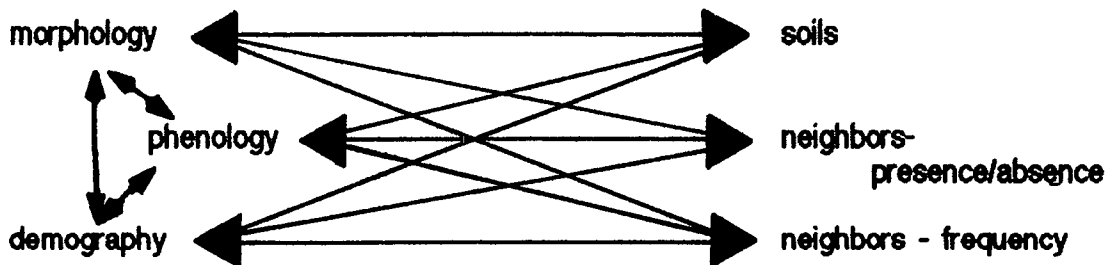
VI RESULTS

6.1 ENVIRONMENTAL RESULTS

6.1.1 CANOPY COVER

All sites range from little or no cover to a dense canopy overhead (Figure 5). The WED and DC sites have the most dense canopy cover with most quadrats having over 60 percent cover. Due to the alder girdling at the KIT site, most quadrats have less than 30 percent cover. The higher cover values at KIT quadrats 3, 8 and 14 are due to adjacent willows, which were not girdled. Quadrats 18 and 5 are shaded by elderberry.

Figure 5.   Percentage canopy cover over 63 quadrats at KIT, WED and DC in July 1987. Numbers refer to the quadrats at each site.
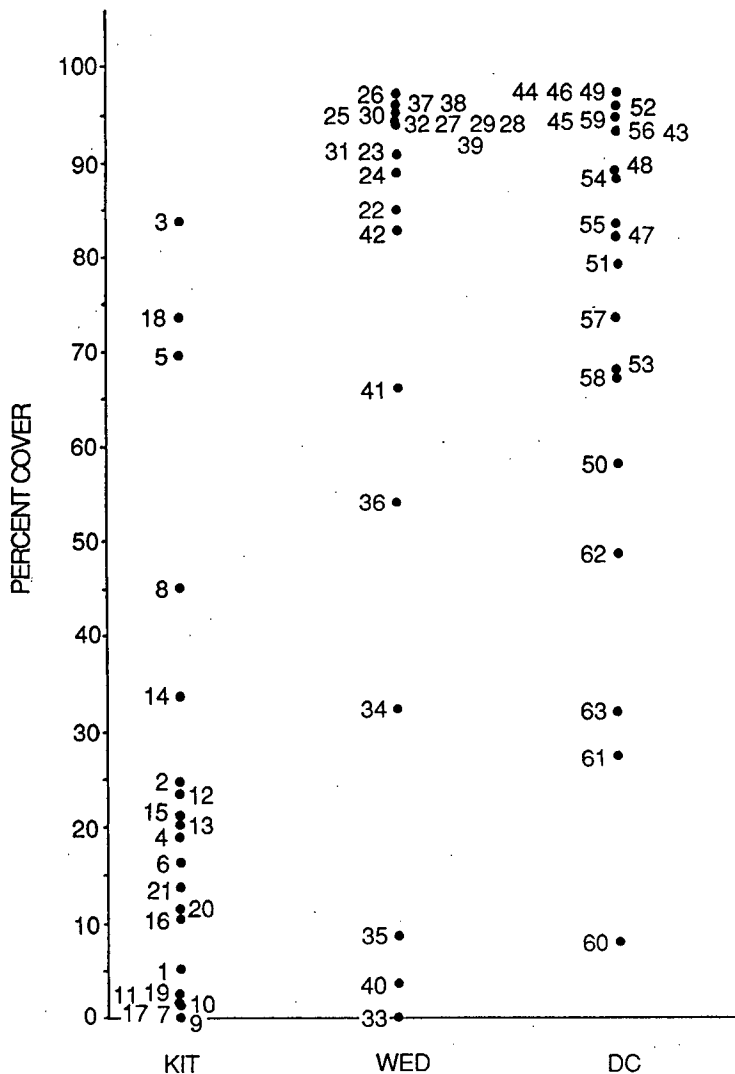
6.1.2 SOILS VARIABLES

Axis I, of the TB soils PCA, may represent a nutrient gradient (Table 7). The soils are more basic with a higher percentage of sand at the positive end of the axis and are acidic, have more nitrogen, organic material and coarse fragments at the negative end of the axis (Table 7). Axis II suggests a textural gradient or the time since the site was flooded and mineral soil was covered with a layer of silt and clay (Table 7). The percentage of clay and silt are negatively correlated with axis II whereas the depth to mineral soil, the percent organic matter and the percentage of sand in the soil are positively correlated with the axis. Axis III may be a gradient of drainage conditions or the amount of time that quadrats are submerged (Table 7). The percentage of clay and the depth to mineral soil are positively correlated with the axis (Table 7). As smaller clay sized particles retain water and limit drainage, biological processes may be inhibited and organic matter may accumulate on the surface.

There is some separation between the two sites on both axes (Figure 6). The KIT scores are mostly positive for axis I and negative for axis II (Figure 6). This suggests that KIT may have less rich soils and may have been flooded more frequently than WED (Figure 6). The WED site is further from the river and has a blanket of rich alder leaves covering the ground, which supports this interpretation.
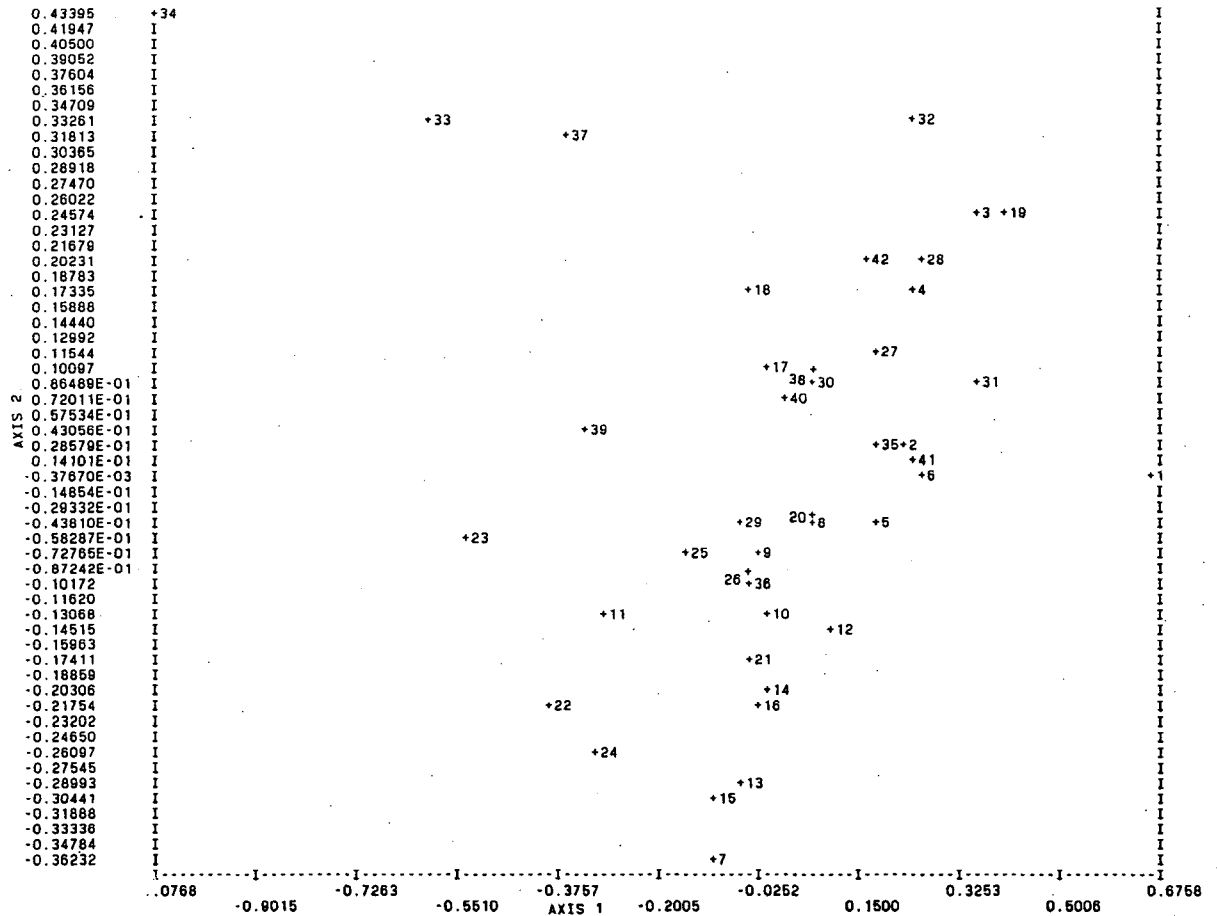
Table 7.   TB soils - PCA axes relationships.
            Correlation coefficients relating soils variables to PCA axes
            I-III.

Axis	I	II	III
% variation	47.78	18.33	13.99
soils variables			
pH	.7313	-.0863	.0539
%coarse	-.7825	.3885	-.0809
%sand	.6942	.6520	-.0999
%silt	-.6311	-.6363	-.2357
%clay	-.0965	-.3349	.8882
organic matter	-.8663	.3409	.0264
nitrogen	-.9189	.0063	-.1492
depth to mineral soil	-.4372	.4992	.4820

The KIT soils PCA axes are similar to the TB data set (Table 8). Axis I may be a nutrient gradient. Total soil nitrogen, the percentage of organic matter and the percentage of silt are negatively correlated with the axis whereas the percentage of sand and pH are positively correlated with the axis (Table 8). Axis II represents a textural gradient or the time since flooding. The percentage of silt is negatively correlated with the axis and the percentages of coarser fragments and clay and the depth to mineral soil are positively correlated with the axis (Table 8). Axis III suggests a drainage gradient or the duration of flooding. The percentage of clay is positively correlated with the axis, whereas, the percentage of coarse fragments are negatively correlated with the axis (Table 8).

Figure 6.   Graph of axes I and II of the soils PCA for TB showing individual quadrats.

Table 8.   KIT soils - PCA axes relationships.
            Correlation coefficients relating soils variables to PCA axes
            I-III.

Axis	I	II	III
% variation	42.79	20.84	13.55
soils variables			
pH	.7250	-.0978	-.4170
%coarse	-.4674	.6439	-.5359
%sand	.8479	.1526	-.1780
%silt	-.6564	-.6614	.2186
%clay	-.0914	.5730	.5306
organic matter	-.7784	.3758	-.2135
nitrogen	-.9133	.0064	-.1095
depth to mineral soil	.2844	.5596	.4520

Axis I of the WED soils PCA suggests a nutrient gradient (Table 9). The percentages of soil nitrogen, organic matter, coarse fragments, silt and clay are negatively correlated with the axis, while the pH and sand content are positively correlated (Table 9). Axis II again suggests a textural gradient or the time since the site was flooded. The percent silt and clay are negatively correlated with the axis and the percent sand is positively correlated with the axis (Table 9). Axis III suggests a drainage gradient or a gradient of standing water, being positively correlated with the depth to mineral soil (Table 9).

Table 9.   WED soils - PCA axes relationships.
            Correlation coefficients relating soils variables to PCA axes
            I-III.

Axis	I	II	III
% variation	59.96	18.92	10.47
soils variables			
pH	.8346	-.3089	.2380
%coarse	-.7898	.3767	-.3823
%sand	.8030	.5190	.1158
%silt	-.7886	-.5441	-.1002
%clay	-.5112	-.6580	.3830
organic matter	-.8695	.3231	.0118
nitrogen	-.8867	.0989	-.3449
depth to mineral soil	-.6379	.4050	.5879

Axis I of the DC soils PCA may represent a drainage gradient. The depth to mineral soil and the clay content are positively correlated with the axis and the sand content and the percentage of organic fragments are negatively correlated (Table 10). The pH is also postively correlated with axis I (Table 10); however, it is consistently acidic at this site and varies little. Most of the soils samples also contained a high percentage of organic matter from fallen trees and branches. Axis II is correlated with the soil nitrogen content and the percent coarse fragments and organic matter (Table 10). The underlying biological significance of the correlations to Axis II is not clear. Axis III suggests the time since the time site, which is located adjacent to the river, was flooded. The percentage silt has a strong negative correlation with this axis (Table 10).

Table 10.   DC soils - PCA axes relationships.
            Correlation coefficients relating soils variables to PCA axes
            I-III.

Axis	I	II	III
% variation	32.25	22.06	18.89
soils variables			
pH	.5778	.2860	-.4400
%coarse	-.3988	.6240	.1185
%sand	-.8243	-.3483	-.0486
%silt	.2226	.0480	-.9018
%clay	.6350	.2835	.6330
organic matter	-.6801	.5930	.1095
nitrogen	-.3813	.7139	-.2689
depth to mineral soil	.5888	.4777	.0544

Most quadrats to the northeast of the ditch running between the two transect lines have positive scores on axis I of the DC soils PCA, suggesting that they may have poorer drainage (Figure 7). Those quadrats closer to the river have more negative scores (Figure 7). These quadrats are somewhat less boggy and may be higher in elevation (Figure 7), though this was not measured. Transects are dissimilar (Figure 7).

Figure 7. Graph of axes I and II of the soils PCA for DC showing individual quadrats.
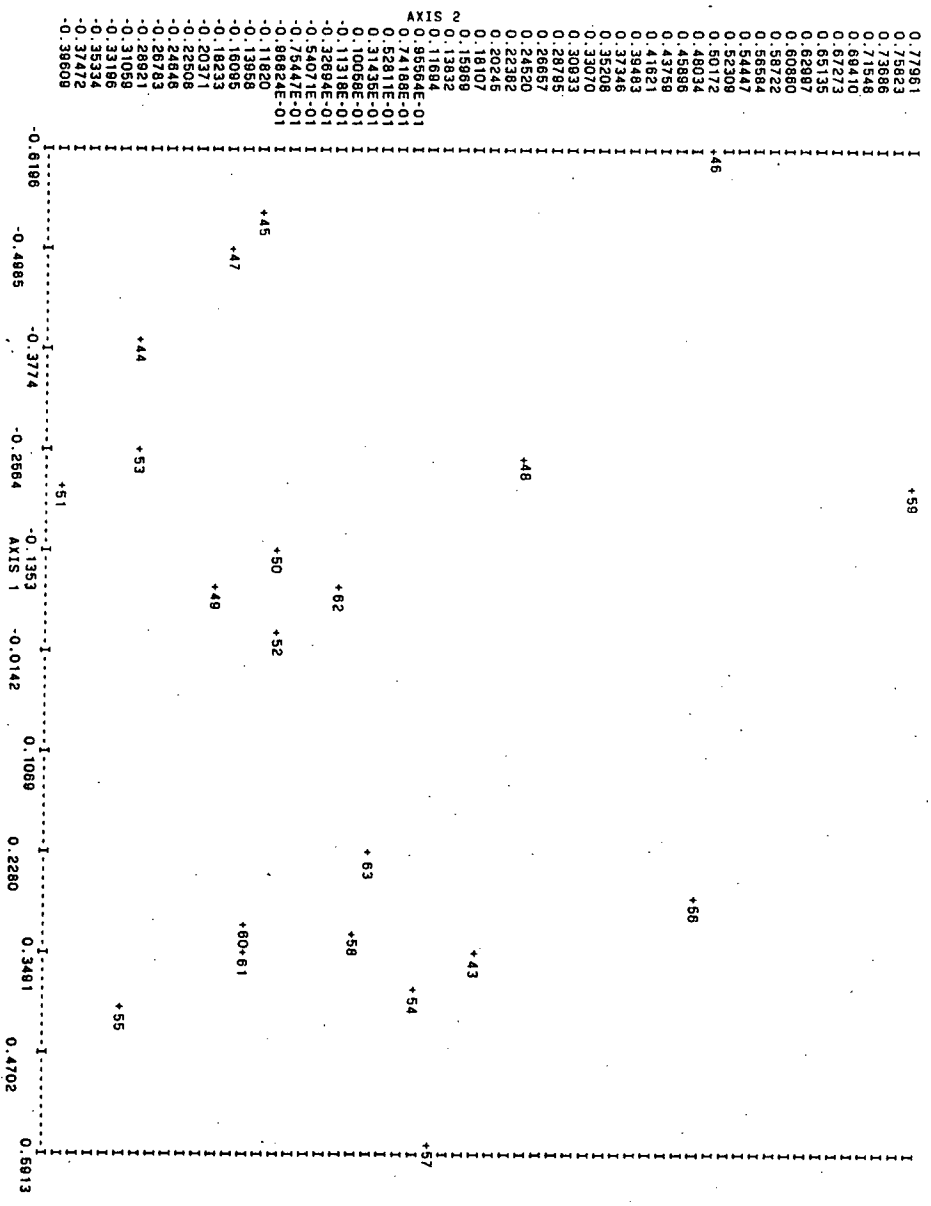
6.1.3 PLANT NEIGHBOURS-PRESENCE/ABSENCE

Although the PCA of the total thimbleberry data set of presence/absence data represents only 30 percent of the total variation on the first three axes (Table 11), these axes can nonetheless be ascribed with environmental processes. Axis I may be a gradient of disturbance due to girdling and a fluctuating water table. The axis is positively correlated with Sambucus racemosa, Osmorhiza chilensis and Epilobium watsonii (Table 11). Sambucus racemosa is characteristic of disturbed sites whereas Osmorhiza chilensis is frequently indicative of a fluctuating water table (Klinka et al 1989). The axis is negatively correlated with Dryopteris assimilis, Tiarella unifoliata and Cornus canadensis (Table 11), which are usually found in moist woods in the Skeena area (Coupé et al 1982). Axis II is negatively correlated with Equisetum arvense, Thelypteris phegopteris, Galium triflorum and Athyrium filix-femina (Table 11), which are characteristic of moist, nutrient rich areas (Klinka et al. 1989).

Axis III may be a disturbance gradient representing changing moisture regimes and nitrogen content. The axis is positively correlated with Epilobium angustifolium (Table 11), characteristic of disturbed sites (Klinka et al. 1989) and Cornus sericea (Table 11), found in flooded areas (Klinka et al. 1989). Streptopus roseus and Gymnocarpium dryopteris are negatively correlated with the axis (Table 11) and common in stable, moist, rich sites (Klinka et al. 1989).

The KIT quadrats are more positive on axis I than the WED quadrats (Figure 8). This agrees with the previous interpretation of the axis as a disturbance gradient. There is no separation between the sites on axis II (Figure 8). Quadrats 21 and 38, at KIT and WED, have most negative scores and both are located in wet, sunken areas. Quadrats 1 and 36, which are most positive, are located in open areas which may be subject to flooding and drying. This suggests that axis II may be interpreted as a disturbance gradient due to moisture. Maianthemum dilatatum and Ribes laxiflorum are positively correlated with this axis (Table 11) and both are characteristic of flooded sites and shaded moist stream banks (Klinka et al. 1989).
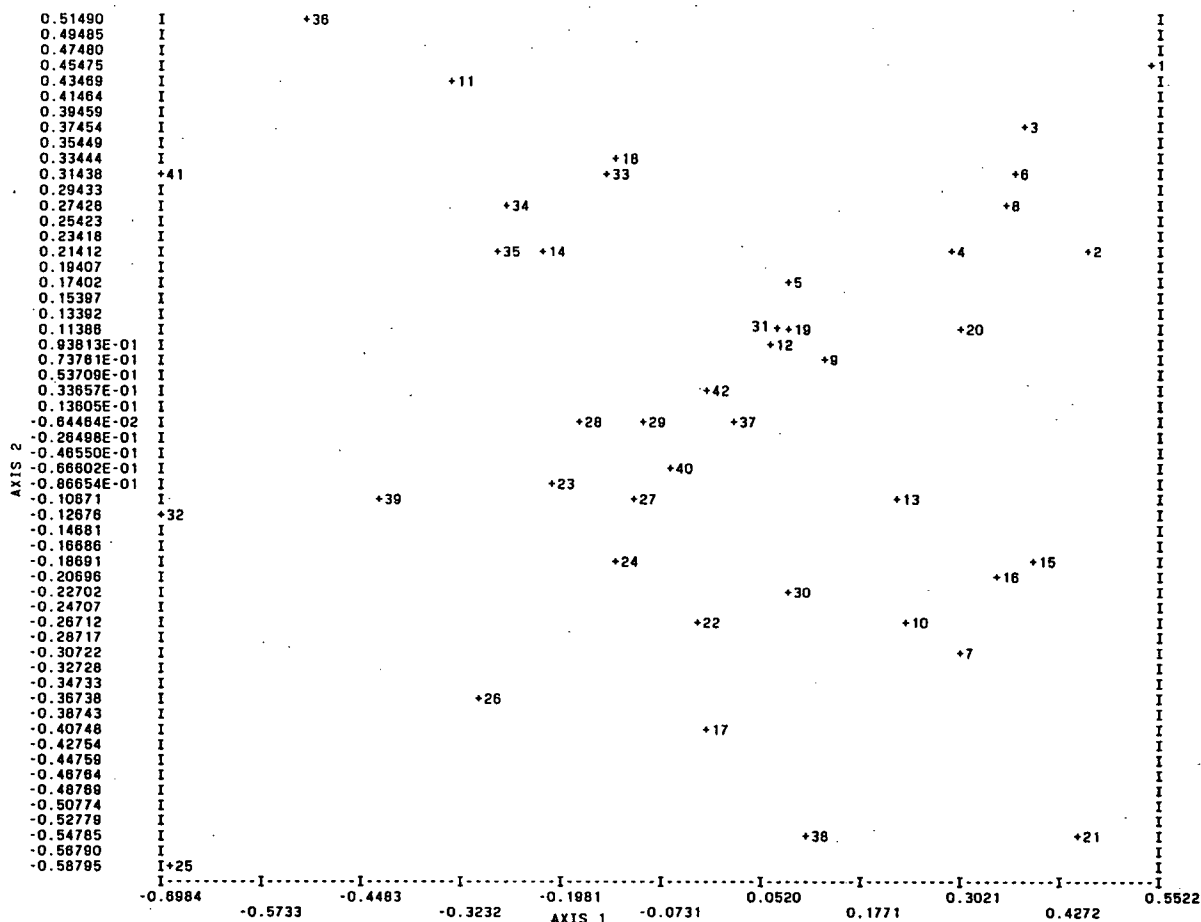
Table 11.   TB plant neighbours - PCA axes relationships.
Correlation coefficients relating the presence/absence of plant neighbours to
PCA axes I - III.

