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Observations on the Ecology of _Vaccinium membranaceum_ Dougl. on the Southeast Slope of the Washington Cascades

by

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Master's Thesis

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TABLE OF CONTENTS

LIST OF FIGURES

List of Figures (Continued)

LIST OF TABLES

List of Tables (Continued)

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CHAPTER ONE

Introduction

Vaccinium membranaceum[1] is a recreationally, economically, and ecologically important plant species of the southern Washington Cascades. Recreational values include berry picking and, where present in open fields, association with scenic vistas and diversity of flora and fauna. On some sites the fruit crop of *V. membranaceum* may surpass the timber crop in economic value. Growing on marginal timber producing sites it may yield annual values up to $741 per hectare (Minore 1972a). Additionally, *Vaccinium* species are a valuable food source for wildlife. Bears, grouse and other birds and mammals rely on the berries, while the foliage, high in carotene and energy content, provides browse for deer, elk and mountain goats (Hamilton and Gilbert 1966, Reed 1983, Grier et al. 1981, Viereck and Little 1972). The ecological importance of *V. membranaceum* is suggested by its use (by virtue of species dominance) in the epithet, *Tsuga-Abies/Vaccinium membranaceum* (Franklin 1966), which describes one of the

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[1] For plant species referred to in this thesis, Appendix A contains a list of scientific names, authors and common names after Hitchcock and Cronquist (1973).

most widespread subalpine plant associations of the Cascade Range (Franklin and Dyrness 1973).

Populations of V. membranaceum which have elicited most attention are those existing in large open fields, probably initiated by wildfire and maintained by Indian burning (Franklin and Dyrness 1973, Barrett 1980). Most research has attempted to enhance fruit production on these preexisting fields or document postfire sprouting (Minore et al. 1979, Miller 1977). Unfortunately, the size and productivity of these fields are declining, largely due to increasingly efficient wildfire suppression and subsequent tree encroachment (Minore 1972a).

Although knowledge and interest exist to maintain these fields with prescribed fire, economic and political constraints may preclude operational programs. Thus, it is important that some attention be given the behavior of V. membranaceum beneath a forest canopy. The purpose of the study described in this thesis is to:

1. Identify patterns of variation in V. membranaceum vegetative production and fruit yield in a variety of forest understories.
2. Relate this variation to existing combinations of disturbance history (stand age), floristic composition/structure and certain environmental factors.

CHAPTER TWO

Literature Review

Taxonomy of Vaccinium Species of the Northwest United States

The genus Vaccinium is divided into two subgenera: Cyanococcus, the true blueberries; and Euvaccinium, commonly referred to as bilberries in the eastern United States and huckleberries, whortleberries or blueberries in the west. In the east, huckleberry is the name commonly applied to the genus Gaylussacia.

There are 12 native species of Vaccinium in the northwest which produce blueberry-like fruit (Minore 1972a, Camp 1942, Hitchcock and Cronquist 1973). Camp (1942) organized nine of these into four taxonomic complexes. Because their inflorescences consist of more than one axillary flower, three species were ignored: V. occidentale, V. uliginosum, V. ovatum. None of these three are significant berry producers (Minore 1972a).

The Myrtillae complex includes V. myrtillus and V. scoparium. The former is conspecific with the economically significant Euro-Asiatic V. myrtillus (Ingestad 1973 citing Teär 1972, Camp 1942). Vaccinium myrtillus is more common in the Rocky Mountains while V. scoparium is abundant in the Pacific Northwest as well, often associated with P. contorta. The most widespread complex in North America is the low statured Caespitosae: V. caespitosum and V. deliciosum. Vaccinium caespitosum, with the greatest North American distribution, is relatively uncommon in Oregon and Washington (Camp 1942). On the other hand, V. deliciosum is a characteristic shrub of alpine meadows and open subalpine forest above 1350 m in the Cascade and Olympic Mountains. It produces a popular but bland and poorly textured berry. Camp (1942) refers to the third complex as the highbush huckleberries. The type species of this complex, V. ovalifolium occurs sporadically between 600 and 1200 m throughout the Pacific Northwest. A morphologically similar species, not found east of the Cascades, is V. alaskaense. The latter generally occupies more mesic lowland sites than V. ovalifolium, Vaccinium parvifolium is a well-differentiated species confined to lowlands, valleys and foothills west of the Cascade Crest. Two additional high bushlike species comprise the fourth, Vaccinium membranaceum-globulare, complex: V. globulare and V. membranaceum. Camp (1942) suggests that V. membranaceum, as a hexaploid derivative of V. globulare and V. myrtillus is genetically isolated. This heteroploidy was implied on Mount Rainier where adjacent clones of V. membranaceum, V. deliciosum and V. scoparium had failed to hybridize (Camp 1942). The same evidence of isolation was apparent on my own study site.