Axis	I	II	III
% variation	12.19	9.40	8.33
species			
Rubus spectabilis	.0854	.2837	.0800
Sambucus racemosa	.5836	-.0510	-.0843
Galium triflorum	.3215	-.5328	.0414
Stachys mexicana	.2714	.0376	.3529
Osmorhiza chilensis	.5129	.2123	-.0035
Cinna latifolia	.2155	.2725	.1789
Epilobium watsonii	.5024	.2251	.0419
Agrostis capillaris (tenuis)	.3440	-.1157	.1807
Picea sitchensis	-.3586	.2739	-.0516
Aruncus dioicus	.3342	-.1595	-.2461
Epilobium angustifolium	-.1255	.2600	.5834
Chamaecyparis nootkatensis	.3194	-.4551	.0202
Ribes bracteosum	-.3301	-.0844	.1160
Dryopteris assimilis	-.5591	-.0492	.2067
Bromus vulgaris	.3570	-.2046	.0640
Salix sitchensis	.4335	.2583	.4013
Oplopanax horridus	-.0270	.1951	-.4560
Streptopus roseus	-.3283	.2372	-.5260
Athyrium filix-femina	.0394	-.5268	-.0014
Gymnocarpium dryopteris	-.1835	-.0395	-.5340
Equisetum arvense	-.0269	-.7446	-.1356
Smilacina racemosa	-.0019	.1305	-.2269
Tiarella trifoliata	-.0089	-.3162	-.2312

Table 11 continued

Tiarella unifoliata	-.5379	-.4020	-.3290
Viola glabella	-.3148	-.1537	.4333
Tellima grandiflora	.4133	-.1849	-.1962
Maianthemum dilatatum	-.4351	.3535	-.2194
Clintonia uniflora	-.3917	.0948	-.3827
Circaea alpina	-.2330	-.3989	.0624
Thelypteris phegopteris	-.1894	-.5918	.1824
Ribes laxiflorum	-.3474	.4359	.0374
Cornus sericea	-.1820	-.0900	.5035
Alnus rubra	.0251	-.2684	-.2450
Vaccinium ovalifolium	-.4858	-.2419	.4546
Cornus canadensis	-.6626	-.0859	.3205

Axis I of the KIT presence/absence of plant neighbors PCA may represent a disturbance gradient. It is positively correlated with devil's club, Streptopus roseus, Gymnocarpium dryopteris, Tiarella unifoliata and Tiarella trifoliata (Table 12), which tend to occur in rich, moist, less disturbed areas (Klinka et al. 1989). The axis also has a weak negative correlation with Epilobium watsonii (Table 12), which is an introduced species found in open and disturbed areas. Axis II is positively correlated with Galium triflorum, Athyrium filix-femina, Bromus vulgaris and Equisetum arvense and negatively correlated with Piceae sitchensis (Table 12). No obvious interpretation emerges due to the ecological dissimilarity between these species (Klinka et al. 1989). This distribution of Picea sitchensis, however, could be due to planting; though no records of this were available. Axis III has no strong positive correlations (Table 12) and was not interpreted.

Figure 8.   Graph of axes I and II of the presence/absence of plant neighbors PCA for TB
              showing individual quadrats.

Table 12.   KIT plant neighbours - PCA axes relationships.
Correlation coefficients relating the presence/absence of plant neighbours to PCA axes I - III.

Axis	I	II	III
% variation	19.67	18.63	11.83
species			
Sambucus racemosa	-.3970	.3668	-.1649
Galium triflorum	-.1548	.5626	-.5009
Osmorhiza chilensis	-.1832	-.3430	-.7068
Epilobium watsonii	-.4622	-.2936	.2127
Agrostis capillaris (tenuis)	-.3195	.4803	.0899
Picea sitchensis	-.0248	-.5994	.3235
Epilobium angustifolium	-.1238	.1974	-.4163
Bromus vulgaris	.1421	.5891	-.4879
Oplopanax horridus	.6937	-.3376	-.2420
Streptopus roseus	.5574	-.4177	-.2635
Athyrium filix-femina	.1424	.6429	.4820
Gymnocarpium dryopteris	.6788	-.0104	.2274
Equisetum arvense	.2461	.7097	.0820
Tiarella trifoliata	.6685	-.0115	-.0618
Tiarella unifoliata	.7725	.2604	.0660
Tellima grandiflora	.0456	.3212	.0132

Only axis I of the WED PCA for the presence/absence of plant neighbours, can be fully interpreted. Axis III has no strong negative correlations while the species both negatively and positively correlated with axis II (Table 13) commonly co-occur and do not differ ecologically (Klinka et al. 1989). Axis I is positively correlated with Galium triflorum and Alnus rubra and negatively correlated with Epilobium angustifolium (Table 13) and may represent a moisture gradient. Both Cornus canadensis and Epilobium angustifolium are only found in open, drier areas of the site and Equisetum arvense and Alnus rubra are commonly found in areas of standing water. Alnus is also an indicator of a fluctuating water table (Klinka et al. 1989).

Table 13. WED plant neighbours - PCA axes relationships.
Correlation coefficients relating the presence/absence of plant neighbours to PCA axes I - III.

Axis	I	II	III
% variation	19.84	15.20	13.00
species			
Sambucus racemosa	.4287	.0547	-.2309
Galium triflorum	.6096	.1469	.4766
Agrostis capillaris (tenuis)	.2565	.1690	.3811
Picea sitchensis	-.1399	-.4197	-.2917
Epilobium angustifolium	-.7787	.2349	-.1067
Dryopertis assimilis	-.3990	.4933	.4947
Oplopanax horridus	-.0814	-.6145	.1860
Streptopus roseus	-.1938	-.4485	.6517
Athyrium filix-femina	.4027	.2207	-.1371
Gymnocarpium dryopteris	.2007	-.6562	.1813
Equisetum arvense	.5369	.2915	.4892
Tiarella trifoliata	.2378	.6460	.0546

Table 13 continued

|	-.3852	-.0143	-.0494
Tsuga heterophylla			
Clintonia uniflora	.1106	-.5627	.5963
Alnus rubra	.7621	.1135	-.1649
Vaccinium ovalifolium	-.4758	.4834	.2704
Cornus canadensis	-.5467	.2591	.4352

Although the first three axes of the devil's club presence/absence data summarize over 55 percent of the total variation in the data set, only axis I can be ascribed with any underlying pattern (Table 14). Axes II and III have no strong negative correlations with any species (Table 14). Axis I may be a moisture gradient from damp to very moist to wet conditions. Rubus spectabilis, Maianthemum dilatatum and Cornus sericea are all indicators of very moist to wet sites with either fluctuating groundwater or flood conditions (Klinka et al. 1989). The axis is negatively correlated with Gymnocarpium dryopteris (Table 14), which is indicative of fresh to very moist sites, as used by Klinka et al. (1989).

Most quadrats are widely separated on axes I and II (Figure 9). Like the graph of the soils scores (Figure 7), quadrats 60, 61 and 63 are at the wet end of the PCA axis and quadrats 46 and 47 are at the negative drier end (Figures 7 and 9). The first axes of these two PCAs are not equivalent, however, as relationships between all quadrats on both graphs are not identical (Figures 7 and 9).

Table 14.   DC plant neighbours - PCA axes relationships.
Correlation coefficients relating the presence/absence of plant neighbours to
PCA axes I - III.

Axis	I	II	III
% variation	27.23	18.13	10.16
species			
Rubus spectabilis	.7378	-.4237	.4150
Galium triflorum	.4870	.6877	-.1108
Osmorhiza chilensis	-.0415	.7604	.0406
Agrostis capillaris (tenuis)	.6314	.2450	-.1358
Dryopteris assimilis	-.4705	.3535	.5595
Actaea rubra	.4376	.0990	-.1886
Gymnocarpium dryopteris	-.7630	-.2359	-.1837
Streptopus roseus	-.2106	.2546	-.0111
Tiarella unifoliata	.6930	-.4262	-.1148
Viola glabella	-.1866	.2869	.0285
Maianthemum dilatatum	.6776	.2762	.2235
Clintonia uniflora	-.4406	.0767	-.1213
Circaea alpina	.4320	-.0638	.5034
Streptopus amplexifolius	-.0090	.1340	.6875
Matteuccia struthiopteris	.4514	.7035	-.2773
Cornus sericea	.5788	-.4367	-.2479

Figure 9. Graph of axes I and II of the presence/absence of plant neighbors PCA for DC showing individual quadrats.
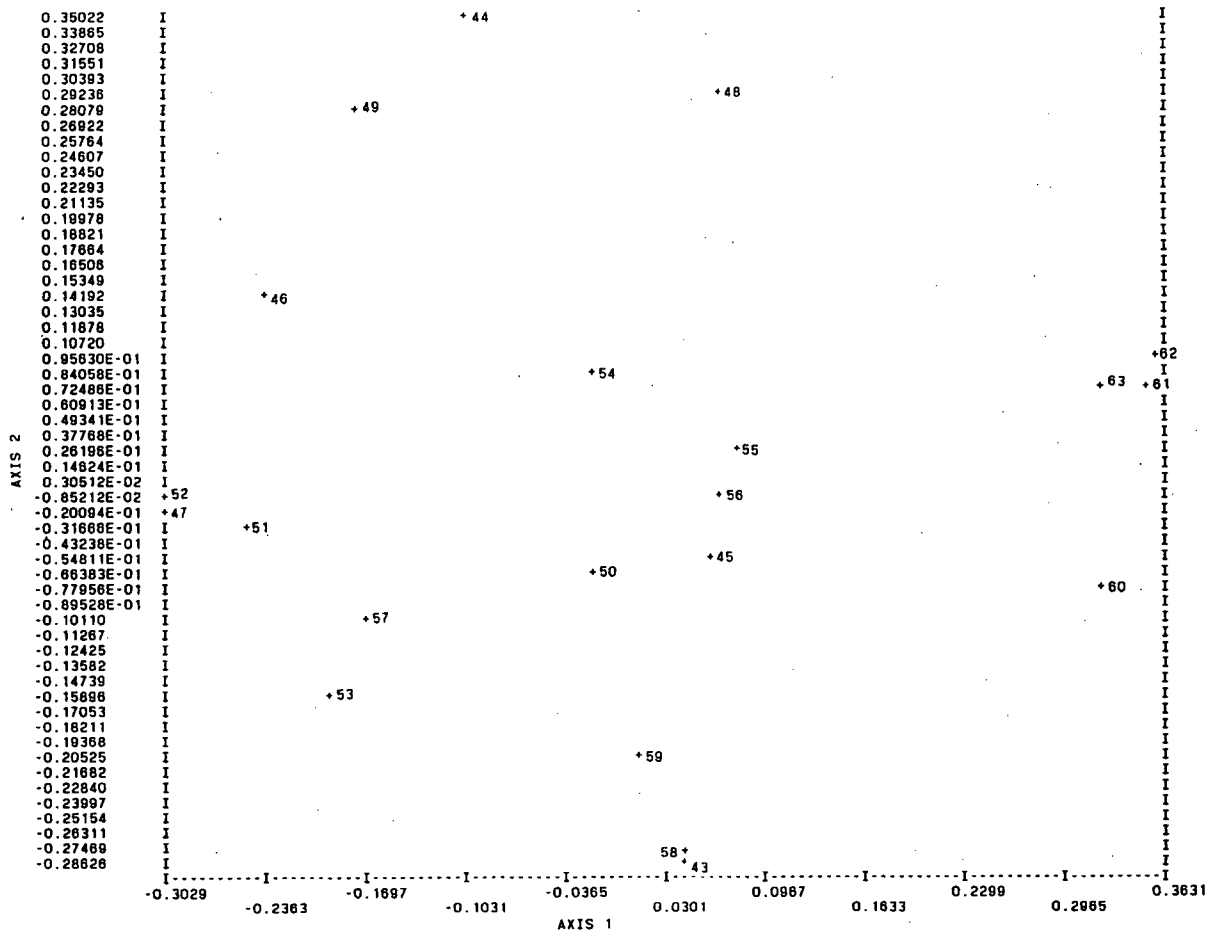
6.1.4 PLANT NEIGHBOURS-FREQUENCY

Like the presence/absence PCA for the TB data, the PCA axes for the frequency data reflect disturbance. Axis I of the TB PCA of the frequency of plant neighbours data, is positively correlated with Sambucus racemosa and Epilobium watsonii and negatively correlated with Tiarella unifoliata, Clintonia uniflora and Cornus canadensis (Table 15) and suggests a disturbance gradient. Axis II may also be a disturbance gradient. Epilobium angustifolium and Cornus canadensis are positively correlated with the axis (Table 15) and are indicative of disturbance and poor nutrient conditions respectively (Klinka et al. 1989). The axis is negatively correlated with Streptopus roseus, and Tiarella trifoliata (Table 15), which are characteristic of rich, moist, somewhat stable areas (Klinka et al. 1989). As axis III has no positive correlations (Table 15), an ecological gradient was not ascribed to the axis.

The graph of axes I and II scores corroborates the interpretation that axis I is a disturbance gradient and may be due to girdling (Figure 10). Most quadrats, numbered from 1 to 21 at the KIT or ungirdled alder site, have positive scores and most quadrats, numbered from 22 to 42 at the WED or ungirdled alder site, have negative scores. Although axis II was also interpreted as a disturbance gradient, it is not a gradient due to girdling. Both KIT and WED quadrats have positive and negative scores on the axis (Figure 10).

Table 15.   TB plant neighbours - PCA axes relationships.
Correlation coefficients relating the frequency of plant neighbours to PCA axes I - III.

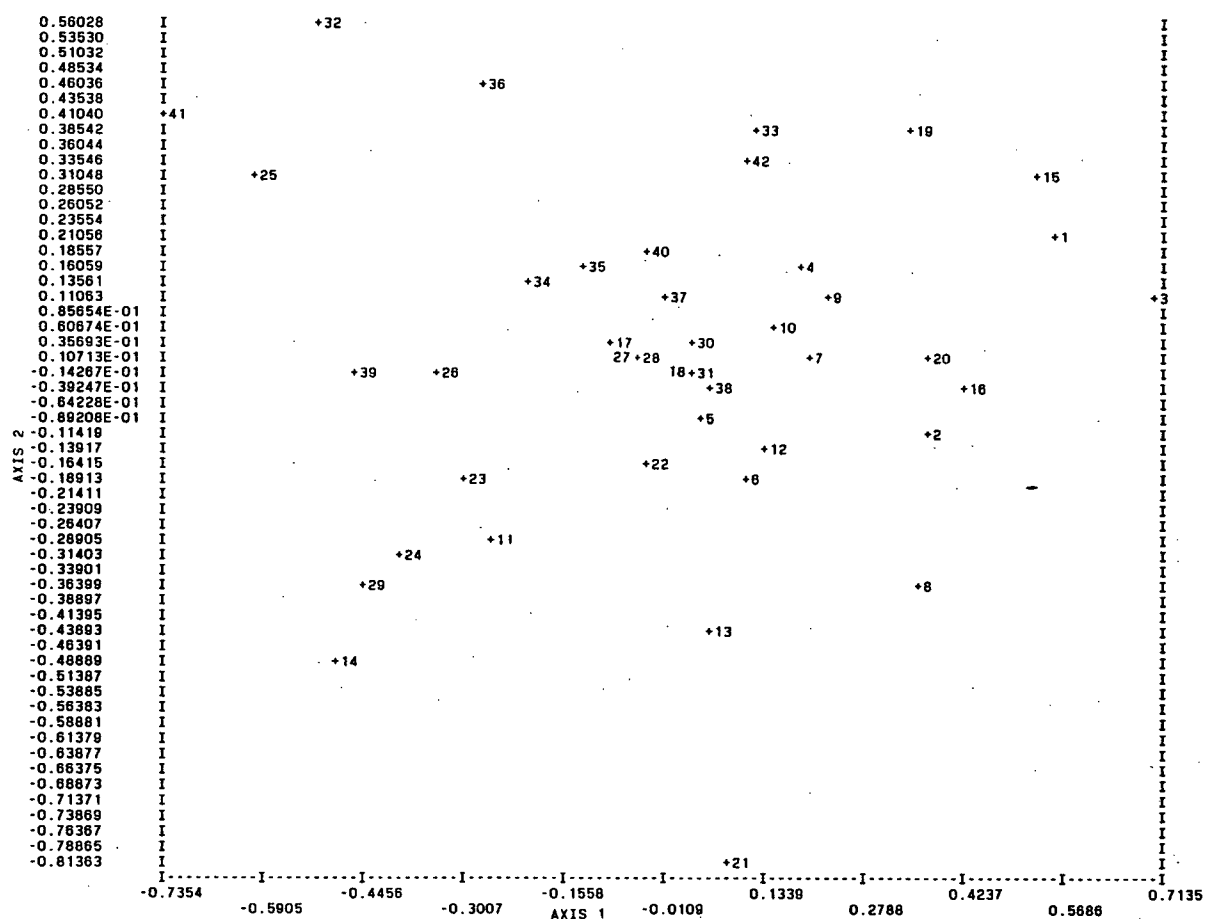| Axis	I	II	III
% variation	12.21	8.80	7.91
species			
Rubus spectabilis	.4160	-.0378	-.2049
Sambucus racemosa	.5355	-.3650	.2805
Galium triflorum	.2516	.0930	-.5276
Stachys mexicana	.3035	.2529	-.1424
Osmorhiza chilensis	.3621	-.3255	.2141

Table 15 continued

Cinna latifolia	.2882	.0118	.1410
Epilobium watsonii	.5148	-.0612	.0784
Agrostis capillaris (tenuis)	.4727	.1477	-.4046
Picea sitchensis	-.3167	-.0215	.1197
Aruncus dioicus	.1513	-.4686	-.0590
Epilobium angustifolium	.0755	.6146	.1801
Chamaecyparis nootkatensis	.2411	-.0454	-.0804
Ribes bracteosum	-.3318	.2678	.0453
Dryopteris assimilis	-.4366	.0319	.1031
Bromus vulgaris	.3106	.1818	-.0924
Salix sitchensis	.4977	.1439	.0065
Oplopanax horridus	-.2871	-.3843	.3111
Streptopus roseus	-.3703	-.5361	.2861
Athyrium filix-femina	-.0591	-.0671	-.4242
Gymnocarpium dryopteris	-.4391	-.4823	.0907
Equisetum arvense	-.2537	-.1628	-.7616
Smilacina racemosa	.0678	.0187	.2891
Tiarella trifoliata	-.1572	-.5540	.0706
Tiarella unifoliata	-6904	-.2777	-.2931
Viola glabella	.2170	-.4121	-.0419
Tellima grandiflora	.3297	-.1399	-.0029
Tsuga heterophylla	-.3330	.4145	.1135
Maianthemum dilatatum	-.3267	.1631	.4595
Clintonia uniflora	-.5065	-.0540	.0890
Circaea alpina	-.1981	-.0642	-.3927

Table 15 continued

Thelypteris phegopteris	-.2368	.0071	-.3634
Ribes laxiflorum	-.1527	.3487	.4555
Cornus sericea	.0024	.2939	-.1479
Alnus rubra	-.2634	-.2741	-.4263
Vaccinium ovalifolium	-.3666	.2743	-.2424
Cornus canadensis	-.5536	.5168	-.0645

Figure 10.   Graph of axes I and II of the frequency of plant neighbors PCA for TB showing individual quadrats.

```
0.56028  I                    +32
0.53530  I
0.51032  I
0.48534  I
0.46036  I                              +36
0.43538  I
0.41040  +41
0.38542  I                                        +33        +19
0.36044  I
0.33546  I                                      +42
0.31048  I          +25                                            +15
0.28550  I
0.26052  I
0.23554  I
0.21056  I                                                            +1
0.18557  I                              +40
0.16059  I                          +35         +4
0.13561  I                      +34                    +9
0.11063  I                              +37                              +3
0.85654E-01  I
0.60874E-01  I                                      +10
0.35693E-01  I                        +17  +30
0.10713E-01  I                      27 +28      +7          +20
-0.14267E-01  I      +39    +28      18+31
-0.39247E-01  I                          +38              +16
-0.64228E-01  I
-0.89208E-01  I                          +5
-0.11419  I
-0.13917  I                                  +12              +2
-0.16415  I
-0.18913  I              +23          +22      +6
-0.21411  I
-0.23909  I
-0.26407  I
-0.28905  I              +11
-0.31403  I          +24
-0.33901  I
-0.36399  I      +29                              +8
-0.38897  I
-0.41395  I
-0.43893  I                          +13
-0.46391  I
-0.48889  I    +14
-0.51387  I
-0.53885  I
-0.56383  I
-0.58881  I
-0.61379  I
-0.63877  I
-0.66375  I
-0.68873  I
-0.71371  I
-0.73869  I
-0.76367  I
-0.78865  I
-0.81363  I                          +21
         I-------I--------I--------I--------I-------I-------I--------I--------I--------I
       -0.7354   -0.4456   -0.3007   -0.1558   0.1339         0.4237        0.7135
             -0.5905             AXIS 1  -0.0109     0.2788        0.5686
```

Axis I of the KIT frequency PCA may, like axis I of the TB frequency data, represent a disturbance gradient. Streptopus roseus, devil's club, Gymnocarpium dryopteris, Tiarella trifoliata and Tiarella unifoliata, which are negatively correlated with the axis (Table 16), tend to occur in rich, moist, less disturbed areas (Klinka et al. 1989). Agrostis capillaris (tenuis) is generally found at open, more disturbed quadrats at KIT. Axis II is positively correlated with Galium triflorum, Epilobium angustifolium and Bromus vulgaris and negatively correlated with Sambucus racemosa (Table 16) and may represent a light gradient of illumination. Bromus is found in quadrats with less cover at this site and Epilobium is shade intolerant while Sambucus is known to be shade tolerant (Klinka et al. 1989). Axis III has no strong negative correlations (Table 16) and was therefore not interpreted.

Table 16.   KIT plant neighbours - PCA axes relationships.
Correlation coefficients relating the frequency of plant neighbours to PCA axes scores I - III.

Axis	I	II	III
% variation	31.01	14.33	12.39
species			
Sambucus racemosa	.0669	-.5211	.5119
Galium triflorum	.4897	.6031	.2689
Osmorhiza chilensis	-.0506	.0098	-.2953
Epilobium watsonii	.2904	-.4081	-.2893
Agrostis capillaris (tenuis)	.7158	.1431	.1094
Picea sitchensis	-.3338	-.0026	-.1899
Epilobium angustifolium	.4121	.6946	.4461
Bromus vulgaris	.2747	.5470	.4804
Oplopanax horridus	-.6557	.4664	-.3577
Streptopus roseus	-.7550	.0793	-.1237

Table 16 continued

Athyrium filix-femina	-.0155	-.4442	.5610
Gymnocarpium dryopteris	-.7266	.1230	.1250
Equisetum arvense	-.1027	-.1935	.4544
Tiarella trifoliata	-.7690	.0083	.4185
Tiarella unifoliata	-.8198	.1149	.3241
Tellima grandiflora	.2299	-.4407	-.1264

Axis I,of the WED data set, is a moisture gradient. The axis is negatively correlated with Epilobium angustifolium (Table 17), which is characteristic of open moist, disturbed sites and positively correlated with Alnus rubra, Equisetum arvense and Galium triflorum (Table 17). Equisetum arvense and Alnus rubra co-occur in areas of standing water at the WED site. Alnus rubra also shades and cools the site reducing surface evaporation and is an indicator of a fluctuating water table (Klinka et al. 1989). Biological significance cannot be readily ascribed to axis II. The axis is positively correlated with devil's club, Streptopus roseus, Gymnocarpium dryopteris and Clintonia uniflora and negatively correlated with Athyrium filix-femina (Table 17). All these species co-occur. Klinka et al. (1989) also states that Gymnocarpium dryopteris and Streptopus roseus are indicative of damp, very moist soils, devil's club and Athyrium filix-femina are indicative of very moist to wet soils, and Clintonia uniflora is indicative of moderately dry to damp soils. Axis III may be a light gradient of illumination. It is positively correlated with Agrostis tenuis (tenuis) and Epilobium angustifolium (Table 17), a shade intolerant species (Klinka et al. 1989) and negatively correlated with Sambucus racemosa (Table 17), a shade tolerant species (Klinka et al. 1989).

Table 17. WED plant neighbour - PCA axes relationships.
Correlation coefficients relating the frequency of plant neighbours to PCA axes
scores I - III.

Axis	I	II	III
% variation	24.50	15.91	13.43
species			
Sambucus racemosa	.0686	-.0742	-.8424
Galium triflorum	.5780	-.1158	.2318
Agrostis capillaris (tenuis)	.4459	-.3469	.6402
Picea sitchensis	-.1382	.3635	.0003
Epilobium angustifolium	-.7949	-.0125	.5105
Dryopertis assimilis	-.1055	-.0024	-.0629
Oplopanax horridus	.3095	.6046	-.0884
Streptopus roseus	.2356	.6007	.1514
Athyrium filix-femina	.2786	-.6690	-.3210
Gymnocarpium dryopteris	.3697	.8120	.1419
Equisetum arvense	.7074	-.2385	.4144
Tiarella trifoliata	.1820	-.4410	-.0250
Tsuga heterophylla	-.2277	.1532	-.3255
Clintonia uniflora	.2526	.5182	-.1290
Alnus rubra	.7595	.1162	.1152
Vaccinium ovalifolium	-.0763	-.1215	.1048
Cornus canadensis	-.4103	.0032	.1977

The first three axes of the devil's club frequency of plant neighbours data represent
almost sixty-five percent of the total variance in the data (Table 18). Axis I is a moisture gradient
which is positively correlated with Gymnocarpium dryopteris (Table 18), an indicator of damp to
very moist conditions (Klinka et al.1989). Galium triflorum, Actaea rubra, Maianthemum

dilatatum, Cornus sericea and Agrostis capillaris (tenuis) are negatively correlated with this axis (Table 18). Both Cornus sericea and Maianthemum dilatatum are tolerant of a fluctuating water table or flood conditions and indicate very moist to wet conditions (Klinka et al. 1989). Axis II is strongly correlated with Dryopteris assimilis (Table 18), an indicator of rich damp to very moist sites (Coupé et al. 1982, Klinka et al. 1989). Circaea alpina is aso correlated with the axis (Table 18) and is found on moist, nutrient medium sites (Klinka et al. 1989). As this axis has no negative correlations greater than .5, it was not interpreted further (Table 18). Axis III has positive correlations with Osmorhiza chilensis and Smilacina stellata and is negatively correlated with Rubus spectabilis (Table 18). These species, however, are ecologically similar (Klinka et al. 1989) and a biological interpretation was not ascribed to the axis.

Table 18.   DC plant neighbour - PCA axes relationships.
Correlation coefficients relating the frequency of plant neighbours to PCA axes I -
III.

Axis	I	II	III
% variation	36.36	14.68	13.43
species			
Rubus spectabilis	-.3625	-.1487	-.7717
Galium triflorum	-.7618	.0906	.0848
Osmorhiza chilensis	-.2362	.2648	.5465
Agrostis capillaris (tenuis)	-.7527	-.2176	-.3105
Dryopteris assimilis	.2197	.9365	.0020
Actaea rubra	-.6274	-.1904	.4649
Gymnocarpium dryopteris	.8485	-.2115	.0275
Smilacina stellata	-.0805	-.0302	.5514
Tiarella unifoliata	-.2662	-.1623	-.4137
Viola glabella	-.2093	.0176	.3972
Tsuga heterophylla	.0705	.3043	.0656
Maianthemum dilatatum	-.8504	-.1068	-.2139

Table 15 continued

<u>Clintonia uniflora</u>	.2543	-.1435	.2580
<u>Circaea alpina</u>	-.2004	.6742	-.3596
<u>Streptopus amplexifolius</u>	.1202	.3608	.0103
<u>Matteuccia struthiopteris</u>	.1949	-.0015	.0417
<u>Cornus sericea</u>	-.7692	.0764	.4569

Like the DC presence/absence graph (Figure 9), quadrats 61 to 63 and quadrats 46 and 47 are at opposite extremes of the moisture gradient on the graph of the axes scores (Figure 11). The quadrat relationships shown in the graph, however, do not suggest an ecological interpretation of axis II.

Figure 11.   Graph of axes I and II of the frequency of plant neighbors PCA for DC showing individual quadrats.
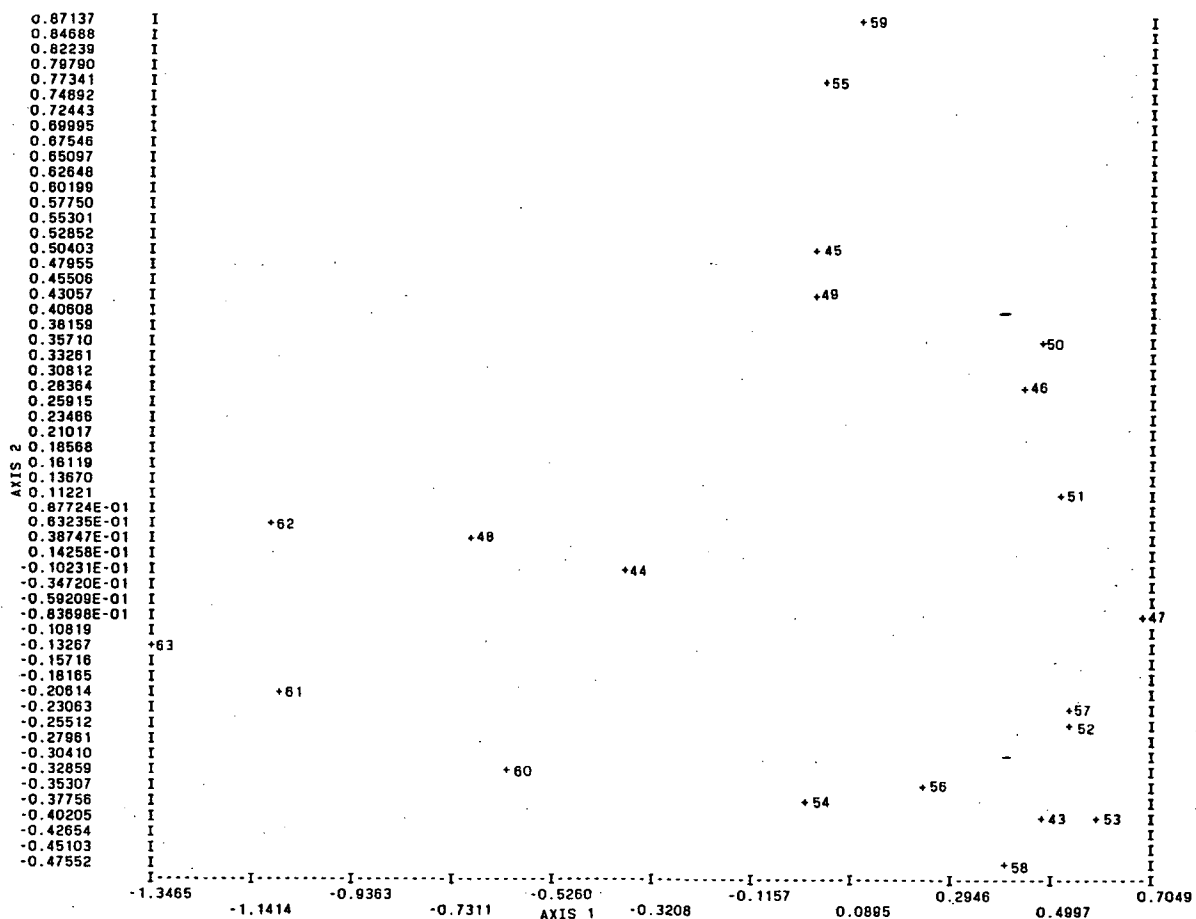
6.2   MORPHOLOGY

6.2.1   UNIVARIATE ANALYSES AND GRAPHS

Although the number of thimbleberry flowers per stem was not significantly different between KIT and WED in 1987 (Appendix I), many more quadrats lacked flowering stems at WED as compared to KIT (Figure 12). At those quadrats at WED with flowers, there were fewer flowering stems and therefore fewer flowers and fruit (Appendix 1). The number of flowers per quadrat did not differ between sites in 1986, whereas differences between years were significant (Appendix 1).

Figure 12.   Number of thimbleberry flowers per quadrat at WED and KIT on June 22, 1987.
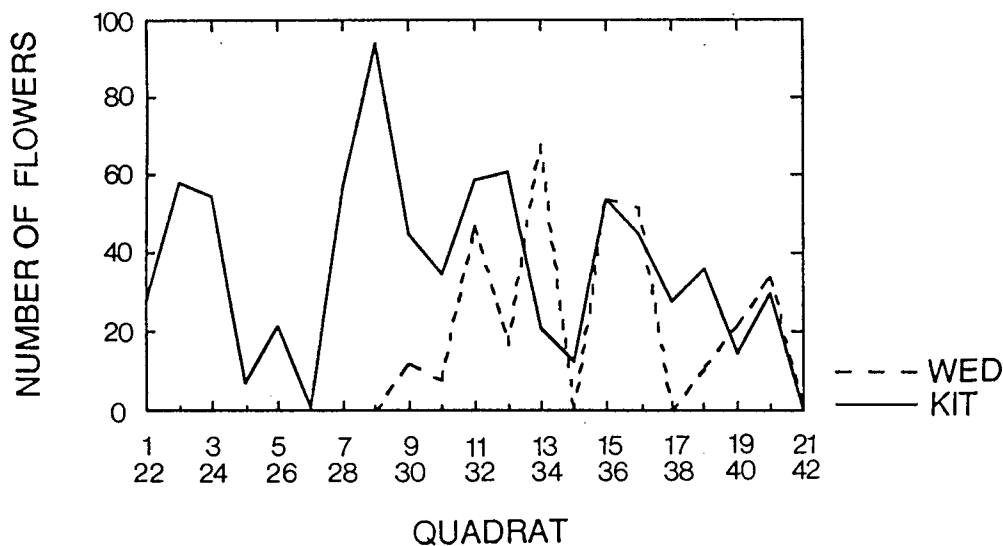
Annual differences and site differences were also apparent for the number of thimbleberry stems per quadrat. In 1987 more stems were produced at both thimbleberry sites than in 1986 (Appendix 1). Stem density was also higher at KIT than WED for two-year-old stems in 1987 (Appendix 1). One-year-old stem density in 1987 and the density of all stems in 1986 did not differ significantly between sites (Appendix 1).

The number of leaves produced by thimbleberry also varied, with site differences and stem differences observed (Appendix 1). In both 1986 and 1987, the number of leaves produced by one-year-old, two-year-old stems and branches differed (Appendix 1). Two-year-old stems had most leaves and branches had least . In 1987, site differences were also apparent, though these were not observed in 1986 (Appendix 1). KIT had more leaves per stem than WED in 1987 (Appendix 1). The number of leaves per stem did not differ between years (Appendix 1).

Differences in stems length were also observed for thimbleberry. One- and two-year-old stems are significantly longer than branches in both 1986 and 1987 (Appendix 1). Stems, however, did not differ in length; neither did they differ between years, though in 1987 two-year-old stems differed between sites (Appendix 1).

The number of devil's club flowers per quadrat did not differ in 1986 and 1987 (Appendix 1) and little variation is apparent between years (Figure 13). Only 1987 values were used to apportion variation between species or to correlate morphology with environment.

Unlike thimbleberry, the number of devil's club stems per quadrat does not annually fluctuate (Figure 14)(Appendix 1). Only six new stems were produced from 1986 to 1987. None of the quadrats with less than five stems increased in stem number (Figure 14). Stems and branches also produced the same amount of new growth at the growing tip in each quadrat, though stems are significantly longer than branches (Appendix 1). There is also no difference between years for the number of leaves per stem or per branch (Appendix 1).

Figure 13. Number of devil's club racemes per quadrat in 1986 and 1987.
All filled circles indicating a negative number of inflorescences show quadrats which were not sampled in 1986.
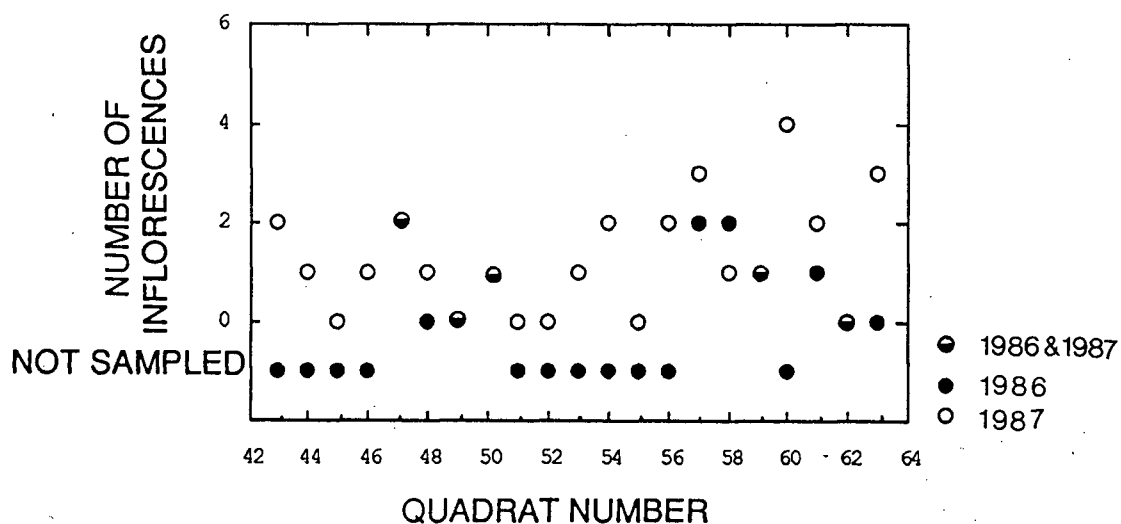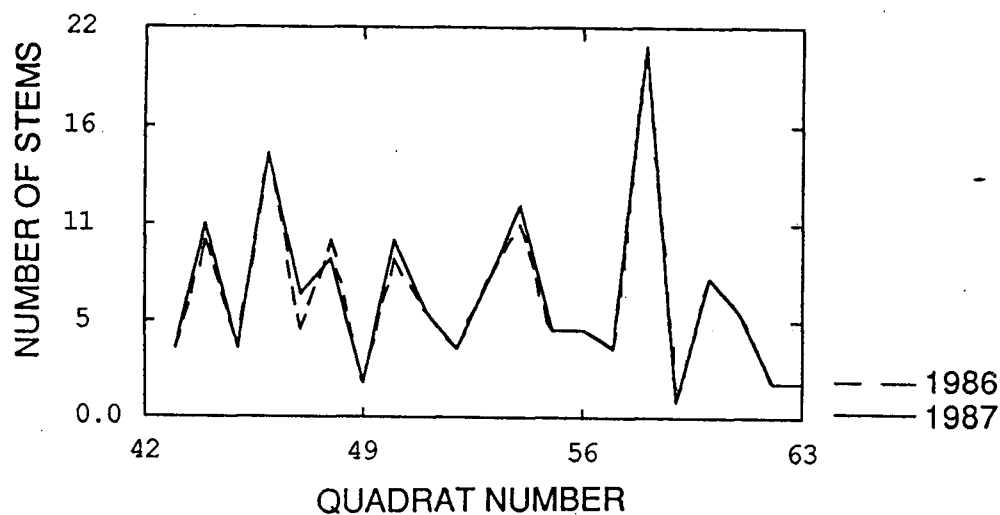(O = quadrats sampled in 1987, ●= quadrats sampled in 1987, ◐ = quadrats sampled in both 1986 and 1987)

Figure 14. Total number of stems per quadrat for devil's club on June 30, 1986 and 1987.

6.2.2   PRINCIPAL COMPONENT ANALYSES

PCA was used to generate scores to subject to ANOVA. This was done to summarize

the data set and to capture some of the interactions among the morphological variables. These

PCAs accounted for at least 70 percent of the variation in the data on the first three axes (Table

19).

Table 19.   Percent variance explained by PCA axes of the morphological data used in
                 ANOVA only:
                 1) 1986 and 1987 Thimbleberry data
                 2) 1986 and 1987 Devil's club data
                 3) 1987 - both thimbleberry and devil's club data

	1986 & 7 TB	1986 & 7 DC	1987 DC & TB
Axis I	44.20	46.68	31.30
Axis II	14.12	17.02	30.49
Axis III	10.91	13.40	13.00

The PCA of the the 1987 TB data summarized 67 percent of the total variation on the first

three axes (Table 20). Axis I has a positive correlation greater than .5 with all morphological

variables except for the number of stems per quadrat and the number of branch leaves (Table

20). This axis represents the size and the number of parts on each stem. Axis II is a gradient of

stem number per quadrat. It is strongly positively correlated with the number of one-year-old

and two-year-old stems (Table 20). Axis III is positively correlated with the number of branch

leaves (Table 20). No other correlations between axis III and the input data are greater than .5

and the axis was not considered to reflect sufficient variation for interpretation (Table 20).

Table 20. Morphology - PCA axes relationships for TB data in 1987. Correlation coefficients relating morphological data to PCA axes I - III.

Axis	I	II	III
% variation	47.89	9.98	9.03
morphological variables			
#branches/stem	.7059	-.2951	-.1066
# flowers/inflorescence	.6628	.1117	.1602
# flowering stems	.6803	.1926	-.0279
# flowers/quadrat	.6215	.1072	.2702
# 2-year-old stems	.3980	.6831	-.0580
# 1-year-old stems	.2420	.7493	-.1229
# leaves/quadrat	.7970	.2666	-.0827
# leaves/branch	.4931	-.0674	.7106
# leaves/1-year-old stem	.7400	-.2955	-.4086
# leaves/2-year-old stem	.6366	.2920	-.0202
1-year-old stem length	.8277	-.2349	-.3735
2-year-old stem length	.8502	-.0038	-.0341
1-year-old stem diameter	.6948	-.1824	-.4303
2-year-old stem diameter	.8910	-.0378	-.0544
branch length	.7302	-.1645	.4253
branch diameter	.7808	-.2368	.3571

Axis I of the KIT PCA for 1987 is a vegetative size gradient representing the size of stems and branches and the number of parts attached to them at each quadrat. The axis is positively correlated with stem and branch lengths and diameters, the number of leaves per quadrat and per one-year-old stem and the number and the number of flowers per inflorescence (Table 21). Axis II has positive correlations with the number of branch leaves and the branch length and has a weak negative correlation with the number of flowering stems per quadrat (Table 21). Axis III is a reproductive axis which is correlated with the number of flowers per inflorescence, the number of flowers per quadrat and the number of two-year-old stems (Table 21). This PCA accounts for almost 65 percent of the raw variation on the first three axes (Table 21).

Table 21. Morphology-PCA axes relationships for KIT data in 1987. Correlation coefficients relating morphological data to PCA axes I - III.