Considering the three species' alleged historical relationship, their distributional patterns are curious. *Vaccinium myrtillus* and *V. globulare* are generally associated with the Rocky Mountains, *V. membranaceum* with the Pacific Northwest. However, ambiguities and contradictions exist. According to Camp (1942), the ranges of *V. globulare* and *V. membranaceum* overlap in the northern Rocky Mountains and central British Columbia where the two species are virtually indistinguishable. During an extensive vegetation classification project in western Montana, Pfister et al. (1977) identified specimens from the *V. membranaceum-globulare* complex as *V. globulare*. Stark (1980) however, reports the occurrence of *V. membranaceum* in the same region. Franklin and Dyrness (1973) report *V. membranaceum* in the Blue Mountains of Oregon and Washington and the *Tsuga heterophylla* and *Abies lasiocarpa* forests of eastern Washington and northern Idaho. Camp (1942) acknowledges the appearance of *V. globulare* in the Cascades no further south than Chelan County, Washington yet Minore (1972) and Minore and Dubrasich (1978) cite its occurrence near Mount Adams, Washington. Hitchcock and Cronquist (1973) abbreviate the northwest range of *V. globulare* as "e Wn and Ore through Ida to Mont and Wyo" and Franklin and Dyrness (1973) do not cite its occurrence in the Cascades of Oregon and Washington. During extensive reconnaissance I found no specimens of *V. globulare* in

Yakima County, Washington. If it does occur in the Cascades, its distribution must be limited and insular. This is surprising considering the habitat and floristic similarities of the eastern Cascades and northern Rockies (Douglas and Bliss 1977, Franklin 1966). In any case, V. membranaceum is the most ubiquitous Vaccinium species of Pacific Northwest subalpine forests.

Subalpine Closed-Forest Zones of the Pacific Northwest

Although V. membranaceum is often associated with A. lasiocarpa, P. menziesii, and P. engelmannii, it achieves greatest importance in more mesic subalpine communities of A. amabilis and T. mertensiana (Del Moral and Watson 1978, Arno and Habeck 1972, Fonda and Bliss 1969, Brooke et al. 1970, Franklin and Dyrness 1973). Franklin and Dyrness (1973) subdivide the high elevation closed forests of the Cascades into two zones defined by and named after their characteristic climatic climax tree species. Near Mount Rainier, the Abies amabilis Zone has its lower boundary at about 900 m, abutting the montane Tsuga heterophylla Zone. In the same region its upper elevational limit is at about 1300 m where it meets the subalpine Tsuga mertensiana Zone which in turn extends to about 1850 m. Where these two zones occur on drier and warmer sites, e.g. east of the Cascade Crest, they can be expected to occur at compensatingly higher elevations (Franklin and Dyrness

1973). According to Packee et al. (1981), A. amabilis does not occur below the subalpine zone east of the Cascade Crest.

The combined presence of T. mertensiana and A. amabilis in some communities makes it difficult to force them into one zone or the other. Franklin and Dyrness (1973) consider any community with a component of T. mertensiana as a member of the Tsuga mertensiana Zone, regardless of that species' seral or climax role. Because A. amabilis is the major climax dominant where the two species occur together, Douglas (personal communication cited by Franklin and Dyrness 1973) considers such closed subalpine T. mertensiana forests as components of the Abies amabilis Zone. Zobel et al. (1976) used direct environmental gradient analysis to evaluate several A. amabilis stands in the central Oregon Cascades and found that temperature and vegetation were well correlated. However, the temperature and moisture conditions of the highest elevation stand, floristically included in the Tsuga mertensiana Zone, were not significantly different from lower elevation pure A. amabilis stands. Based on these results they included their Abies amabilis-Tsuga mertensiana/Xerophyllum tenax stand in the Abies amabilis Zone. This study will follow their definition of the Abies amabilis Zone as that zone where the preponderance of regeneration is A. amabilis.

The *Abies amabilis* Zone, characterized by relatively cool temperatures with little seasonal variation, receives abundant moisture from rain, fog, or snow (Packee et al. 1981). The deep and lingering snowpack at higher elevations moderates the soil moisture regime and shortens the growing season relative to lower elevation communities, even though soil temperature increase is dramatic after snowmelt (Zobel et al. 1976). Zobel et al. (1976) found that vegetation zones in the western Oregon Cascades are differentiated by temperature regime and, within the *Abies amabilis* Zone, moisture stress is insignificant during the growing season. However, there was a significant decrease in temperature from a *Tsuga heterophylla-Abies amabilis*/*Linnaea borealis* community to adjacent pure *A. amabilis* communities. On the east slopes of the Cascades, as temperature decreases, *A. amabilis* is replaced by *T. mertensiana* which in turn gives way to *A. lasiocarpa* under conditions of increasing plant moisture stress.

Leaf area accumulations of *A. amabilis* forests are among the largest of all coniferous forests, indicating they have the potential for considerable production (Waring et al. 1978). However, climatic conditions result in generally low productivity and total live biomass for *A. amabilis* forests relative to montane coniferous forests (Grier and Running 1977). In addition, their biomass accumulation is retarded. Grier et al. (1981) report that it may take as long as 180 years for the canopy of an *A. amabilis* community to reach biomass equilibrium.

In particular, communities characterized by *Vaccinium* species are not remarkably productive. Of seven commercial forest communities in the *Abies amabilis* Zone of the southwest Washington Cascades, stands with an understory dominated by *Vaccinium* are among the least productive (Emmingham and Halverson 1981). In the Blue Mountains of Oregon, Hall (1973) defined an *Abies grandis*/*Vaccinium membranaceum* community with a site index of only 50. The characteristic occurrence of *Vaccinium* species on less productive sites is apparent in the Scandia-Fenno countries as well, where a *V. myrtillus* site type indicates intermediate fertility in Cajander's understory site-typing scheme (Kellomäki 1977).

Vaccinium species have been identified as understory dominants in several Pacific Northwest forest communities (Table 2.1). The *Tsuga mertensiana-Abies amabilis*/*Vaccinium membranaceum* community is a most widespread community of the *Abies amabilis* Zone from British Columbia to central Oregon (Franklin and Dyrness 1973). In the Cascade Range, *V. membranaceum* frequently occurs on dry subalpine sites where it is often associated with *X. tenax* (Franklin 1966, Minore and Smart 1975, Grier et al 1981, Vogt et al 1983). However, *V. membranaceum* is not confined to such xeric habitats. Among five southern Washington Cascade plant

TABLE 2.1

Pacific Northwest plant communities in which *V. membranaceum* has been identified as an understory dominant.

Community	Location	Author
A. amabilis - T. mertensiana/V. membranaceum	Northern Oregon Cascades Southern Washington Cascades	Franklin 1966
A. amabilis - T. heterophylla/V. membranaceum	Southern Washington Cascades	Franklin 1966
A. grandis/V. membranaceum	Northern Idaho Rocky Mountains	Daubenmire & Daubenmire 1968
	Northwest Oregon Blue Mountains	Hall 1967
T. heterophylla/V. membranaceum - X.tenax	Northern Oregon Coast Range	Hines 1971
T. mertensiana/V. membranaceum	Southern British Columbia Cascades	Brooke et al. 1970
	Central Washington Cascades	Del Moral & Watson 1978
P. engelmannii/V. membranaceum	Central Washington Cascades	Del Moral & Watson 1978
A. amabilis/V. membranaceum	Central Washington Cascades	Del Moral & Watson 1978
P. menziesii/V. membranaceum	Central Washington Cascades	Del Moral & Watson 1978
P. menziesii/V. membranaceum - R. lasiococcus	Central Washington Cascades	Del Moral & Watson 1978
A. amabilis/V. membranaceum - V. ovalifolium	Western Washington Cascades	Del Moral & Long 1976
V. membranaceum - R. albiflorum	Northern Washington Cascades	Douglas 1972
V. membranaceum - X. tenax	Southern Washington Cascades	Franklin 1966