Axis	I	II	III
% variation	37.45	14.57	12.35
morphological variables			
# branches/stem	.6594	-.2730	-.3827
# flowers/inflorescence	.5738	-.1298	.6628
# flowering stems	.2951	-.5085	.1207
# flowers/quadrat	.4503	.1050	.6818
# 2-year-old stems	-.0911	-.3650	.6258
# 1-year-old stems	-.2405	-.4614	.1539
# leaves/quadrat	.7400	.1772	-.0624
# branch leaves	.2623	.6709	.5274
# leaves/1-year-old stem	.7322	-.3853	-.1976

Table 21 continued

# leaves/2-year-old stem	.4915	.3651	-.1199
1-year-old stem length	.8147	-.3958	-.1954
2-year-old stem length	.8787	-.0617	.2089
1-year-old stem diameter	.7043	-.4507	-.0412
1-year-old stem diameter	.8779	.1167	-.0211
branch length	.5025	.5045	-.1429
branch diameter	.7232	.4795	-.2353

The PCA of the WED morphological data in 1987 summarizes over 70 percent of the total variation on the first three axes (Table 22). Axis I is positively correlated with the length and diameter of one- and two-year-old stems and branches, the number of branches per stem, the number of leaves per branch, per one-year-old stem and per quadrat and the number of flowers per inflorescence and the number of flowering stems (Table 22). Like axis I of the TB data, this axis may summarize the size of stems and branches and the number of their component parts at each quadrat. Axis II is positively correlated with the number of leaves on two-year-old stems and the number of two-year-old stems per quadrat and negatively correlated with the number of branch leaves and branches per stem and branch sizes (Table 22). This axis reflects differing vegetative possibilities of a two-year-old stem. Axis III is a reproductive gradient. It is negatively correlated with the number of flowers per quadrat (Table 22). Together axes II and III summarize the vegetative and reproductive alternatives of the two-year-old stems; to flower or to branch.

Table 22.   Morphology-PCA axes relationships for WED data in 1987.
Correlation coefficients relating morphological data to PCA axes I - III.

Axis	I	II	III
% variation	41.70	18.56	10.90
morphological variables			
# branches/stem	.6106	-.6583	.1105
# flowers/inflorescence	.6790	.0702	-.3300
# flowering stems	.6981	.1972	-.3724
# flowers/quadrat	.3958	.2258	-.7458
# 2-year-old stems	.3061	.5643	.5664
# 1-year-old stems	.4146	.3964	.2956
# leaves/quadrat	.6308	.6315	.3329
# branch leaves	.7012	-.5635	-.0841
# leaves/1-year-old stem	.6058	-.1532	.3810
# leaves/2-year-old stem	.4889	.7406	-.1915
1-year-old stem length	.7864	-.0882	.3283
2-year-old stem length	.8105	.1536	-.1498
1-year-old stem diameter	.6370	.1768	-.2713
1-year-old stem diameter	.8526	.1447	.0805
branch length	.6616	-.5760	.0356
branch diameter	.7663	-.5120	.0933

The first three axes of the 1987 DC PCA account for 73 percent of the total variation in the raw data (Table 23). Axis I is positively correlated with the number and size of branches, stem sizes, the number of branch leaves and the number of flowers per quadrat (Table 23). The axis focuses on older stems and their component vegetative parts. Axis II is positively correlated with the number of stems and negatively correlated with the number of branches per stem and the stem length (Table 23). Larger older stems often have more branches while in quadrats with many stems, the stems were often younger and smaller. Axis III is negatively correlated to the stem length increment and the number of flowers per quadrat (Table 23).

Table 23.   Morphology-PCA axes relationships for DC data in 1987. Correlation coefficients relating morphological data to PCA axes I - III.

Axis	I	II	III
% variation	40.82	21.70	10.56
morphological variables			
# branches/stem	.6018	-.6517	.1858
# flowers/quadrat	.5872	.3003	-.5590
# stems	-.0890	.6927	.0541
# leaves/stem	.2897	.3819	.3021
# leaves/branch	.6986	.4210	.3073
stem length increment	.1224	-.3095	-.7101
stem length	.6816	-.6706	.1710
stem diameter	.7375	-.4927	.0612
branch length increment	.7756	.4145	-.1890
branch diameter	.8842	.1911	-.1689
branch length	.8925	.2697	.1572

6.2.3 PARTITIONING OF VARIATION

For both devil's club and thimbleberry, little variation was accounted for by differences between years suggesting that annual temporal heterogeneity actually influenced the two species very little in 1986 and 1987 (Table 24). Large-scale spatial heterogeneity had little effect upon thimbleberry morphology (Table 24), the percent variation accounted for by site differences being only 15 percent (Table 24). Most of the variation in the total data set was accounted for by within-site influences (error term)(Table 24). Species were not included in the previous comparison because only one site was sampled for devil's club. The percentage of variation due to species differences was only 20 percent (Table 24), suggesting that there was more variation within each species for the parameters measured than between the two species.

Variation within- and among-quadrats was analyzed to further characterize the patterns of observation. Only stem length and the number and size of leaves were analyzed because sample sizes were greater than 3 at all quadrats, and each sample could be obtained from more than 1 stem, thereby measuring variation within genets rather than within ramets. In most cases the majority of variation is within quadrats suggesting environmental or developmental influences were a large component of the morphology.

Table 24.   Morphological variation apportioned between years, species, sites and within and among quadrats by ANOVA.

	Thimbleberry	Devil's Club
Years	6.29%	3.88%
Sites	15.74%	n/a
Error	75.88%	95.81%

Species	20.36%	Error	80.66%

Within and among Quadrats

	KIT	WED	DC
1987 stem leaves			
among	16.84	21.43	23.04
error	83.16	78.57	76.96
1987 stem length			
among	53.24	48.25	18.77
error	46.76	51.75	81.23
1986 leaf length			
among	10.57	9.87	16.30
error	89.43	90.13	83.70
1986 leaf width			
among	16.10	8.63	18.39
error	83.90	91.37	81.61

6.2.4 MORPHOLOGICAL-ENVIRONMENTAL RELATIONSHIPS

Morphological PCA axes are not strongly correlated with 1986 or 1987 canopy cover (Table 25).

Table 25. Canopy cover-morphological PCA relationships.
Correlations between canopy cover in 1986 and 197 and morphology axes I - III for KIT, LWED, TB and DC (* ,p<.05).

PCA Axis	TB		KIT	
	1987 cover	1986 cover	1987 cover	1986 cover
I	-.4059*	-.4891*	.3083	-.1349
II	-.1004	-.0013	-.1262	-.1429
III	-.1033	-.2709	-.0808	-.3770

PCA Axis	WED		DC	
	1987 cover	1986 cover	1987 cover	1986 cover
I	-.0607	-.0229	.3083	.1349
II	-.1015	.0419	-.1262	-.1429
III	.4669*	.4630*	-.0808	-.3770

Although canonical correlation coefficients are large (Appendix III), CANCORR indicates little if any relationship occurs between the devil's club and thimbleberry morphology and the soils matrices (Table 26)(Appendix III).

Table 26. Summary of relationships between TB, KIT, WED and DC morphological variables and environmental characters. (+) positive relationship, (-) no relationship.

	SOILS		PLANT NEIGHBOURS			
			FREQUENCY		PRESENCE/ABSENCE	
	CANCORR	WMDS	CANCORR	WMDS	CANCORR	WMDS
TB	-		+	+	+	
KIT	-		-		-	
WED	-		+	+	-	
DC	-		-		-	-

Both CANCORR and WMDS imply a relationship between the TB and WED morphology and frequency of plant neighbours matrices (Table 26). The first TB morphological canonical axis is positively correlated with the first PCA axis (Appendix III), a gradient of stem size and number and size of stem component parts (Table 20). The first frequency canonical axis is positively correlated with the first PCA axis (Appendix III), a disturbance gradient due to girdling (Table 15). The third PCA axis was also correlated with this canonical axis , however, this could not be interpreted (Table 15). When both TB sites are examined together, larger stems with more leaves and flowers and more and longer branches are found at more disturbed sites. Nondisturbed quadrats have smaller stems with fewer smaller vegetative component parts.

At WED the second canonical axis pair is correlated with the first PCA axes for both morphology and frequency of plant neighbours (Appendix III). The first WED morphology PCA axis is correlated with the length and diameter of one- and two-year-old stems and branches,the number of branches per stem, the number of leaves per branch, per on-year-old stem and per quadrat and the number of flowers per inflorescence and per stem (Table 22). The first plant neighbour frequency PCA axis is a moisture gradient (Table 17). CANCORR therefore suggests that in drier quadrats one and two year old stems are larger, have more, larger branches, more leaves and more flowers than in wetter quadrats.

The CANCORR of the morphological and presence/absence of plant neighbours matrices all indicate little relationship between each matrix pair, except for the TB data set (Table 26). The size of stems and the number and size of stem components increases as moisture or flooding increases. The morphological canonical variables are most strongly correlated with PCA axis I (Appendix III), which is positively correlated with stem size and the number and size of stem components (Table 20). The presence/absence canonical variables are correlated with the second PCA axis (Appendix III), a disturbance gradient due to moisture (Table 11).

6.3   PHENOLOGY

6.3.1   UNIVARIATE ANALYSES AND GRAPHS

In 1986 the rate of vegetative development appears similar at both thimbleberry sites (Figure 15) and the slopes of regression were not significantly different between sites (Appendix II). In 1987, on the other hand, the vegetative development appeared to occur more rapidly at KIT than WED (Figure 15) and the slopes of regression lines for vegetative phenological codes were significantly different (Appendix II).

Thimbleberry was not vegetatively different between years (Appendix II) suggesting that annual climatic differences may have little affect on the rate of development. Significant differences were found between the vegetative phenologies of one-year-old and two-year-old stems and branches, however (Appendix II).

Figure 15.   Vegetative phenological codes at KIT and WED in 1986 and 1987. The numbers within the circles represent the number of quadrats with the code on the y-axis at the sampling time.
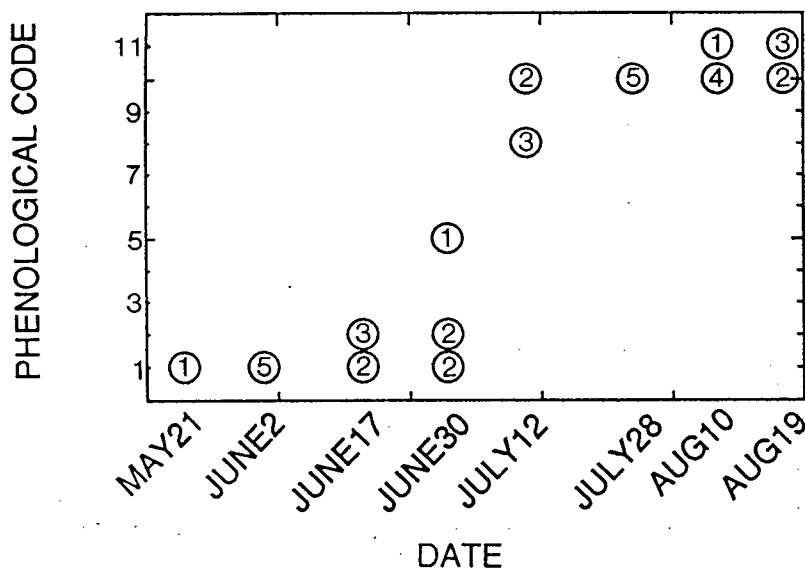
a) KIT - 1986

b) WED - 1986

Figure 15 continued

PHENOLOGICAL CODE

c) KIT - 1987

PHENOLOGICAL CODE

Figure 15 continued

d) WED - 1987
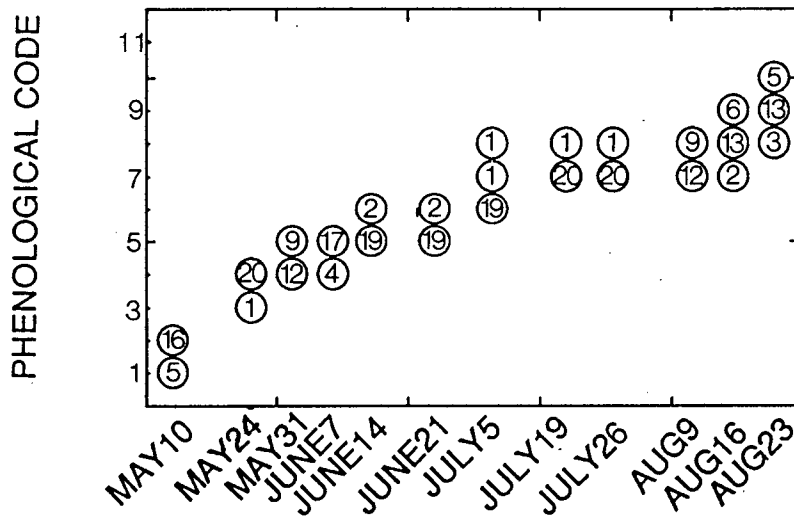
Unlike thimbleberry, the slopes of regression lines of devil's club vegetative phenology differed between years (Appendix II) and phenology may have initially proceeded more rapidly in 1986 than 1987 (Figure 16). Devil's club stems and branches were not vegetatively different (Appendix II).

Figure 16. Vegetative phenological codes for devil's club in 1987 and 1987. The number within the circles represent the number of quadrats with the code on the y-axis at the sampling time.

a) DC - 1986

DATE
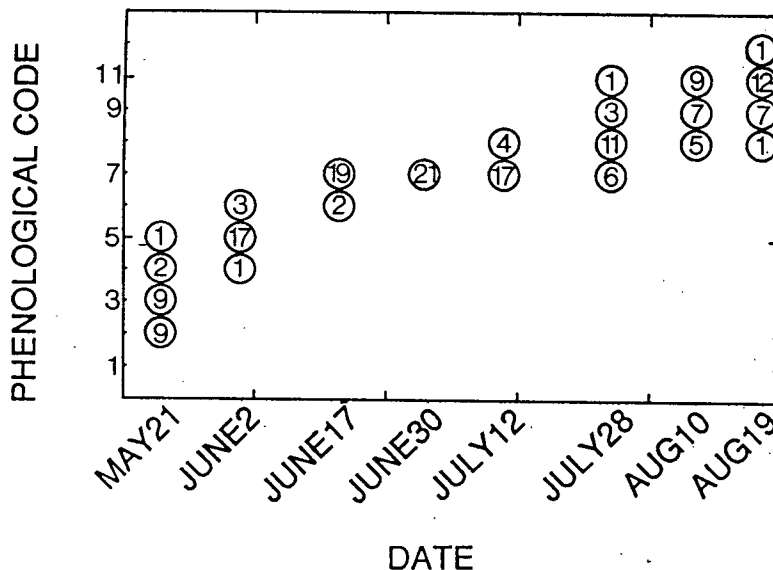
Figure 16 continued

b) DC - 1987
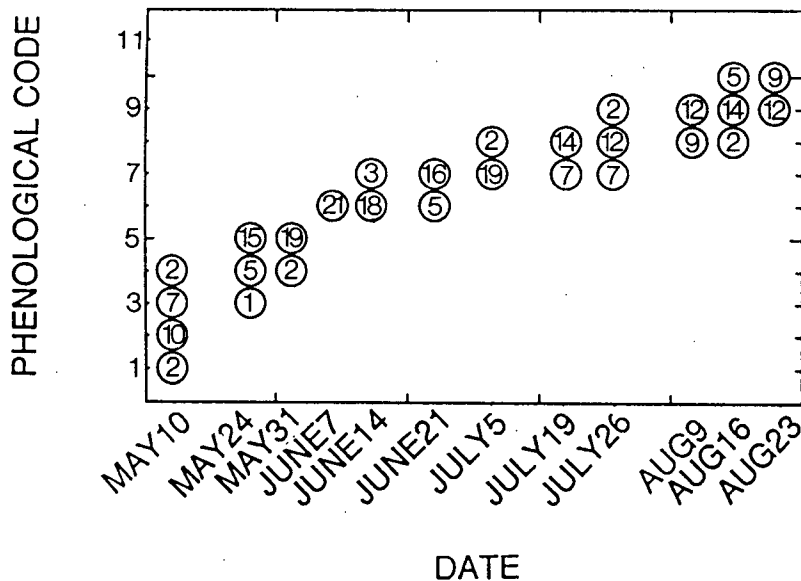
Reproductive phenologies differed between thimbleberry sites in both years (Appendix II). In 1986 at WED few plants bore fruit (Figure 17), and of those that did many became moldy. At KIT most plants flowered and produced fruit (Figure 17). Flowering and fruit ripening occurred at a rapid rate in 1986 (Figure 17). By the end of June, most plants at KIT had begun to bloom and within two weeks the same flowers had faded and had developed fruit (Figure 17). During this short period when flowers were opening, variability between quadrats was substantial (Figure 17).

In 1987, although KIT again produced most fruit, WED had more flowers than in 1986. Flowers were also seen earlier at KIT than at WED (Figure 17). By June 21, most plants were in full bloom (code 7) or fading at KIT while at WED flowering was just beginning (code 4)(Figure 17). These differences between sites continued and although most plants bore fruit at both sites by July 26, at KIT some fruit had already ripened (Figure 17).

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Reproductive phenologies were also different between years (Appendix II), with
flowering beginning two or three weeks earlier in 1987 (Figure 17). Fruit also matured earlier in
1987 (Figure 17). Few plants had ripe fruit by mid-August in 1986 (Figure 17).

Figure 17.　Reproductive phenological codes at KIT and WED in 1986 and 1987. The
number within the circles represent the number of quadrats with the code on the
y-axis at the sampling time.
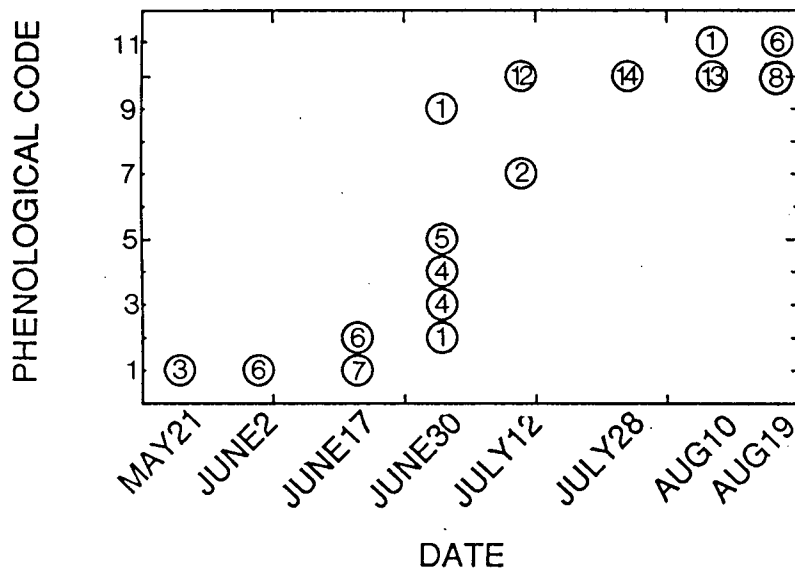
a) KIT - 1986

b) WED - 1986

Figure 17 continued

c) KIT - 1987
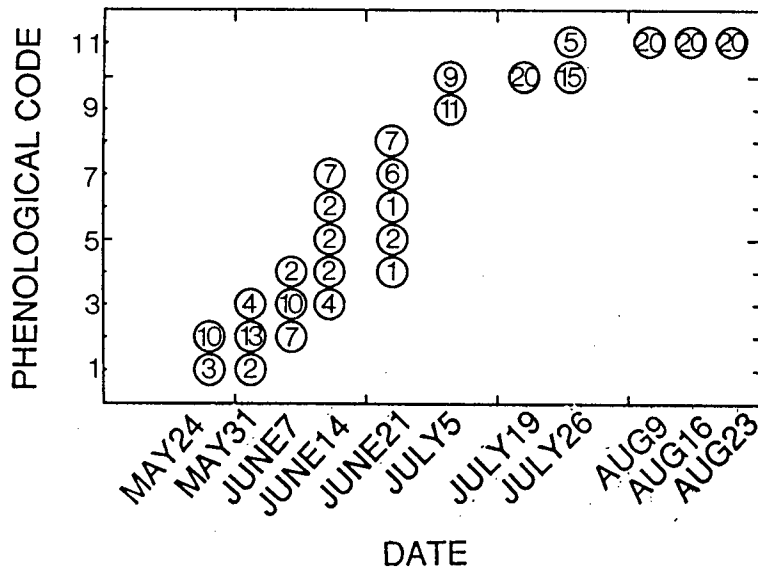
d) WED - 1987
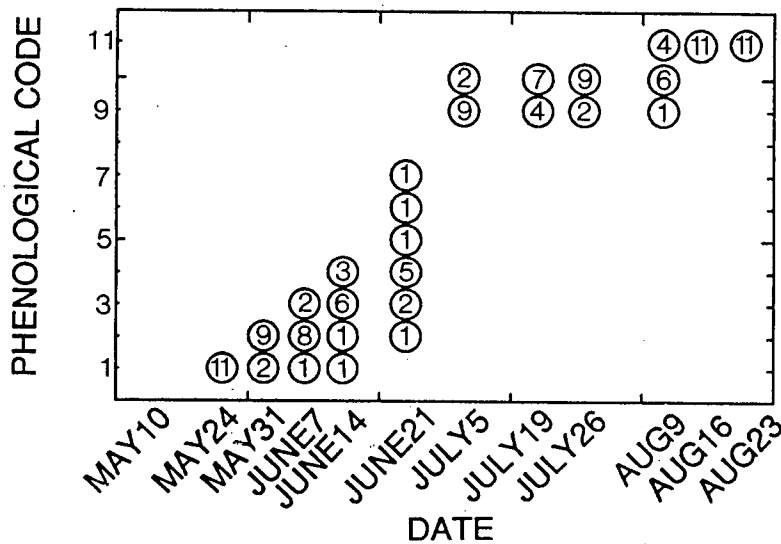
Unlike thimbleberry, devil's club branches and stems did not exhibit different reproductive phenological rates (Appendix II). Like thimbleberry though, devil's club reproductive phenology was significantly different between 1986 and 1987 (Appendix II), with

development occurring more rapidly in 1986 (Figure 18). In both years floral development was rapid (Figure 18).

Figure 18. Reproductive phenological codes for devil's club in 1986 and 1987. The number within the circles represent the number of quadrats with the code on the y-axis at the sampling time.
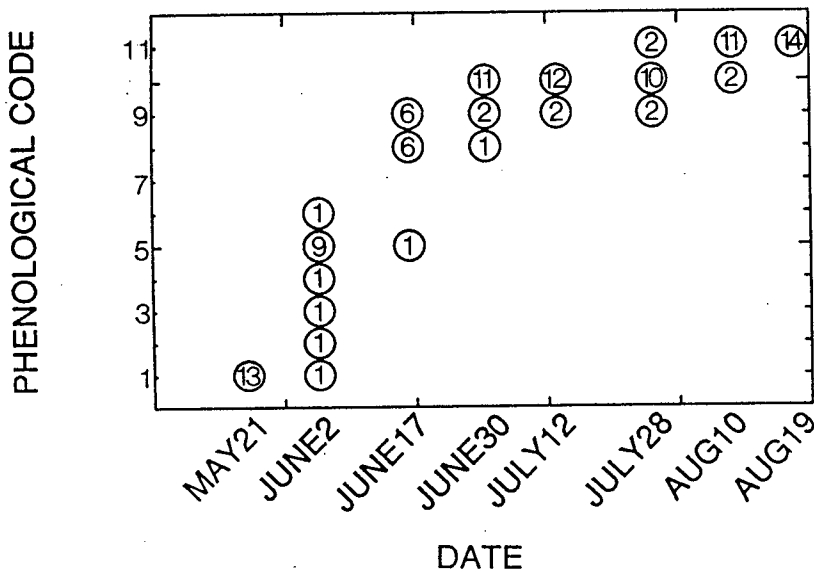
a) DC - 1986

b) DC - 1987
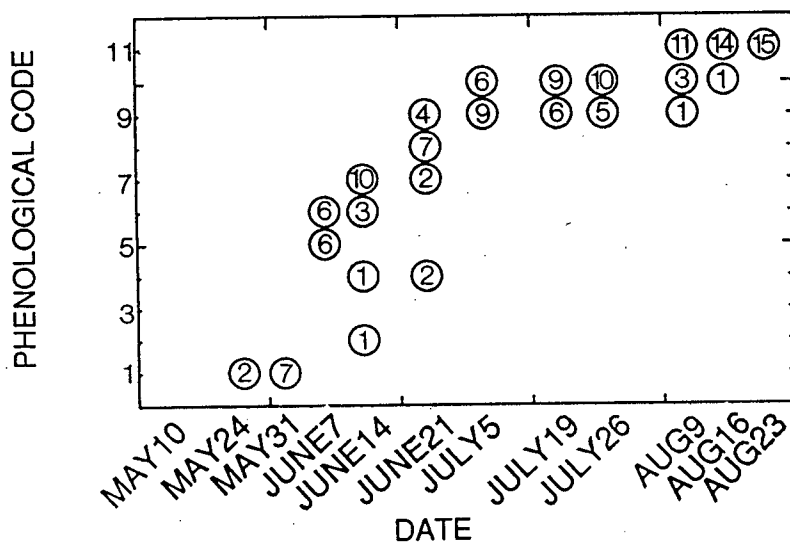
In all cases of regression of vegetative phenology at each quadrat coefficients of determination were greater than .80 and with the exception of 15 quadrats in both 1986 and 1987 all were greater than .85. Reproductive phenology for each quadrat was not as efficiently summarized by a regression equation. Seven quadrats had r^2 values between .7 and .8 though, in most cases, the simple regression represented greater than 90 percent of the variation in the total data set.

6.3.2 PRINCIPAL COMPONENTS ANALYSES

The PCA of the thimbleberry data reduce the data to three axes which represent over 90 percent of the variation in the total data set. Axis I is highly correlated with reproductive phenology in both 1986 and 1987 and vegetative phenology in 1987 (Table 27). Axis II is strongly correlated with the vegetative phenology in 1986 (Table 27). Axis III is not strongly correlated with any raw variable (Table 27).

Table 27.   Phenology - PCA relationships for TB data. Correlation coefficients relating phenological data to PCA axes I - III.

Axis	I	II	III
% variation	56.16	25.54	11.24
phenological variables			
reproductive 1987	.8962	.1353	.0737
vegetative 1987	.8019	-.3491	.4250
reproductive 1986	.8226	-.1991	.5116
vegetative 1986	.3516	.9174	.0398

As with the TB PCA data set, KIT PCA represents over 90 percent of the variance of the whole data set on the first three axes (Table 28). Axis I is positively correlated with the vegetative and reproductive phenological codes for 1986 and 1987 (Table 28). Axis II is positively correlated with the reproductive phenology and negatively correlated with vegetative phenology in 1986 (Table 28). Axis III is a vegetative axis and is positively correlated with the vegetative phenology in 1986 (Table 28).

Table 28.   Phenology - PCA relationships for KIT data. Correlation coefficients relating phenological data to PCA axes I - III.

Axis	I	II	III
% variation	55.11	23.11	14.73
phenological variables			
reproductive 1987	.8598	-.2103	-.2857
vegetative 1987	.7136	.3461	.6048
reproductive 1986	.7128	.5457	-.3608
vegetative 1986	.6691	-.6803	.1065

Axis I, of the WED PCA, is correlated with all the phenological variables, especially the phenology in 1987 (Table 29). Axis II summarizes the 1986 phenological data being negatively correlated with the 1986 vegetative phenology and positively correlated with the reproductive phenology (Table 29). Axis III is negatively correlated with the 1987 vegetative phenology (Table 29).

Table 29.   Phenology - PCA relationships for WED data. Correlation coefficients relating phenological data to PCA axes I - III.

Axis	I	II	III
% variation	56.63	20.94	12.70
phenological variables			
reproductive 1987	.8584	-.0051	.0444
vegetative 1987	.7947	.1843	-.5454
reproductive 1986	.7563	.4119	.4447
vegetative 1986	.5697	-.7963	.1036

Axis I, of the devil's club PCA, is strongly correlated with all the phenological variables and summarizes most of the variation in the data (Table 30). Axis II is a vegetative axis and is negatively correlated with the vegetative phenology in 1987 (Table 30). No interpretation of axis III is possible as it is not strongly correlated with any of the phenological variables (Table 30).

Table 30.   Phenology - PCA relationships for DC data. Correlation coefficients relating phenological data to PCA axes I - III.

Axis	I	II	III
% variation	74.81	15.45	7.05
phenological variables			
reproductive 1987	.9088	.2611	.2536
vegetative 1987	.7014	-.7079	.0825
reproductive 1986	.9381	.2085	.1148
vegetative 1986	.8914	.0715	-.4445

6.3.3 PARTITIONING OF VARIATION

Examination of the variation apportioned to years, sites and quadrats for vegetative development reveals that little variation within the thimbleberry data is accounted for by annual temporal fluctuations (Table 31). Annual fluctuations seem to have a larger impact on devil's club vegetative phenology (Table 31). For thimbleberry most variation (77.18%) is accounted for by site differences, indicating that large-scale environmental patterns affect vegetative developmental rates substantially. Of the remaining variation most is accounted for by the within-site or error term for devil's club and 22.72% is due to within-site variation for thimbleberry (Table 31). For both species the within-quadrat term represents a substantial proportion of the variability within sites (Table 31). This suggests that more variation is due to phenotypic rather than genotypic differences assuming each quadrat represents a single genet.

Reproductive patterns are somewhat different from vegetative patterns. Annual climatic fluctuations have a larger effect on the reproductive phenology of thimbleberry; however almost none of the variation in the data is accounted for by differences between years for devil's club (Table 31). The ANOVA suggests that annual temporal fluctuations are important to thimbleberry reproductive developmental rates but not devil's club (Table 31). As the regression equation for nonflowering plants had no slope, 1986 would have more zero values for the input data to ANOVA. These zero values may increase the proportion of the reproductive variation accounted for by annual differences and the annual variation accounted for by those plants with flowers may be larger than 10.77 % indicated by ANOVA (Table 31).

The variation accounted for by site differences is not as large for thimbleberry reproductive data as for vegetative data (Table 31). Of the remaining variation within sites, both devil's club and thimbleberry are strongly affected by within-quadrat environmental differences as suggested by the large proportion of variation accounted for by the within-quadrat term and less affected by environmental and genotypic differences between quadrats (Table 31). Quadrat differences also account for a substantial proportion of reproductive phenology for thimbleberry, suggesting that genotypic effects are also important. Most reproductive characters are considered to be conservative and less susceptible to environmental fluctuations and

therefore useful in taxonomy. Perhaps reproductive phenology is subject to the same selection pressures and is also less variable in a fluctuating environment than other vegetative characters.

Table 31.   Percentage of phenological variation apportioned between years, species, sites and within and among quadrats for devil's club and thimbleberry.

Thimbleberry	Vegetative	Reproductive
between years	0.00	10.77
between sites	77.18	18.97
error	22.72	70.26
among quadrats	.12	20.38
error	99.88	79.62

Devil's club		
between years	18.45	.41
error	81.55	99.59
among quadrats	7.98	11.94
error	92.02	88.06

Devil's club and thimbleberry	Vegetative 1987	Reproductive 1987
between species	40.01	3.64
error	59.99	96.36

6.3.4   PHENOLOGICAL-ENVIRONMENTAL RELATIONSHIPS

The 1987 vegetative phenology for TB and the 1986 reproductive phenology for WED were both significantly correlated with canopy cover (Table 32). As canopy cover decreases the developmental rate increases in these cases. ANOVA indicates a large proportion of the vegetative phenological variation is accounted for by site differences (Table 31). Perhaps the open canopy at the KIT site let snow melt and soils warm earlier in 1987 than at WED so vegetative development proceeded sooner. In 1986, when spring was warmer and drier (Figure 2), differences in temperature and snow cover may not have been so critical between sites. Certainly the vegetative development is more advanced at KIT from spring through to the end of August, 1987 (Figure 15).

Table 32.   Canopy cover - phenology relationships. Correlations between canopy in 1986 and 1987 and reproductive and vegetative phenology summary variables for KIT, WED, TB and DC. (*,p<.05).

	1987 CANOPY COVER	1986 CANOPY COVER
TB		
reproductive 1987	-.4275	-.4443
vegetative 1987	-.7107*	-.7452*
reproductive 1986		-.4703
vegetative 1986		-.0485
KIT		
reproductive 1987	.1325	-.0656
vegetative 1987	-.1985	-.1084
reproductive 1986		.1939
vegetative 1986		-.1810
WED		
reproductive 1987	-.3050	-.1893
vegetative 1987	-.4046	-.3341
reproductive 1986		-.5703*
vegetative 1986		-.1405
DC		
reproductive 1987	-.2545	-.2490
vegetative 1987	-.4132	-.4874
reproductive 1986		-.2646
vegetative 1986		-.5916*

Devil's club vegetative phenology was also negatively correlated with canopy cover in 1986 (Table 33). In 1986, spring was sunnier and drier than 1987 (Figure 3). This suggests that canopy cover and climate may have jointly affected phenology. Warmer spring temperatures in 1986 would melt snow more rapidly under open canopies than under conifer trees allowing devil's club to develop earlier than in 1987. Phenological codes add credence to these findings as they were greater in early May, 1986 than in 1987 (Figure 16).

Little relationship is apparent between phenology and soils for either devil's club or thimbleberry as suggested by CANCORR , though an overlap between the phenology and frequency of plant neighbour matrices for thimbleberry is strongly indicated (Appendix III)(Table 33). Only the CANCORRs for WED and TB were interpretable, however as the PCA axes correlated with the KIT canonical axes were not ascribed with biological significance (Table 15).

Table 33.   Summary of relationships between TB, KIT, WED and DC phenological variables and environmental characters. (+) relationship occurs, (-) no relationship, (?) possible relationship indicated by CANCORR.

| | SOILS | | FREQUENCY | | PRESENCE/ABSENCE | |
	CANCORR	WMDS	CANCORR	WMDS	CANCORR	WMDS
TB	-		+		+	+
KIT	-		+		-	
WED	-		+		+	+
DC	-		-		-	

PLANT NEIGHBOURS

The CANCORR for the TB data set suggested that the rate of reproductive development and vegetative development in 1987 for thimbleberry increased with disturbance, as suggested by the frequency of plant neighbours PCA. The first canonical axes are correlated with the first PCA axis (Appendix III), which are correlated with the reproductive phenology in 1986 and 1987 and the vegetative phenology in 1987 (Table 27). The first PCA axes of the plant frequency

axes is correlated with the canonical axes (Appendix III) and represents disturbance gradient due to alder girdling (Table 15).

CANCORR also indicated a relationship between TB phenology and disturbance, as suggested by the presence/absence of plant neighbours (Table 33), with developmental rates increasing with increasing disturbance. The first canonical axis is correlated with the first and third phenological PCA axes (Appendix III), which are positively correlated with reproductive phenologies in 1986 and 1987 and the vegetative phenology in 1987 (Table 27). The first plant presence/absence PCA axis, which is correlated with the first canonical axes (Appendix III), may be a disturbance gradient due to alder girdling and a fluctuating water table (Table 11).

CANCORR also suggested a relationship between phenology and the frequency of plant neighbours for the KIT data. The first canonical axes were correlated with the first phenological and frequency of plant neighbours PCA axes (Appendix III). The first phenological axis is positively correlated with all phenological variables (Table 28) whereas, the first frequency of plant neighbours PCA axis was a disturbance gradient (Table 16). This relationship suggests that all developmental rates are increased in more open and disturbed sites at KIT.

Both the CANCORR for the WED phenology-frequency of plant neighbours and the WED phenology-presence/absence of plant neighbour matrices indicated a relationship between phenology and moisture, with developmental rates decreasing as moisture increases and evaporation decreases due to shading by alder. The first WED phenology canonical axis for the frequency-phenology CANCORR is correlated with the first phenology PCA axis (Appendix III), which summarizes all the phenological variables (Table 29). The first plant frequency canonical axis is negatively correlated with the first PCA axis (Appendix III), a moisture gradient (Table 17). This relationship suggests that as moisture increases and evaporation decreases due to shading by alder, all developmental rates decrease.

Redundancies indicate that the strongest relationship between the canonical axes and the PCA axes occurs between the second canonical axis pair for the WED phenology-presence/absence of plant neighbours (Appendix III). The second canonical axes for the WED presence/absence-phenology CANCORR are correlated with the first phenological and plant

presence/absence PCA axes (Appendix III). The first phenological axis summarizes all phenological variables (Table 29), whereas the first plant presence/absence axis represents a moisture gradient (Table 13).

## 6.4   DEMOGRAPHY

6.4.1   UNIVARIATE ANALYSES AND GRAPHS

Though the rate of demise differs for thimbleberry between years, the shape of the survivorship curve is similar (Figure 19). The curve (Figure 19) indicates that each thimbleberry cohort has a relatively constant risk of mortality throughout its lifespan and suggests a type II demographic curve, which is common for perennial species (Hutchings 1976). There are still changes, however, in the risk of mortality through time.

In 1986 the slope of the curve between the two sites was similar though the number of recruits was far larger at KIT (Figure 19). Approximately 10 percent of the stems die within the first month and a half of growth or from May 21 to mid-June (Figure 19). The next deaths occur from the end of August, 1986, to the beginning of the following May, 1987 though approximately 78 percent of the stems survived to the second year (Figure 19). From this point on, most stems lived only until the period from August,1987, to August,1988, though almost 10 percent of stems were still alive by the end of the third summer of growth (Figure 19). In many Rubus species canes live for only two years but thimbleberry this is not necessarily the case. Of those 54 stems known to survive from 1985 to 1986, three were still alive at the end of 1988.

The longevity of stems produced in 1987 did not appear to differ substantially between sites though the slope of the line appeared more steep than for 1986 stems (Figure 19). Recruitment was obviously greater in 1987 at both sites (Figure 19). Unlike 1986, 65 percent of the stems were dead by the end of August of the second year (Figure 20). Forty-five percent more stems produced in 1987 had died between August of the first summer of growth and August of the second year than those produced in 1986. Most stems die from August ,1987, to August, 1988, regardless of which year they were produced in. Some mortalities may be explained by clearing done by forestry crews at WED early in the summer of 1988. However this effect was not substantial as the slope between KIT and WED does not appear to differ to any great degree during this time (Figure 19).

Figure 19.   Survivorship of thimbleberry stems produced in 1986 and 1987 at the WED and KIT sites.

a) 1986
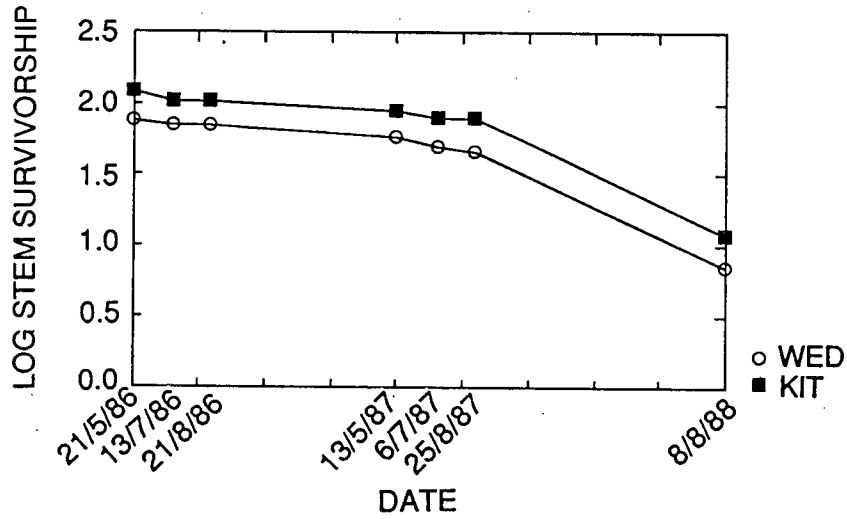
b) 1987
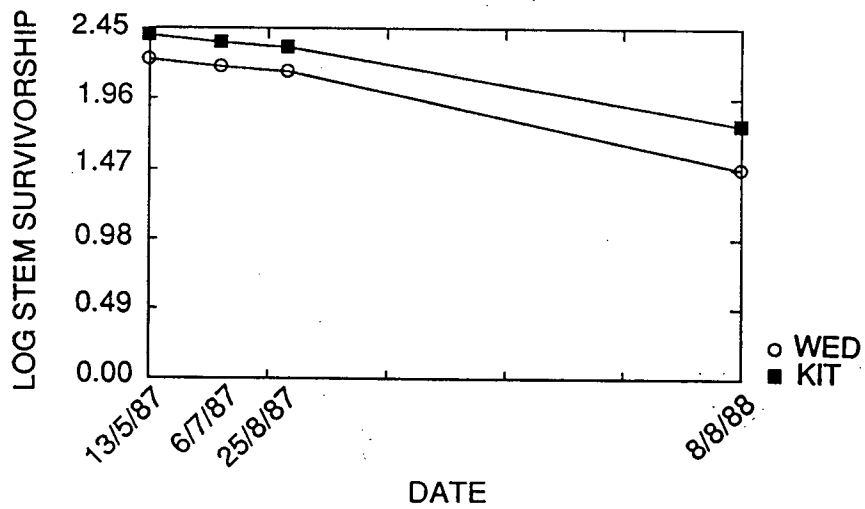
As indicated by the survivorship curves, the KIT histograms of the percentage of stems dying within distinct time intervals also indicates that the largest percentage die during the period from August, 1987 to August ,1988 (105-450 days)(Figure 20). These graphs also suggest that each quadrat, except those at WED for which no stems were produced, contained a range of stem ages in each year (Figure 20). Few general patterns are evident among sites though some relationship within quadrats is suggested (Figure 20). Quadrats with a large percentage of stems which die by the end of June, 1986 produce stems with greatest longevity in 1987. For example, in 1986 at quadrat 2, almost 60 percent of the stems produced die by the end of June whereas of those produced in 1987, 100 percent live longer than August ,1987 and 25 percent are alive in August, 1988 (Figure 20).

Figure 20. Percentage of stems dying within distinct time periods at KIT and WED sites in 1986 and 1987.