associations arrayed along a moisture gradient, *V. membranaceum* maintained similar frequency and cover values for all but the wettest habitat (Franklin 1965). Similar behavior was noted by Hines (1971) in northwest Oregon and Minore (1972b) in the South Umpqua River Basin of Oregon. *V. membranaceum* achieves its best development on cool, moderately moist sites intermediate between those typified by its occasional associates, *R. albiflorum* on cold-wet sites and *X. tenax* on cold-dry sites.

Vaccinium membranaceum often occurs in open parklike *T. mertensiana* forests of the subalpine zone. These communities are characterized by scattered tree clumps surrounded by *V. membranaceum* with *V. deliciosum* dominating elsewhere (Brooke et al. 1970, Douglas 1972). Minore and Smart (1978) have reported that *V. deliciosum* is more frost tolerant than *V. membranaceum*. Where these meadowlike communities are not fire initiated, *V. membranaceum* will remain confined to the shelter of tree clumps. The increase in clonal height approaching the shelter of these clumps also suggests that such habitats are not climatically optimum. Including *V. membranaceum* in the epithet for these communities is misleading. Because *V. deliciosum* is more suited to these environments it should be cited as the understory dominant.

V. Membranaceum-Fire Succession Interactions

Fire and Early Succession

According to Yakima Indian legend, the Great Spirit provided each tribe with its own huckleberry field, a reliable late-season food source (Tony Washines 1981, personal communication). An alternative explanation for the occurrence of widespread V. membranaceum fields of the southern Washington Cascades is large and repeated wildfire (Franklin and Dyrness 1973), similar to those documented for the extensive brushfields of northern Idaho (Orme and Leege 1974).

Many species present in the prefire community are represented in postfire seres (Franklin and Dyrness 1973, Reed 1983). For three wildfires, all burning to mineral soil, Lyon and Stickney (1974) observed that about 80% of the first-growing-season community was derived from the prefire community and these same species were dominant in the same proportion after five years. The most effective mechanism for this dominance was sprouting from below ground organs. In fact, the appearance of V. membranaceum as a seedling is rare and not significant in recolonization (Miller 1977, citing personal communication from Stickney). Even though prefire species do not always dominate immediately, they may reassert dominance after a period of dominance by invading species. Dyrness (1973) reports that two to four years after a slash fire, invading herbs were dominant but after five years, prefire species were restored to dominance.

Dominance of early seres by V. membranaceum is not assured. Many investigators indicate that one of several different and unpredictable communities each with different rates of development, leading to the same or in some cases different potential climax forests, may occur on the same area (Franklin and Hemstrom 1981, Oliver 1981). According to Franklin and Hemstrom (1981), fire frequency and, especially fire intensity have the greatest influence on post fire communities. Dyrness (1973) found that, in general, herbaceous invasion was more characteristic of severely burned areas.

In addition to factors such as season of burning, with its effect on forest floor and debris moisture contents, the intensity of wildfire is a function of stand successional status. The general trend is for Vaccinium rhizomes to concentrate in the organic forest floor (Miller 1977, Smith 1962). This is particularly significant in mature A. amabilis forests where the concentration of fine and mycorrhizal roots in the forest floor cause their marked sensitivity to fire (Vogt and Grier 1981).

Site factors also influence the establishment of V. membranaceum in early seres. Minore (1972a) indicates that clear cut logging, which leaves the understory intact, does not consistently initiate a productive berry field. He cites postharvest water relations, as well as preharvest floristics, as influential conditions. An obvious effect of site is apparent in the response of the seral brushfields originating from the 1910-1920 fire episodes in northern Idaho. Although *V. membranaceum* is present in these brushfields (*Thuja plicata*/*Pachistima myrsinites* and *Abies grandis*/*Pachistima myrsinites* associations (Daubenmire and Daubenmire 1968)) they are dominated by *C. sanguineus* and shrubs other than *Vaccinium* (Orme and Leege 1974). Rowe (1983) reports that tolerant sprouting species, such as *Vaccinium*, dominate sites ranked third most mesic on a scale of four. Increasing sensitivity to microsite is demonstrated by herbs, then shrubs, then trees (Cattelino et al. 1979). If conditions are appropriate, the shrub stage of succession may be bypassed as herbs assert dominance until their subordination to trees (Dyrness 1973). On the other hand, Alaback (1982) reports that in a *P. sitchensis*/*T. heterophylla* forest of southeast Alaska, *Vaccinium* was the dominant post disturbance genus. In any case, the influence of site is obscure. In a study of a variety of huckleberry communities Minore and Dubrasich (1978) found no correlation between *V. membranaceum* abundance or fruit production and *P. menziesii* site index.

Fire integrates climate, previous stand structure and composition, recolonization pattern and site to create the potential for a productive *V. membranaceum* community. Only the potential exists. These factors must all interact to allow the appearance of a V. membranaceum sere.

In spite of the stochastic processes affecting postfire community composition, environmental factors ultimately determine the success or failure of individual plants and species, thus successional composition and structure. Fruit production by a dominant V. membranaceum stand is more strongly influenced by random weather anomalies such as freezing, hail and drought (Minore and Dubrasich 1978, Nelson 1974) than is vegetative production. Although Minore and Dubrasich assign greater significance to these more dramatic events, suitable quantities of light, heat and precipitation, and their timing are probably more influential in the long term and should not be overlooked.

When water and nutrients are adequate, light and temperature determine a plant's photosynthetic rate (Väisänen et al. 1977) and thus its carbon assimilation rate and competitive and successional fortunes (Kellomäki et al. 1977). Light is the factor most influencing cultivated (Hall 1958) Vaccinium production and most likely wild production as well. Väisänen et al. (1977) found that photosynthetic rates of V. myrtillus and V. vitis-idaea showed a strong linear increase with light and temperature increasing from zero.

Many investigators report that early season temperature regime significantly affects phenologic development of most plants, especially at high elevation (Douglas and Bliss 1977, Fowler and Tiedmann 1980). Even though floral buds are initiated on the current season's shoot, growing conditions of the previous season are influential. Abundant carbohydrate stored in roots will provide a head start for growth the next season. Fowler and Tiedemann (1980) monitored the effect of temperature regime on S. betulifolia in the east Cascades of Washington. Although retarded growing degree accumulation delayed phenological development by three to four weeks, its effect on flowering was more profound. During a season of reduced temperature, relative to the previous season when all plants developed seed, all plants showed sparse or absent bloom and none set seed. While total growing degree accumulation is important their distribution must be significant (Fowler and Tiedemann 1980).

In early succession, light and temperature are abundant and carbon assimilation and allocation of resources to reproductive structures are probably limited by other factors. Emmingham and Halverson (1981) report predawn plant moisture stresses, the rough equivalent of soil matric potential, as negative as minus seven bars on recent Abies amabilis Zone clear cuts. Although permanent wilting probably doesn't occur above -10 to -20 bars (Fitter and Hay 1981), V. membranaceum fruit production may be significantly reduced at values more negative than minus seven bars. Investigations by Minore (1975b) reveal that V. membranaceum may prospect for water into the lower A horizons. Although he found no taproots, sinker roots occurred to 100 cm beneath the soil surface.

Although Zobel et al. (1976) cite several studies indicating that soil chemistry has a secondary effect in determining vegetation patterns, it is probably more significant in postfire conditions where light is not limiting (Väisänen et al. 1977). However, early-seral communities have more available nutrients with turnover rates twice those of mature *A. amabilis* forests (Vogt et al. 1983). Nutrients may or may not be especially important for fruit production. Silvertown (1982) monitored the reproductive allocation (RA = annual assimilated resources allocated to reproduction/annual total assimilated resources) of plants subjected to a range of simulated competitive conditions. An observed decline in RA by *Chamaesyce hirta* (sic, valid scientific name *Euphorbia serpyllifolia* Pers. var. *hirtula* (Engelm), Munz and Keck 1965) was reversed by the addition of nutrients. Conversely, *S. vulgaris* maintained an RA of about 21% without added nutrients, although plant weight varied by a factor of seven. In any case, highbush-cultivated *Vaccinium* spp. require lower levels of most nutrients than many other fruit producers (Bailey et al. 1949). The relative infertility of established berry-producing fields (Minore et al. 1979) suggests that site nutrient status may not limit fruit production by V. membranaceum.