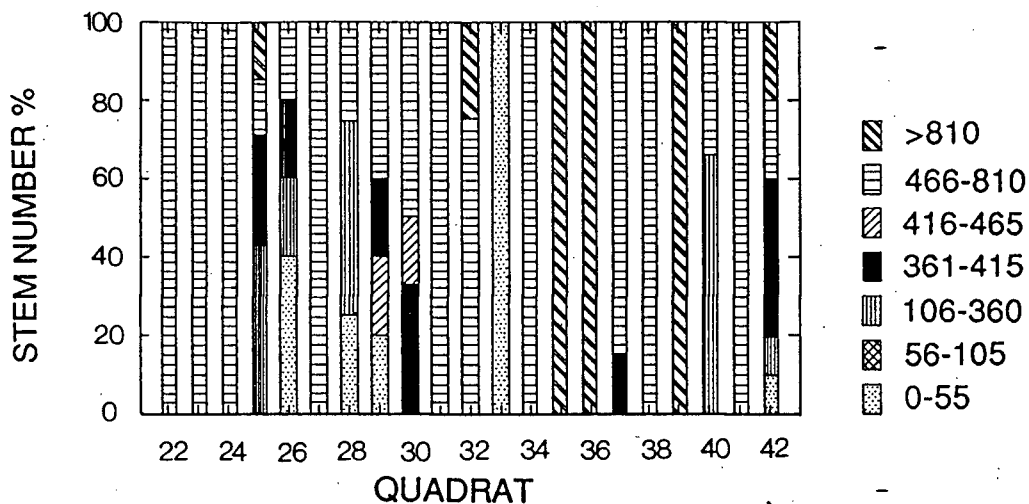a) KIT 1987
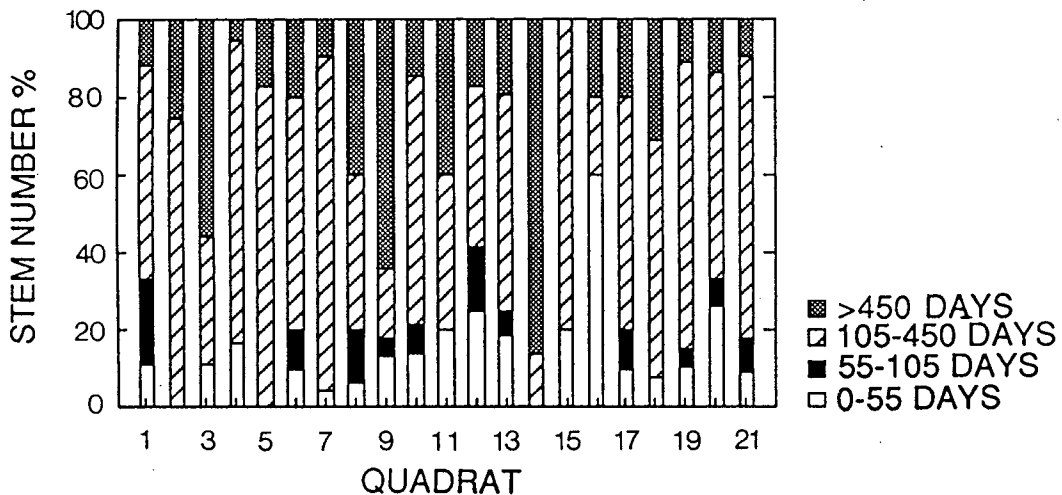
Figure 20 continued

b) WED 1987
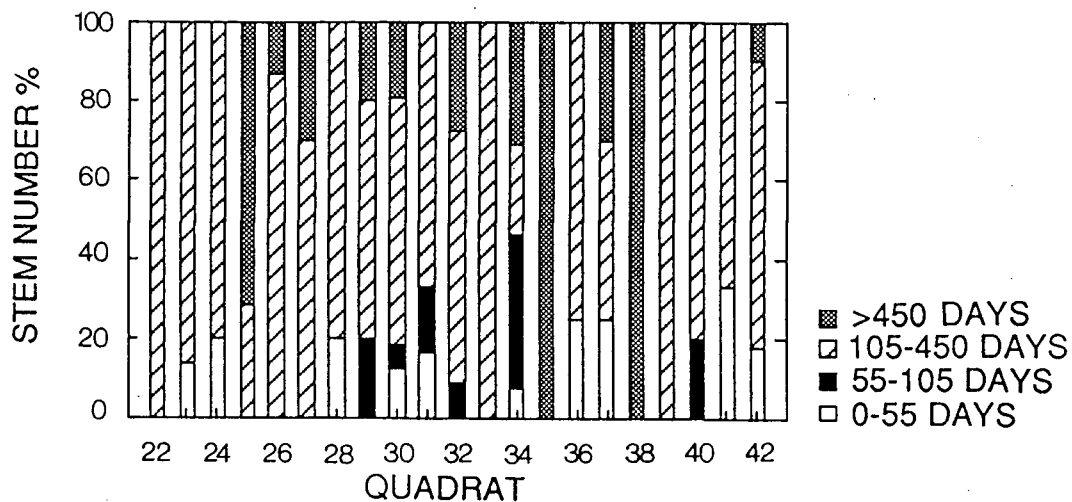
c) KIT 1986
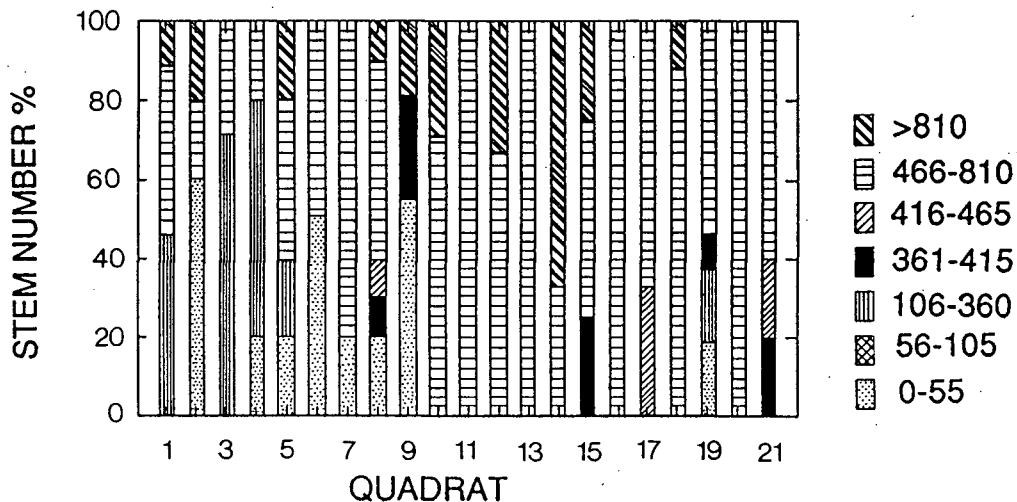
d) WED 1986

In the devil's club site, only six stems were produced in 1987 and only one stem was still alive by August. This large rate of early mortality and the graph of the age distribution (Figure 21) suggest a Deevey Type III curve (Hutchings 1976). A type III distribution implies that youngest plants have the greatest risks of mortality. This risk of mortality declines with age so that some very old individuals will be found in the population (Hutchings 1976). A type III curve is common for longlived species (Balogh and Grigal 1988). The cumulative distribution, however, shows stem ages at one time only (Figure 21) and is not identical to a Deevey survivorship curve which shows the change in cohort numbers through time (Hutchings 1976). Devil's club populations do not necessarily have the same age distribution at all times as factors determining longevity may change. It was also impossible to determine the age of this longlived population accurately and it may be hundreds of years old. Indeed aging stems by counting terminal bud scars probably underestimates each stem by at least five years as these scars are obliterated by stem thickening.

Figure 21.   Cumulative number of devil's club stems older than the time indicated on the x-axis.
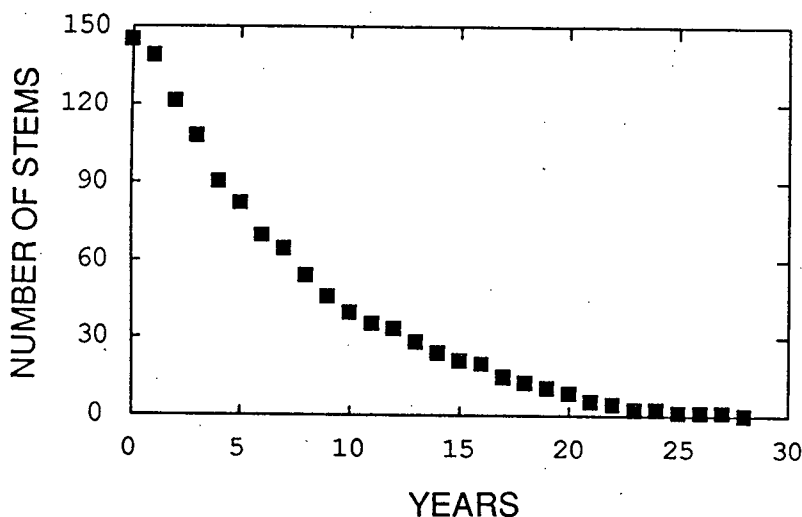
In comparison with thimbleberry, the devil's club population consists of a mixture of ages (Figure 22). The largest overall proportion of stems are less than five years old indicating that although the risks of mortality are high early in life sufficient numbers are produced to ensure that many stems reach reproductive maturity. Few stems were observed to be greater than 22 years old, indicating the maximum time period before stems become stoloniferous and fragment.

Figure 22.   Percentage of devils' club stems in distinct age classes on June 30, 1987.
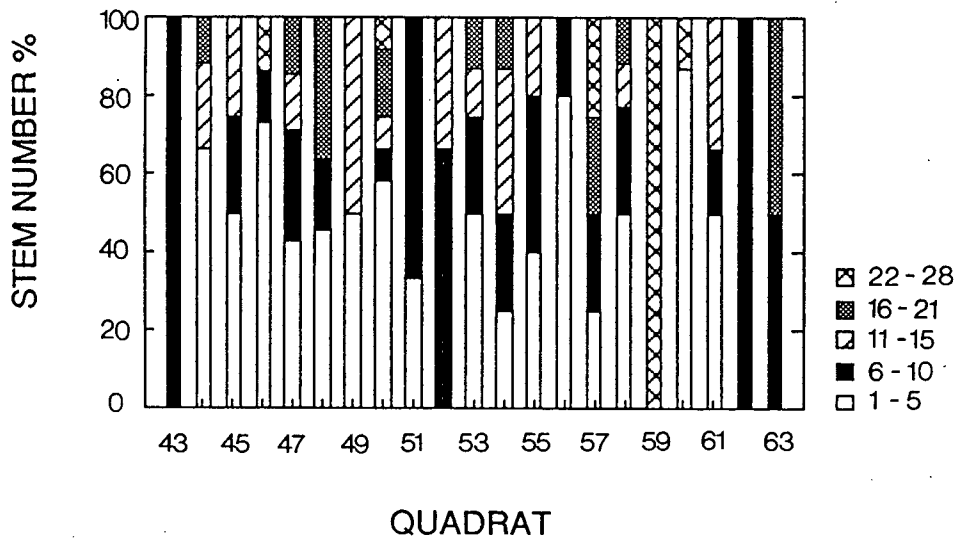
There appears to be little relationship between the density of thimbleberry at each quadrat and the percentage of stems surviving to each age class. As density increases a concomitant change in the longevity at each quadrat does not occur (Table 34). In most cases the slope of the regression is not significantly different from zero (Table 34), indicating no relationship. In those cases where the regression is significant (1986 - all periods from 106 - 810 days) (Table 34), the variation in the data accounted for by the regression is less than 30 percent.

Table 34.   Regression analysis of thimbleberry stem longevity and stem density.
Y=a+bx where y = percentage of the total number of stems in quadrat surviving to
the time period, a = intercept, b = slope and x = total number of stems in quadrat.
($*$, p<.05)

Time period (days)	r-square	slope	significance
(1986) 0-55	.07	-.014	.10
(1986) 55-105	.07	-.014	.10
(1986) 105-360	.14	-.033	.01$*$
(1986) 361-415	.26	-.015	.00$*$
(1986) 416-465	.26	-.052	.00$*$
(1986) 466-810	.10	-.033	.04$*$
(1987) 0-55	.06	-.013	.10
(1987) 56-105	.03	-.003	.26
(1987) 106-450	.03	-.004	.25

The regression of the proportion of the total number of devil's club stems in each class against the total number of stems in the quadrat suggests that density has little or no effect on the proportion of stems of each age class observed (Table 35). As the density of stems increases the proportion of stems in each age class does not also increase (Table 35).

Table 35.   Regression analysis of devil's club stem age and density.
Y=a+bx where Y = ratio of number of stems in age class to total number of stems
in quadrat, a = intercept, b = slope and x = total number of stems in quadrat. ($*$,
p<.05)

Age class (years)	r-square	slope	significance
1-5	.33	.035	.00$*$
6-10	.12	-.019	.12
11-15	.02	-.004	.60
16-21	.01	-.003	.61
22-28	.05	-.011	.32

6.4.2   PRINCIPAL COMPONENT ANALYSES

The PCA of the number of thimbleberry stems alive in each age class in 1986 and 1987 was used to generate axes scores for use in ANOVA only. The PCA summarized over 99 percent of the variation in the data on the first three axes, (Table 36). No biological interpretation was ascribed to these axes.

Table 36.   Eigenvalues of 1986 and 1987 PCA for the number of stems surviving to each age class.

	Axis I	Axis II	Axis III
Eigenvalues	66.90	31.99	.73

The PCA of the number of stems dying in the age classes in 1986 and 1987 was used in subsequent CANCORR analysis, though only 54.81 percent of the variation in the total data were explained by the first three axes (Table 37). Axis I reiterates the relationship observed graphically and groups together those quadrats with the shortest living stems in 1986 and longer lived stems in 1987, all of which are vegetative and not sexually reproductive (Table 37). Axis II implies that quadrats with the longest living stems in 1986 produce shorter living stems in 1987 (Table 37). Axis I and II suggest at tradeoff between younger vegetative and older generative stems and indicate that the plant may alternately channel resources between vegetative and generative stem production. Axis III has no strong positive correlations and is negatively correlated with stem deaths during the period from July to August, 1987 (1986 416-465, 1987 56-105 days), the period where least deaths occur whether these stems were produced in 1986 and 1987 (Table 37).

Table 37.   Demography - PCA axes for TB data for the number of stems dying during each age class. Correlation coefficients relating demographic data to PCA axis I - III.

Axis	I	II	III
% variation	22.59	18.75	13.47
demographic variables (days)			
(1986) 0-55	.7844	-.1013	.1101
(1986) 106-360	-.0299	-.1217	.3179
(1986) 361-415	.7699	-.0014	.0117
(1986) 416-465	.1497	.1669	-.7688
(1986) 466-810	-.0005	.7069	-.7260
(1986) >810	.5506	-.3978	.1878
(1987) 0-55	.2144	.7417	.2930
(1987) 56-105	.1659	.1929	-.6575
(1987) 106-450	.0202	.7551	.2875
(1987) >450	.8065	.0806	-.0419

PCA of the KIT data represents approximately 60 percent of the variation on the first three axes (Table 38). Axis I of the KIT PCA, like axis I of the TB PCA, groups together those stems dying early in 1986 and 1987, before they can flower and those stems living longest, perhaps because they have also not yet flowered. Axis II is correlated with those stems produced in 1986 and 1987 which die by the end of the summer of 1987 (1986 416-465 days and 1987 56-105 days), the period when stem mortality is at a minimum (Table 38). Axis III is negatively correlated with the stems produced in May, 1986 which die by August 1987 (416-465 days) and positively correlated with those stems from 1987 which die by the end of June, 1987 (0-55) days (Table 38). These opposite correlations suggest that reproductive and vegetative

stems are not produced at the same time, assuming two year old stems which die by the end of the summer were reproductive.

Table 38.   Demography - PCA axes for KIT data for the number of stems dying during each age class. Correlation coefficients relating demographic data to PCA axes I - III.

Axis	I	II	III
%variation	29.34	15.46	13.86
Demographic variables (days)			
(1986) 0-55	.8451	.0327	.2632
(1986) 106-360	-.2022	-.3099	.1540
(1986) 361-415	.8491	.2917	.1522
(1986) 416-465	.0709	.5411	-.6937
(1986) 466-810	-.4316	.3863	.0465
(1986) >810	.6313	-.3334	-.2176
(1987) 0-55	.0474	.4642	.6203
(1987) 56-105	.2247	.6464	-.3244
(1987) 106-450	-.2908	.4180	.4921
(1987) >450	.8547	-.0525	.0851

The PCA of the WED summarizes 58 percent of the total variation in the data on the first three axes (Table 39). It is most strongly correlated with the stems from 1986 which die after August,1987 (466-810 days) perhaps after flowering and producing fruit, and those vegetative stems produced in 1987 which die within two months of their emergence or after June,1987 (0-55 days)(Table 39). Axis I is also correlated with those stems produced in 1987 which live past the first summer (106-450 and >450 days). Axis II is correlated with stems produced in spring, 1986, which die in all age categories before July, 1987, or before they can produce fruit. The stems from spring, 1987, are most strongly correlated with axis III. The stems which die during the time period from August, 1987, to August, 1988, (106-450 days) may have died between

August and June, 1988, and can be assumed to be vegetative as fruit did not ripen until mid-July in 1987. Those stems dying from June to August, 1987, were most probably reproductive as stems which produce fruit common died shortly afterwards. This axis may therefore be a continuum showing the differing longevities of vegetative to reproductive stems.

Table 39. Demographic - PCA axes for WED data for the number of stems dying during each age class. Correlation coefficients relating demographic data to PCA axes I -III.

Axis	I	II	III
%variation	24.24	19.36	14.82
Demographic variables (days)			
(1986) 0-55	-.1990	.6001	-.0732
(1986) 106-360	-.3150	.6035	.1233
(1986) 361-415	.2046	.8998	.0729
(1986) 416-465	.2634	.1967	.3081
(1986) 466-810	.8283	-.0041	.1637
(1986) >810	-.2773	.4813	-.0848
(1987) 0-55	.7542	.0723	-.4665
(1987) 56-105	.2234	-.2414	.6754
(1987) 106-450	.6532	.0977	-.5737
(1987) >450	.6048	.2414	.5701_

The devil's club PCA of the number of stems of each age category recorded in quadrats on June 30, 1987, explains 80 percent of the total variation on the first three axes (Table 40). Axis I is negatively correlated with the oldest class, those stems aged from 22 to 28 years (Table 40). Stems greater than 16 years old tend to be stoloniferous and those younger than 10 years old are not reproductive. Axis II may, therefore, be a vegetative gradient for those two vegetative states. Axis III may represent the differences between vegetative and generative

stems, certainly that is the most noticeable difference between these two age classes correlated with the axis.

Table 40. Demography - PCA axes for DC data for the number of stems in each age class. Correlation coefficients relating demographic data to PCA axes I - III.

Axis	I	II	III
%variation	31.47	30.92	18.33
Demographic variables (years)			
0-5	-4856	.7846	.1465
6-10	.3962	.4771	-.6568
11-15	.5427	.3919	.6739
16-21	.1104	.7329	-.0935
22-28	-.9349	.1087	.0257

6.4.3 PARTITIONING OF VARIATION

The ANOVA results for thimbleberry indicate that a substantial proportion of the total variation is accounted for by annual differences (Table 41). This agrees with trends suggested by PCA which indicated that vegetative and generative patterns were not maximized every year. The variation accounted for by differences between sites is less than 10 percent and suggests a relatively small effect due to large scale environmental differences (Table 41). The genetic component in demographic heterogeneity is also small as suggested by the proportion of variation accounted for by among-quadrat differences (Table 41). Most variation is accounted for by differences between stems within quadrats (Table 41), indicating that small scale environmental or developmental influences are an important component of longevity, and may be the major impetus determining age structure within populations.

Although almost 20 percent of the variation in devil's club stem ages on June 30, 1987, is accounted for among quadrats, most variation is within quadrats or between stems, suggesting that small scale environmental or developmental influences are a large component in population age structure (Table 41).

Table 41. Demographic variation apportioned between years, sites and within and among quadrats by ANOVA.

	Thimbleberry	Devil's club
Years	29.10	n/a
Sites	8.27	–
Error	62.63	
Within and among quadrats		
quadrats	7.10	17.18
error	92.09	82.82

6.4.4 DEMOGRAPHIC-ENVIRONMENTAL RELATIONS

Correlations between canopy cover and the longevity of thimbleberry stems are all less than .50 and indicate little relationship (Table 42).

Table 42. Canopy cover - demographic relationships. Correlations between the number of stems dying in each time period and the canopy cover in 1986 and 1987 for TB, KIT and WED. (*,p<.05).

Time period (days)	KIT		WED		TB	
	1986	1987	1986	1987	1986	1987
(1986)						
0-55	.11		.19		-.11	
106-360	-.05		.23		-.05	
361-415	-08	-.21	.15	.27	.14	.15
416-465	-.20	-.05	.26	.21	-.01	.01
466-810	-.22	.07	.45*	.45*	-.13	.04
>810	.11	.10	-.35	-.06	-.23	-.10
(1987)						
0-55		-.41		.21		-.18
56-105		-.28		-.26		-.27
106-450		-.28		.30		-.06
>450		.07		.23		-.11

Canopy cover also seems to have little effect on the longevity of devil's club stems, as correlations are small (Table 43).

Table 43.   Canopy cover - age distribution relationships. Correlation between the age distribution of stems and the canopy cover in 1987 for devil's club. (*,p<.05).

age class (years)	correlation
1-5	.18
6-10	.06
11-15	.00
16-21	-.07
22-28	-.01

CANCORR suggests little or no relationship exists between all the demography and environmental matrices (Table 44). Although the canonical correlation coefficients are frequently large, redundancies often do not support any overlap between point swarms or correlation structure is not conclusive (Appendix IIII). CANCORR also implies a relationship between the WED demography-soils and the WED and KIT demography-frequency of plant neighbours matrices, but WMDS refutes these relationships (Table 44)(Appendices III and IV). A relationship is also indicated between the phenology and the presence/absence of plant neighbours at KIT; however, the second PCA axis which is correlated with the first canonical axis (Appendix III) could not be interpreted (Table 12).

Table 44.   Summary of relationships between TB, KIT, WED and DC demographic variables and environmental characters. (+) relationship occurs, (-) no relationship, (?) possible relationship indicated by CANCORR.

	SOILS		PLANT NEIGHBOURS FREQUENCY		PRESENCE/ABSENCE	
	CANCORR	WMDS	CANCORR	WMDS	CANCORR	WMDS
TB	-		-		-	
KIT	-		?	-	?	
WED	?	-	?	-	-	
DC	-		-		-	

6.5 MORPHOLOGY-PHENOLOGY-DEMOGRAPHYINTERACTIONS

Morphology and phenology appear to be related at each level in the nested hierarchy for both thimbleberry and devil's club, as suggested by CANCORR (Table 45). CANCORR also suggests a relationship between demography and morphology for both devil's club and the thimbleberry data set (Table 45), though WMDS refutes these relationships at KIT and WED (Appendix IV). In no case, though, is phenology related to demography (Table 45), suggesting that longevity has little relationship to the rate of development.

Table 45.   Summary of relationships between TB, KIT, WED and DC morphological, phenological and demographic variables. (+) relationship occurs, (-) no relationship.

	PHENOLOGY		DEMOGRAPHY	
	CANCORR	WMDS	CANCORR	WMDS
TB -				
MORPHOLOGY	+		+	
PHENOLOGY			-	
KIT -				
MORPHOLOGY	+		+	-
PHENOLOGY			-	
WED -				
MORPHOLOGY	+		+	-
PHENOLOGY			-	
DC -				
MORPHOLOGY	+		+	
PHENOLOGY			-	

CANCORR suggests that both vegetative and reproductive developmental rates in 1986 and vegetative developmental rates in 1987 are more rapid at those quadrats with larger stems with more, larger branches and leaves and more flowers for the TB data set. The first canonical

axes for the TB morphology-phenology CANCORR are correlated with the first morphological and phenological axes (Appendix III). Axis I of the morphological PCA data is correlated with all morphological variables except the number of stems per quadrat and the number of branch leaves (Table 20). The first phenological axis is correlated with the reproductive phenology in 1986 and 1987 and the vegetative phenology in 1986 (Table 27).

For the KIT morphology-phenology data, CANCORR indicates that quadrats with more flowers have more rapid developmental rates. In those quadrats, where phenology does not proceed as rapidly, there are fewer flowers. The first canonical axis is correlated with the first phenological PCA axis and the third morphological PCA axis (Appendix III). The first phenological PCA axis is correlated with all the phenological variables (Table 28), whereas the third morphological PCA axis is a reproductive axis and is correlated with the number of flowers per inflorescence and per quadrat and the number of two-year-old stems per quadrat (Table 21). As those quadrats with no flowers have no change in reproductive phenological code, the slope of the regression line between the phenological code and time is zero (Table 5). Phenological summary slopes would be larger than zero at those quadrats with flowers, regardless of how rapidly they matured. Only two-year-old stems produced flowers and they also had the most rapid rate of vegetative development. Quadrats with most two-year-old stems would therefore be expected to have greatest overall developmental rates or slopes of the regression.

At WED, the CANCORR indicates a relationship between phenology and vegetative and reproductive morphological features. Those quadrats with more flowers and larger amounts of vegetative tissue have most rapid developmental rates and at those quadrats where there are fewer flowers and smaller vegetative parts, the developmental rates are less rapid. The first canonical axis pair is strongly positively correlated with the first morphological and phenological PCA axes (Appendix III). The first morphological PCA axis is, like axis I of the TB data, a gradient of vegetative tissue size and is also less strongly correlated with the number of flowering stems and the number of flowers per inflorescence (Table 22). The first phenological axis is correlated with all the phenological variables, especially the 1987 phenological variables (Table 29).

CANCORR between the TB morphology-demography matrices indicates a relationship between the number of stems in each quadrat and the number of stems in most demographic time periods. The first morphological canonical axis is correlated with the second morphological PCA axis (Appendix III), a gradient of the number of stems per quadrat (Table 20). The first demographic canonical axis is correlated with the first and second PCA axes (Appendix III). These PCA axes are correlated with most stem age classes, except those from July to August in either 1986 or 1987, and from August, 1986, to May, 1987, (Table 37), the time periods when fewest stems die(Figure 20). As the number of stems dying is related to the number of stems in each quadrat, this relationship is not surprising though perhaps it does attest to the validity of the method. It also reiterates the regression analysis between each demographic age class and the stem density (Table 34). The regression indicates that as the number of stems per quadrat increases more stems die but the proportion dying in any one age class does not change (Table 34). According to CANCORR (Appendix III), as stem number per quadrat increases, no stem age class emerges when stems die.

Phenology is unrelated to demography (Table 30), suggesting that the rate of annual periodic development is uncorrelated to the longevity of stems and may also be subject to different environmental contraints. As suggested for morphology and demography, a relationship between longevity and reproductive phenology may be expected as stems usually die after flowering and flowering stems tend to be oldest in the population. Regardless, CANCORR does not strongly indicate a relationship (Appendix III). The type II survivorship curve for thimbleberry also suggests that the risk of mortality is relatively constant through time for each cohort (Figure 37).

Developmental rates increase in devil's club quadrats where there are more flowers and stems are larger with more vegetative tissue. CANCORR further indicates that plants with smaller stems and branches with fewer leaves may have slower developmental rates. The first canonical axes are correlated with the first morphological and phenological PCA axes (Appendix III). The first morphological PCA axis is correlated with stem sizes and the number and size of branches and the number of branch leaves and the number of flowers per quadrat

(Table 23). The first phenological axis is correlated with the vegetative and reproductive phenological codes in 1986 and 1987 (Table 30). As with the thimbleberry data, quadrats lacking flowers generate a zero slope from the regression of phenological slope against time (Table 5). Reproductive developmental rates will therefore be perceived as more rapid at those quadrats with flowers, regardless of the rate at which flowers and fruit mature. Although, larger devil's club stems mature more rapidly or larger stems may initiate growth earlier than smaller stems, no correlation is apparent for the stem length increment and the rate of development. Branches, though, increase more in length at quadrats with more rapid developmental rates and larger stems (Appendix III). As branches represent the next generation of stems and the means of clonal expansion, their increased growth may indicate that conditions are most favorable for vegetative reproduction at sites where developmental rates are maximized.

CANCORR also indicates a relationship between devil's club morphology and demography. The first canonical axis is correlated with the second morphological and demographic PCA axes (Appendix III). The second morphological axis is negatively correlated with the number of branches per stems and the stem length and positively correlated with the number of stems per quadrat (Table 23). The second demographic axis is correlated with those stems between 0 and 5 years of age and 16 and 21 years of age (Table 40). This correlation links together those stems, aged 16 to 21 years, which have become stoloniferous and along which branches have rooted to become independent stems estimated to be between 0 and 5 years old. Although the 16 to 21 year old stems would have the greatest overall stem lengths, nonetheless, the average stem length per quadrat would be low due to the large number of newer, shorter stems.

VII DISCUSSION

7.1 MORPHOLOGY

The environmental characteristics of differing successional niches have been credited with maintaining morphological differences between some species (Lee et al. 1986). Morphological differences are evident between thimbleberry and devil's club with perhaps a palmate leaf shape and a clonal growth habit being the most obvious traits that the two species share. Differences in the successional niche occupied by each species are also apparent. Although thimbleberry is found in clearings in old growth forests with devil's club, it is most abundant at earlier successional stages. This suggests that differing successional environments may correlate with morphological characters unique to devil's club and thimbleberry. Lee et al. (1986) attributed variation in leaf size and shape and plant architecture between two species of Polygonum to differing successional habitats. Thimbleberry morphologies are correlated with disturbance caused by girdling and moisture, whereas devil's club morphology is uncorrelated with any other environmental variables selected (Table 26). Devil's club may be buffered by large trees in the old growth forest against fluctuations in climate and, therefore, may be living in a stable environment.

Though few studies have compared vegetative morphology between species in differing successional environments (Bierzychudek 1982), reproductive effort has frequently been linked to succession (Hancock and Pritts 1987; Stearns 1977). - Harper (1970) indicates that species found earlier in succession devote larger proportions of energy to reproduction than those species found later in succession. Thimbleberry and devil's club suggest that those factors which determine reproductive allocation are complex. Both are vegetatively and sexually reproductive, perennial and iteroparous; as well thimbleberry rhizomatous growth is extensive and devil's club roots are also large and deep (personal observation). However, their flowering responses differ. Devil's club doesn't flower in the first year and each stem may flower thereater, whereas thimbleberry stems produce fruits once in their second or third year of growth and then

die. This diversity of reproductive possibilities suggests that several differing factors may determine reproductive allocation and that reproductive allocation is a complex species-specific phenomena. Both species, however, fit into life history arguments which suggest that earlier successional species flower sooner after germination than later successional species (Stearns, 1977).

Differences between the two thimbleberry populations may be due to environmental differences at each site (Jurik 1985; Van Cauteren and Lefebvre 1986; Maddox et al. 1989; Schwaegerle and Levin 1990). Some site differences are apparent, with WED having greater canopy cover (Figure 7), richer soils and showing less sign of flooding than at KIT (Table 6). In 1987, morphological patterns also differed between sites. KIT had greater numbers of flowers, fruits, leaves and stems per quadrat, longer stems and a larger proportion of fruit per flower produced than WED (Appendix I). Disturbance, due to moisture differences and alder girdling, was correlated with morphological differences between sites. These environmental characters were reflected differently between sites, though. At WED drier quadrats contained plants with more flowers, larger stems and more branches (Appendix III); whereas for the overall TB data set more disturbed, moist quadrats contained larger stems with more leaves and branches (Appendix III). At KIT, where disturbance was greater, moist sites produced more flowers and branches on larger stems; whereas at WED, where disturbance is less, moist sites produce fewer flowers and branches on smaller stems. Relationships between morphology and environment were also found to differ between sites by Schwaegerle and Levin (1990) and between and among sites by Gawler et al. (1987) for Phlox drummondii and Peducularis furbishiae respectively. Menges (1987) also found larger leaves and longer stems produced in canopy gaps for Laportea canadensis to differ between upland forests and floodplains.

Most variation is accounted for within sites or populations, being greater than between sites for thimbleberry and between years for either thimbleberry or devil's club. If, as assumed, each quadrat contains a single unique genet then it would appear that

morphology is strongly influenced by genetic differences between individuals and by small scale environmental heterogeneity. The number and size of leaves are mostly influenced by small scale environmental heterogeneity for both species (Table 24). Variation within other clonal populations for leaf size was also found to be substantial by Barnes (1986) and Herndon (1987). Leaf plasticity has also been observed with such examples as sun versus shade leaves (Schlichting 1986) or different nutrient, moisture and clipping treatments affecting the number and size of Phlox leaves (Schlichting 1989). Plasticity is common for leaf (Oberbauer and Strain 1986) and stem (Schlichting 1986; Pitelka et al. 19865) morphology and may even be predictable in differing environments (Givnish 1982; Menges 1987). Morphological plasticity is also commonly observed in weedy species (Holzner 1982) and has been noted for thimbleberry (Hultén 1974).

Most variation for stem length is apportioned within individuals for devil's club and equally divided within and between individuals for thimbleberry (Table 24). Thimbleberry stem length is influenced by both genetic differences and small scale environmental heterogeneity. Several factors may account for the differences observed. Devil's club stems originate individually and are long-lived stoloniferous stems producing roots and vertical branches along their length. Thimbleberry stems are produced in clumps and remain erect. Each thimbleberry stem may therefore encounter less environmental variation than devil's club, both spatially and temporally. The common origin of each thimbleberry is also assurance that each clump of stems within a quadrat is genetically identical. Devil's club stems within a quadrat may not be genetically identical and may therefore also be influenced by a combination of genotypic and environmental heterogeneity.

The large within-quadrat morphological term suggests that replicate environmental measures made within quadrats might have been informative. If small-scale environmental variability promotes plasticity within individuals as Levin (1986) suggests, this large within-quadrat term (Table 24), indicates that environmental

variation within quadrats may also be significant. Certainly soil characteristics are known to be highly variable, perhaps requiring up to 100 samples in a hectare to accurately estimate soils features (Courtin et al. 1983).

Although the relative allocations to sexual and vegetative reproduction may be important to maintain or spread clonal plants under different environmental conditions (Pitelka et al. 1980; Abrahamson 1980; Loehle 1987), they are difficult to assess for thimbleberry and devil's club. In addition, both plants are long-lived and do not flower every year. Accounting for vegetative costs for years when no seed is produced is not straightforward. Although thimbleberry was found to increase sexual reproduction at KIT, where light levels are greater than WED, vegetative reproduction was also found to increase. Vegetative and sexual reproduction were also found to increase for Acalypha rhomboidea and Pilea pumila (Cid-Benevento 1987) with increasing light.

Physiological integration may be an important strategy for both devil's club and thimbleberry, though devil's club does not maintain the same degree of interconnection between parts as does thimbleberry. Once devil's club stems become stoloniferous, branch and root at stem nodes, the stolon degenerates between nodes, though these connections may be several meters long before degradation occurs. Thimbleberry rhizomes tend to maintain connections between clumps of stems and appear to die at the tip of the growing rhizome (personal observation). Certainly the degree of rhizome branching, primary and secondary root formation and the distance between above ground stems is variable. Architectural differences such as these have been interpreted as a strategy to alleviate stress (Schmid and Bazazz 1987; Hartnett and Bazazz 1985) as stem ramets were found to be longer and fewer through areas of nutrient (Slade and Hutchings 1987a; Slade and Hutchings 1987b) and moisture (Hartnett and Bazazz 1983) stress.

Morphological patterns observed for devil's club and thimbleberry are similar to results reported by Scagel and Maze (1984); more variation is accounted for within individuals rather than between individuals. Environmental correlates reported here do

not parallel those of other studies. Devil's club morphology was uncorrelated with the environmental variables, though thimbleberry showed similar correlations to those reported by Pitelka et al. (1985) and Gawler et al. (1987) for other clonal species. Canopy openings (Pitelka et al. 1985) and moisture (Gawler et al. 1987) were correlated with the number and size of leaves and the number of flowers. Disturbance and moisture were both positively correlated with these traits for thimbleberry. If disturbance equates to girdling of the alder and therefore canopy openings, the relationship between these studies is more apparent. No interaction, as thimbleberry displayed, between moisture and canopy openings, though was observed by Pitelka et al. (1985) for Clintonia borealis or Gawler et al. (1987) for Peducularis furbishiae.

7.2   PHENOLOGY

The different successional niches occupied by thimbleberry and devil's club may account for some of the phenological differences observed (Rathcke and Lacey 1985). Devil's club, as a member of a late successional community may be a stronger competitor than thimbleberry, which is found at earlier stages along a successional gradient (Grime 1979). It has a well defined peak of leaf production during the longest days of summer followed by the rapid production of flowers. Grime (1979) indicates that competitive species generally will produce leaves during periods of maximum productivity and then flower. In contrast, thimbleberry produced leaves early in the summer on two-year-old stems, which may then flower for up to two months. One-year-old stems produce leaves throughout the summer. The strategies of devil's club and thimbleberry are quite different and may indicate stronger differences between the two species, especially reproductively, than the ANOVA indicated.

Little variation is accounted for by species differences in the ANOVA of reproductive phenology (Table 31), these results may partly reflect the coding used. Each thimbleberry had several flowering stems which flowered continuously; whereas devil's club had only one or two flowering stems per quadrat with only one floral spike per stem. Thimbleberry was, therefore, potentially more phenologically varied than devil's club, although the average quadrat value for the two species was similar.

Annual climatic differences appeared to have some effect on thimbleberry reproductive phenology though not on the vegetative phenology. Flowering proceeded at a faster rate in 1987 as compared to 1986 (Figure 17), but in addition far more thimbleberry plants bore fruit at both sites in 1987 than in 1986 (Appendix I). Annual variation in numbers of fruit and flowers was also reported to be substantial by Duke (1990), and the relationship between variation in climatic factors, such as frost (Rathcke 1988), temperature (Helenurm and Barrett 1987; Rathcke 1989) and rainfall (Jackson and Bliss 1984; Gill and Mahall 1986; Heideman 1989), on flowering phenology have been recorded.

In contrast to thimbleberry, annual differences for devil's club were seen for vegetative phenologies only (Figure 18), with phenological development proceeding more rapidly in 1986 than 1987. Annual differences observed for devil's club phenology may be due to interactions of canopy cover and climate, which would affect the rate of snow melt and the temperature at each quadrat (Table 32, Figure 2). Temperature was also linked to annual differences in leaf and flower phenology of Aralia nudicaulis (Flanagan and Moser 1985).

Environmental differences between sites may maintain the phenological differences between two populations (Primack 1985). A large proportion of the phenological variation for thimbleberry is accounted for by site differences (Table 31), with canopy cover negatively correlated with the 1987 vegetative phenology and disturbance due to girdling and fluctuating water conditions positively correlated with all phenological variables (Table 33). Separate populations were also found to exhibit different phenological patterns in different environments by Van Cauteren and Lefebvre (1986) and Nilsen (1986).

Differential responses to environmental factors were also observed at each site for thimbleberry. At WED, phenological development was negatively correlated with moisture and canopy cover due to alder; whereas at KIT phenological development was more rapid at open sites with more fluctuations in water conditions. Site differences and differential responses within sites to moisture were also reported by Heideman (1989).

Studies have indicated that phenology may be affected by pollinator availability (Rathcke and Primack 1985; Rathcke 1988) or the availability of seed dispersers (Rathcke and Primack 1985; Primack 1985). Devil's club was observed to have many different pollinators on the large conspicuous floral stems. The short period of flowering or the narrowing of devil's club's floral niche, may as Rathcke (1988) suggests for several other species, be a result of competition for pollinators. The availability of resources or the presence of seed dispersers, though, are equally likely influences on phenology. Devil's club fruit was favored by bears which distributed these large masses

of berries widely in their droppings. No other plant appeared to be a serious competitor for this mode of dispersal as none bore fruits as large, which offered an equivalent reward. Migrating salmon, however, which arrive in August, would certainly distract bears. In this case, the availability of seed dispersers may shape devil's club fruiting phenology. The large clusters of fruit may also be expensive to produce and resource availability may limit devil's club fruiting phenology. Fruits mature immediately following the longest days of summer. Perhaps increasing levels of photosynthate produced in late July are required for fruit to ripen successfully. Flanagan and Moser (1985) inferred that both resource limitation and the lack of pollinators were important factors in the phenology of Aralia nudicaulis .

Thimbleberry reproductive phenology may also be subject to these constraints. Although flowers are produced continuously for almost two months, nonetheless a peak in floral production is apparent. During this peak in late June (Figure 15), flowers are filled with many (>20 per flower) tiny mating beetles, which may be the main pollinator. Many other pollinators were also observed though none were as plentiful as the beetles. In addition, the availability of seed dispersers may determine when thimbleberry fruit ripen. The main period of fruit ripening is August (Figure 15), coinciding with the arrival of migrating birds. From mid-June on, 1987 was warmer and drier than 1986 (Figure 2) and far more fruit ripened that summer (Appendix I). Reproductive development was also more rapid in 1987 (Figure 17). Perhaps flowering proceeds only after a critical number of degree days is achieved, as has been suggested for many temperate woody species (Lieth 1974; Reader 1983; Rathcke 1985).

7.3 DEMOGRAPHY

The stem demography for thimbleberry varied greatly over the time of the study, whereas devil's club changed little. The Type II survivorship curve for thimbleberry stems (Figure 19), suggests a constant risk of mortality throughout their lifespan (Hutchings 1976). The devil's club cumulative distribution (Figure 20) implies that the risks of stem mortality diminish with age increasing the probability that some very old individuals will be found in the population (Hutchings 1976). Indeed devil's club stems were far older than thimbleberry stems.

While the dynamics of ramet production may differ greatly between the two species, it is possible that genet dynamics may not be too dissimilar. As the characteristic species of an earlier state of forest succession than devil's club, thimbleberry may be expected to have lower survivorship (Bierzychudek 1982; Whitney 1986). However in areas of recurring disturbance, thimbleberry genets may also have long lifespans. Carlsson and Callaghan (1990) indicate that long term observations are necessary to more fully understand genet dynamics.

Annual temporal variation accounts for a larger proportion of the variation in thimbleberry than spatial environmental heterogeneity between populations (Table 41). Given that demography examines changes through time, it is not surprising that temporal influences would be large. Indeed, greater demographic variation between years than between populations was also reported by Weiss (1981) for an annual, and by Waite (1984) and Mack and Pyke (1983) for Plantago coronopus and Bromus tectorum respectively.

Annual climatic differences may partially explain the demographic fluctuations in stem recruitment for thimbleberry. As climate in 1987 was more conducive to flowering, increased stem mortalities in 1987 for both one- and two-year-old stems may be due to this greater floral production. Two-year-old stems generally die after flowering. Perhaps one-year-old stems have two alternatives; either to augment the resources of flowering stems or to flower in later years. Some vegetative stems produced in 1987 may have

transposed resources to flowering stems and subsequently died. This implies that there is a relation between the number of vegetative and flowering stems in a clump, though this was not tested.

Alternatively, this pattern may arise from demographic periodicity which is not annual but longer term. In quadrats where most stems produced in 1986 died by the end of that summer, stem survivability appeared greater in 1987 (Figure 19, Table 37); moreover, quadrats where stems produced in 1986 had the longest lifespans, those produced in 1987 had the shortest lifespans (Table 37). Over the period of this study, thimbleberry may alternately maximize vegetative and reproductive strategies and demographies, producing short-lived vegetative stems in one year and longer-lived flowering stems in the next.

Most of the demographic variation for thimbleberry was found within rather than between sites, suggesting that environmental influences may be operating on a relatively fine scale (Table 41). Spatial demographic variation was also found to be similarly distributed by Huenneke (1987). Billington et al. (1990), Blom and Lotz (1985), Sarukhan and Harper (1973), Matlock (1987) and Watson and Cook (1987) also found extensive demographic plasticity within clonal individuals.

With the exception of the canopy cover at WED for the time interval from 466-810 days, none of the environmental variables were correlated with stem demography (Table 44). Several reasons for this can be advanced. As most demographic variation occurs within individuals, the scale of environmental sampling may have been too large. Perhaps replicate samples within quadrats of the environmental correlates would reflect environmental-demographic correlations more strongly. Stem demographics also fluctuate temporally and environmental variables may have failed to encapsulate these fluctuations. If the demographic periodicity was not synchronized with the periodicity of the environmental correlates, a relationship may not be perceived. In addition, if thimbleberry sites within each year and individuals within each site were not sufficiently

variable, then, as with Garnier and Roy (1988), no environmental correlates at the level of sites or individuals will be perceived.

Finally abundance for thimbleberry and devil's club may, as in other shrub species (Balogh and Grigal 1988), be controlled by shrub regeneration rather than mortality. Recruitment or a compound measure composed of recruitment and mortality may more strongly reflect the environmental correlates assessed rather than a measure based primarily upon mortality.

7.4   NICHE UTILIZATION AND LIFEHISTORY STRATEGY

As the niches occupied by devil's club and thimbleberry differed, so did their life history strategy. Devil's club is located in an area of old growth forest which may be characterized as having longterm stability; in contrast thimbleberry is found where disturbance has occurred.

Perhaps due to the influence of disturbance, thimbleberry's strategy may be more flexible in response to change than devil's club. Most morphological, phenological and demographic variation is apportioned within quadrats (Tables 24, 31 and 41) suggesting that both species are somewhat plastic. Unlike thimbleberry, however, this variation is not readily observable for devil's club. implying that it may be less variable than thimbleberry. If the plasticity observed for thimbleberry is appropriate to the environment, it may, as Levin (1986) suggests for a phenotypically plastic strategy, be a rapid and flexible method of accommodating change in environmental conditions (Levin 1986).

Environmental responses also illustrate thimbleberry's flexibility in that disturbance is correlated with both morphology and phenology (Table 26,33, Appendix III). In contrast devil's club generally does not survive after disturbance and is shade tolerant, a trait more characteristic of a competitor of later successional stages (Grime 1979). Thimbleberry has been reported to be more successful under the open canopy of earlier succession (Barber 1976).

This flexibility is also structurally apparent. Thimbleberry is rhizomatous and may, as Abrahamson (1980) suggests for rhizomatous clonal species, be able to position stem ramets in optimum conditions by growing through less favorable areas. Rhizomes were observed to consist of a complex network with clumps of stems separated by varying rhizome lengths. Devil's club is stoloniferous, with branches produced on erect stems. Once these stems become horizontal, the branches root and become independent. Their position within the site may therefore, be limited by their placement on the stem. If the stolon grows though an unfavorable area, the branch may root in a less desirable location and be unsuccessful. It does like the thimbleberry stem

ramet have the advantage of being physiologically connected to the parent plant, however. Antos and Zobel (1984) also speculate that extensive rhizome systems enable plants to cross unfavorable habitat and provide flexibility in dealing with the heterogeneous forest floor.

Other flexibility expressed by thimbleberry stems and their lateral branches, aside from varying the numbers of leaves produced and lengths grown (Appendix I), is their several developmental potentialities. They may, 1) transfer resources to flowering stems and subsequently die, 2) flower in the second year of growth, or 3) if conditions are not suitable they may branch and flower in later years. Annual demographic differences also suggest that clones may alternatively produce vegetative stems in one year and reproductive stems in the next (Table 37, Figure 19). Stems and branches were also observed to develop at different rates, with two-year-old stems developing most rapidly followed by one-year-old stems and branches (Appendix I).

These same patterns were not observed for devil's club. Branches and stems were not phenologically different, neither did they differ in annual growth or the number of leaves produced (Appendices I and II). Unlike thimbleberry, devil's club stems all shared the same fate, being initially vegetative and finally flowering and branching. This flexibility may allow thimbleberry to react to the rapidly changing site conditions that occur in early successional stages. Certainly the amount and size of vegetative and reproductive tissue was correlated with disturbance and moisture (Appendix III).

Phenological patterns also suggest somewhat more flexibility for thimbleberry. Devil's club produces leaves during the longest days of summer and then flowers (personal observation), a competitive strategy as suggested by Grime (1979). Thimbleberry produces leaves all summer on one-year-old stems and flowers for up to two months (personal observation). While the devil's club strategy may produce more seed if conditions are optimum and may be advantageous in a temporally stable site, this single pulse of seed and leaf production may be risky in a fluctuationing environment. Thimbleberry, by producing flowers and leaves all summer, has a higher probability of

some seed production and some increase in vegetative tissue even if disturbance occurs. A strategy which allows simultaneous and longterm reproductive and vegetative growth may be more suited to an unpredictable growing season (Harper 1977; Rathcke and Lacey 1985).

The differences in modular longevity between species may also be a reflection of the character of their differing niches. Both genets and stem ramets of devil's club are long-lived. Thimbleberry stems lived to be four years old (Table 20) and while genets may survive for lengthy periods (Halpern 1989), they are unlikely to live the hundreds of years which may be the case for devil's club. Devil's club stems flower later in life than thimbleberry and also branch later. This also suggests that environmental fluctuations are perceived in a different time scale than thimbleberry. Although phenological differences were seen between years, perhaps other changes occur at a much larger time scale for devil's club. For example perhaps flowering or branching are influenced by environmental conditions occurring over several seasons. The scale at which temporal fluctuations affect this species may be in the order of decades. Thimbleberry may also be influenced by temporal fluctuations which are not annual, but short-term, such as weather patterns or disturbance events, and longer-term, such as successional patterns. Only long-term monitoring would assess such phenomena, however.

Regardless of niche differences certain similarities emerged between both species. Phenology and morphology were positively correlated; with larger flowering plants having more rapid developmental rates for both species. Slade and Hutchings (1989) found similar relationships between phenology and morphology with Glechoma hederaceae. They suggest that larger stems may initiate growth earlier than smaller stems and may also have a greater probability of flowering. Larger stems were certainly more likely to flower for both devil's club and thimbleberry (Tables 20 and 23).

Morphology was also linked to demography, however this relationship may be somewhat trivial; number of thimbleberry stems in each quadrat was correlated with the

number of stems dying in each time period and for devil's club, the number of stems and their length were correlated with the number of newly produced stems (Appendix III).

The lack of any correlation between floral morphology and demography for thimbleberry was unexpected, as most stems died after flowering whether in their second or third year of growth. In addition, stems which eventually flowered generally had longest lifespans. Bradbury (1981), Hutchings (1983) and Gawler et al. (1987) found that flowering stems had longest lifespans for other clonal species. This has been interpreted as the strong commitment to sexual reproduction by a clone (Slade and Hutchings 1989). There was also no evidence to suggest devil's club stems have longer lives if they flower. The survivorship curve indicated that the risk of mortality declined with age and the rate at which this declines is not altered once stems are mature enough to flower (Figure 21).

7.5 MANAGEMENT

Both devil's club and thimbleberry live longer than the two year scope of this study. Together with the annual differences observed, this implies that only a longterm study will achieve a deep understanding of the population dynamics and autecology of these two species. For example, longer-term studies may discern the demographic pattern of devil's club and determine whether the two year pattern observed for thimbleberry repeats.

The differing environmental relationships inferred for thimbleberry within and between populations also suggests that stringent management rules may be unattainable. Environmental relationships may also be complex at other levels. Certainly the differing developmental possibilities of thimbleberry stems interacting with environment make any demographic prediction tenuous.

The study does suggest, however, that alder girdling may be an effective management practice at some sites. It appeared to affect thimbleberry growth and phenology, though not simply through light relations, and also interacted with moisture conditions (Appendix III). Alder girdling may be a successful management technique for alder and thimbleberry at drier sites. Where flooding occurs or if the site is moist, however, opening up the canopy by girdling may encourage thimbleberry, especially if it persists at the site after logging (Halpern 1989).

7.6   FURTHER RESEARCH

This study was descriptive and hypothesis testing was not performed. Rather the study sought preliminary data to construct a framework for suitable hypothesis generation. Hypotheses based on observation have the advantage of a meaningful relationship to the plant, while not being overly simplistic. Perhaps more importantly, descriptive studies provide criteria to discard unsuitable hypotheses before time and money are spent.

Based on this study, future research could explore the following questions more fully:

1.   How do increasing temperatures occurring under an open canopy increase devil's club's rate of development?

2.   Do longer thimbleberry and devil's club stems begin to develop earlier and do they develop more rapidly? Does earlier development ensure that maximum stem length is attained in a season for thimbleberry?

3.   What quantities and proportions of light, moisture and temperature interact to affect thimbleberry's morphology and phenology?

4.   What is the periodicity of the demographic pattern for thimbleberry? Does the strategy of each thimbleberry clump of stems vary from vegetative to reproductive in a repeatable pattern? Do thimbleberry vegetative stems actively transport resources to reproductive stems? Is there a relationship between the number of reproductive stems and the number of vegetative stems per quadrat?

Finally as with most studies more questions are unanswered than answered. The large within quadrat term in all ANOVA calculations (Tables 24,31,41) and the extent to which this variation is due to plasticity or development may be of interest to assess by examining within quadrat environmental variability and the phenotypic response.

... and they all lived happily ever after...   –

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Appendix 1. Mann Whitney U tests for differences in morphology between thimbleberry sites in 1986 and 1987, between years (1986 and 1987) and within plants between stems and branches.

	THIMBLEBERRY SITES		YEARS	
	1987	1986	DC	TB
# flowers/quadrat	.0019	1.000	.3609	.0240
# flowers/stem	.1982	1.000		
# flowering stems/quadrat	.0004	1.000		
# fruit/quadrat	.0004	1.000		.0084
# stems/quadrat			.7299	
# 1-year-old stems/quadrat	.1010	.3253		.0000
# 2-year-old stems/quadrat	.0000	.2300		
# leaves/branch	.6636	.2378	.5194	.2480
# leaves/1-year-old stem	.0030	.1485		.0829
# leaves/2-year-old stem	.0011	.3845		.5159
# leaves/stem	.0004	.0311	.4494	.8181
1-year-old stem length	.1146	.2568		.8887
2-year-old stem length	.0000	.7622		.3186
branch length	.0029	.6735		.5806

Thimbleberry	branches and 1-year-old stems	branches and 2-year-old stems	1-year-old stems and 2-year-old stems
# stem leaves - 1986	.0061	.0000	.0007
# stems leaves - 1987	.0003	.0000	.0000
leaf length	.0053	.0015	.0000
leaf width	.0045	.0015	.0000
stem length - 1987	.0000	.0000	.9923
stem length - 1986	.0000	.0000	.4285

Devil's club	stems and branches
# leaves - 1987	.0070
# leaves - 1986	.0015
length	.0000
length grown	.8207

Appendix II.   Mann-Whitney U tests for differences in generative and vegetative phenologies between thimbleberry sites in 1986 and 1987, between years (1986 and 1987), and within plants between stems and branches.

	THIMBLEBERRY SITES		YEARS	
	1986	1987	DC	TB
reproductive phenology	.0062	.0000	.0290	.0099
vegetative phenology	.7914	.0000	.0099	.8300

	2-year-old stems vs branches	1-year-old stem vs 2-year-old stems	1-year-old stems vs branches	stems vs branches
vegetative phenology				
KIT	.0000	.0000	.0000	
WED	.0000	.0149	.0000	
TB	.0000	.0000	.0000	
DC				.0653
reproductive phenology KIT				
	.0498			
WED	.0000			
TB	.0000			
DC				.7227

Appendix III. CANCORR relationships between morphological, phenological and demographic characters for TB, KIT, WED and DC and soils, frequency and presence/absence of plant neighbour matrices.

Morphology

A - morphological variance explained morphological variables
B - morphological variance explained environmental variables
C - environmental variance explained by environmental variables
D - environmental variance explained by morphological variables

		TB		KIT		WED		DC	
Canonical axes		I	II	I	II	I	II	I	II
Correlation coefficient		.9654	.9095	.9654	.9095	.9856	.8614	.9908	.9732
Redundancies	A	.0915	.1412	.0915	.1412	.1715	.0707	.0920	.2373
	B	.0853	.2021	.0853	.1168	.1666	.0626	.0904	.2247
	C	.0914	.1011	.0914	.1011	.1116	.1040	.1591	.1885
	D	.0851	.0837	.0851	.0837	.1084	.0921	.1562	.1785

Morphology - Frequency of plant neighbours		TB		KIT		WED		DC	
Canonical axes		I	II	I	II	I	II	I	II
Correlation coefficient		.8589	.7759	.9970	.9876	.9999	.9739	.9996	.9749
Redundancies	A	.3435	.0725	.1270	.0796	.0858	.1441	.0411	.1137
	B	.2534	.0437	.1263	.0776	.0858	.1366	.0411	.1081
	C	.1228	.0849	.0613	.1527	.0984	.1282	-.1018	.1136
	D	.0906	.0511	.0609	.1490	.0984	.1216	.1017	.1080
Correlation to PCA axis morphological axis	I	.8060	.1485			.1891	.5212		
	II	-.3221	.3769			.3254	-.0947		
	III	.0555	-.0637			-.5350	-.3798		
environmental axis	I	.5043	.3371			-.3507	-.5599		
	II	-.0887	.1790			.1971	.2821		
	III	.6190	.0775			-.2998	-.0091		

Morphology - Presence/ absence of plant neighbours	TB		KIT		WED		DC	
Canonical axes	I	II	I	II	I	II	I	II
Correlation coefficient	.8288	.7872	.9982	.9493	.9998	.9964	.9984	.9915
Redundancies								
A	.3258	.0839	.1252	.0837	.1376	.1044	.1169	.0769
B	.2238	.0520	.1248	.0754	.1372	.1037	.1166	.0756
C	.1321	.0821	.1217	.0729	.0932	.1402	.1051	.0918
D	.0908	.0509	.1213	.0657	.0929	.1392	.1047	.0902

Correlation to PCA axes

morphological axis		
I	.7924	.2310
II	-.1123	.1677
III	-.0433	-.0200

environmental axis		
I	.3946	.2725
II	.7307	-.3341
III	.1171	.0872

Phenology

A - phenological variance explained phenological variables
B - phenological variance explained environmental variables
C - environmental variance explained by environmental variables
D - environmental variance explained by phenological variables

Phenology-soils	TB		KIT		WED		DC	
Canonical axes	I	II	I	II	I	II	- I	II
Correlation coefficient	.7322	.5154	.9234	.7426	.8279	.6845	.8973	.7993
Redundancies								
A	.1597	.2063	.1353	.4361	.3708	.3578	.1072	.2059
B	.0856	.0548	.1154	.2405	.2336	.1667	.0863	.1315
C	.0678	.1466	.1869	.1644	.0520	.1042	.0576	.2018
D	.0899	.0390	.1594	.0906	.0356	.0488	.0464	.1289

Phenology - frequency of plant neighbours	TB		KIT		WED		DC	
Canonical axes	I	II	I	II	I	II	I	II
Correlation coefficient	.8032	.7372	.9067	.8529	.9246	.7611	.8914	.8533
Redundancies								
A	.4249	.3057	.5138	.1870	.4619	.1899	.3771	.2599
B	.2741	.1661	.4225	.1360	.3949	.1100	.2996	.1892
C	.1470	.1249	.1280	.0846	.1927	.0920	.0611	.1212
D	.0948	.0679	.1052	.0615	.1648	.2181	.0486	.0883
Correlation to PCA axis								
phenological axis								
I	.8218	.5344	.9555	.0610	.8731	-.2408		
II	-.2846	.6842	-.1676	.7495	.0343	.7338		
III	.4286	-.4466	.0261	-.5647	.4854	.4112		
environmental axis								
I	.7425	-.0902	.5131	.0250	-.7720	.0840		
II	-.1874	.8082	.0371	-.5304	.1928	.2164		
III	.4710	.4863	.1581	.1345	.1482	.6802		

Phenology - presence/ absence of plant neighbours	TB		KIT		WED		DC	
Canonical axes	I	II	I	II	I	II	I	II
Correlation coefficient	.8227	.6983	.9150	.8108	.9083	.8928	.9315	.8837
Redundancies								
A	.2728	.4248	.2677	.4368	.1533	.5198	.1388	.1417
B	.1846	.2071	.2241	.2872	.1264	.4143	.1205	.1106
C	.1513	.1131	.1124	.0853	.1020	.1773	.0818	.1641
D	.1024	.0551	.0941	.0561	.0842	.1413	-.0710	.1281
Correlation to PCA axis								
phenological axis								
I	.5364	.7560	.1095	-.9363				
II	-.4906	.6298	.6490	.3099				
III	.6271	-.0839	.3237	-.1477				
environmental axis								
I	.8281	-.1311	-.2885	.8336				
II	.1215	.6354	-.0245	.1543				
III	-.0517	.4352	.3362	.2228				

Demography

A - demographic variance explained phenological variables
B - demographic variance explained environmental variables
C - environmental variance explained by environmental variables
D - environmental variance explained by demographic variables

Demography - soils		TB		KIT		WED		DC	
Canonical axes		I	II	I	II	I	II	I	II
Correlation coefficient		.8309	.6722	.9912	.9703	.9979	.9841	.9412	.8164
Redundancies	A	.0743	.1100	.0935	.0812	.0968	.0732	.1066	.2731
	B	.0513	.0497	.0919	.0764	.0964	.0709	.0945	.1820
	C	.2217	.2267	.0786	.3359	.0948	.0981	.1169	.0827
	D	.1530	.1024	.0772	.3163	.0944	.0950	.1035	.0551

Demography - frequency of plant neighbours		TB		KIT		WED		DC	
Canonical axes		I	II	I	II	I	II	I	II
Correlation coefficient		.8050	.6747	.9922	.9809	.9733	.9611	.8609	.7381
Redundancies	A	.1026	.0803	.1061	.0885	.0655	.0796	.2784	.1692
	B	.0664	.0366	.1044	.0852	.0621	.0735	.2064	.0922
	C	.1238	.1022	.1386	.0858	.0908	.0886	.1175	.1557
	D	.0803	.0465	.1365	.0826	.0860	.0819	.0871	.0848

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Demography - presence/ absence of plant neighbours	TB		KIT		WED		DC	
Canonical axes	I	II	I	II	I	II	I	II
Correlation coefficient	.8371	.7038	.9995	.9718	.9991	.9799	.8874	.8095
Redundancies								
A	.0896	.0815	.1133	.1164	.0985	.1169	.2252	.1893
B	.0628	.0404	.1132	.1099	.0983	.1123	.1773	.1240
C	.1109	.1074	.1300	.0655	.0802	.1045	.0676	.0732
D	.0777	.0532	.1299	.0619	.0800	.1003	.0532	.0480

Correlation to PCA axis

demographic axis
I -.2530 .2961
II .3311 .2424
III .6960 .2289

environmental axis
I -.0037 -.2249
II .6911 -.1755
III -.2515 -.0837

<u>Morphology - Phenology</u>

A - morphological variance explained morphological variables
B - morphological variance explained phenological variables
C - phenological variance explained by phenological variables
D - phenological variance explained by morphological variables

Morphology - phenology	TB		KIT		WED		DC	
Canonical axes	I	II	I	II	I	II	I	II
Correlation coefficient	.9307	.7803	.9542	.8260	.9738	.8463	-.9620	.8623
Redundancies								
A	.3204	.1432	.1156	.0424	.2551	.0647	.2101	.0641
B	.2776	.0872	.1052	.0289	.2419	.0464	.1944	.0476
C	.5290	.1936	.5065	.1128	.4784	.2000	.6190	.0810
D	.4582	.1179	.4612	.0769	.4536	.1432	.5728	.0602

Correlation to PCA axis

morphological axis
I .7647 .4362 | .1418 -.0561 | .7071 -.1313 | .6104 -.0919
II .2738 -.0786 | -.4546 -.2646 | .1783 .2182 | .2845 -.1627
III .1321 -.0350 | .6749 -.1388 | -.5371 .3786 | -.4476 -.5516

phenological axis
I .9660 .1114 | .9428 .0842 | .9007 -.3961 | .8979 -.2622
II .0238 -.7596 | -.0665 .4895 | .0671 .4883 | -.2285 .1850
III .0279 .4974 | -.3255 .0682 | .0544 .2805 | .3028 -.0602

Morphology-demography

A - morphological variance explained morphological variables
B - morphological variance explained demographic variables
C - demographic variance explained by demographic variables
D - demographic variance explained by morphological variables

Morphology-demography	TB I	TB II	KIT I	KIT II	WED I	WED II	DC I	DC II
Canonical axes	I	II	I	II	I	II	I	II
Correlation coefficient	.9825	.8575	.9999	.9863	.9997	.9994	.9877	.9340
Redundancies A	.1508	.0672	.0835	.1308	.1520	.1069	.1374	.0791
B	.1456	.0494	.0835	.0173	.1519	.1067	.1340	.0690
C	.1991	.0848	.0991	.1260	.1371	.1650	.2897	.1030
D	.1992	.0626	.0991	.1226	.1370	.1648	.2826	.0898
Correlation to PCA axis morphological axis I	.3798	-.2201			.5076	.0134	-.1822	.0467
II	.7712	.1478			.0057	.5531	.6344	.0103
III	-.0557	.2821			.1840	.4581	.0155	.7049
demography axis I	.6945	-.1037			.5790	.7305	-.1548	.2090
II	.6775	.3332			.2872	.2252	.9251	-.1157
III	.0343	-.0985			-.2509	.2110	.1417	.1108

Phenology-demography

A - phenological variance explained phenological variables
B - phenological variance explained demographic variables
C - demographic variance explained by demographic variables
D - demographic variance explained by phenological variables

Phenology-demography	TB I	TB II	KIT I	KIT II	WED I	WED II	DC I	DC II
Canonical axes	I	II	I	II	I	II	I	II
Correlation coefficient	.7147	.6665	.8825	.7804	.8516	.8287	.9551	.7574
Redundancies A	.5280	.1616	.2839	.1933	.3886	.1721	.1033	.2823
B	.2697	.0718	.2211	.1178	.2818	.1182	.0943	.1619
C	.1046	.1240	.0672	.1287	.0763	.1698	.0980	.1198
D	.0534	.0551	.0524	.0784	.0554	.1167	.0894	.0687

Appendix VI. WMDS relationships between morphological, phenological and demographic characters for TB, KIT, WED and DC and soils, frequency and presence/absence of plant neighbour matrices.

TB -morphology-frequency of plant neighbours relationships.

Stress	.195		r-square	.828
Dimension	I		II	III
Importance Weights	.4348		.2016	.1047
morphology	.9101		.0403	.0389
frequency	.2032		.6338	.4559

WED -morphology-frequency of plant neighbours

Stress	.169		r-square	.815
Dimension	I	II	III	IV
Importance Weights	.3228	.2300	.1293	.1330
morphology	.7894	.0868	.1204	.5154
frequency	.1500	.6726	.4940	.0193

TB - phenology-presence/absence of plant neighbours

Stress	.161		r-square	.888
Dimension	I		II	III
Importance Weights	.5146		.2189	.1543
phenology	.9970		.0126	.0073
presence/absence	.1876		.6615	.3555

WED - phenology-presence/absence of plant neighbours

Stress	.150		r-square	.773
Dimension	I		II	III
Importance Weights	.5576		.2331	.0920
phenology	.9963		.0142	.0035
presence/absence	.3502		.6826	.4289

WED - demography-soils

Stress	0.112		r-square	0.958
Dimension	I	II	III	IV
Importance Weights	.4604	.2513	.1994	.0467
demography	.0182	.7086	.6307	.2872
soils	.9594	.0208	.0308	.1042

KIT - demography-frequency of plant neighbours

Stress	.245	r-square	.807
Dimension	I	II	III
Importance	.3228	.8087	0.0
Weights			
morphology	.7959	.0048	.5607
phenology	.1102	.8087	0.0

WED - demography-frequency of plant neighbours

Stress	.179	r-square	.851
Dimension	I	II	III
Importance	.4836	.2488	.1187
Weights			
demography	.9817	.0256	.0277
frequency	.0580	.7044	.4868

KIT - morphology-demography

Stress	.209	r-square	.887
Dimension	I	II	
Importance	.4658	.4217	
Weights			
morphology	.0514	.9182	
demography	.9639	.0169	

WED - morphology-demography

Stress	.136	r-square	.935
Dimension	I	II	– III
Importance	.4810	.3484	.1053
Weights			
morphology	.0736	.8321	.4589
demography	.9781	.0671	0.0