Over 40% of a mature A. amabilis forest's net primary productivity goes to the development of fine and mycorrhizal roots (Grier et al. 1981); most commonly, the ectomycorrhizae formed between conifer roots and the basidiomycete Cenococcum graniforme Fr. (Vogt et al. 1981). Ericaceous plants are typically mycorrhizal (Pearson and Read 1983). Specifically, Largent et al. (1980) report the occurrence of an ericoid mycorrhizal association for V. membranaceum. Ericaceous mycorrhizae are characterized by septate hyphae and intracellular penetration with ultimate digestion of the host cell by the fungal symbiont. Reports of the physiological processes of ericaceous mycorrhizae and Vaccinium spp. are rare. Digestion of the host cell by the endophyte may imply a different process than that of the ectomycorrhizae, common among gymnosperms, that provide enhanced nutrient uptake, drought tolerance and protection against pathogens for the host and carbon metabolites for the ectophyte (Marks and Kozlowski 1973). Regardless of the specific process, Pearson and Read (1973) have demonstrated for V. oxycoccos, in vitro, that phosphorous nutrient and carbon compounds are translocated to the host and fungal symbiont, respectively. Stribley and Read (1976) report that uptake of ammonium nitrogen by V. macrocarpon is enhanced when other nutrients are adequate and that intensity of mycorrhizal infection decreases with increasing ammonium nitrogen. Interestingly, intensity of infection was reduced at low, about one ppm, substrate nitrogen levels as well. They conclude that under such conditions the drain of fixed carbon by the endophyte offsets its nitrogen contribution. Under mature forest conditions the mycorrhizal associations formed by V. membranaceum are probably significant. However, their relationship to production throughout succession is unknown and their effect is probably less significant for young communities.

Although podzolization is still active, an Alh horizon develops above the eluvial A2 within a few year after disturbance (Grier et al. 1981, Ugolini 1981). Minore and Dubrasich (1978) found that soil pH was more strongly correlated with V. membranaceum percent cover than several other environmental variables. However, Nelson (1974) observed shoot and root growth response of V. membranaceum to pH levels ranging from 4.0 to 6.0 and found no significant difference in growth or nutrient uptake. Foliar nutrient levels were similar for all treatments. Fire induced changes in pH probably have an insignificant effect on fruit production.

Arresting Succession to Sustain Fruit Production

Anthropologists have documented Indian caused fire throughout much of North America (Lewis 1977). Its ecologic effect in huckleberry fields of the southern Washington

Cascades was probably determined by harvest patterns. Low elevation-early maturing plants were utilized first with use progressing to plants of higher elevation as they matured (Eugene Hunn 1980, personal communication). The most likely time of Indian burning then, was late September after the berry crop had been harvested. Regardless of the time of ignition or its purposefulness, such fires would have had the effect of arresting succession in favor of V. membranaceum.

Fire exclusion by European-Americans has allowed invasion of these fields by trees and a decline in V. membranaceum productivity (Minore 1972). To maintain their productivity, cultural practices appropriate to domestic Vaccinium species have been modified and applied by Minore and others (Minore et al. 1979). The only treatment associated with a significant increase in fruit production within three growing seasons was elimination of tree competition by application of a silvicide. It should be noted that only this treatment left V. membranaceum stems intact; new seedlings produce neither rhizomes or flowers until their third growing season (Minore et al. 1979). Although borax treatments selectively weed in favor of cultivated V. angustifolium (Smith et al. 1947) its effect here was a one season depression of V. membranaceum cover and fruit production with no significant effect on competition. Test applications of several herbicides--

Casaron, Simazine, Atrazine, and Paraquat--all failed to selectively control competing vegetation (Minore et al. 1979, citing personal communication from Crandall). Cultivated stands of V. corymbosum are regularly pruned to promote fruit production (Brightwell and Johnston 1944). Hypothesizing that grazing would yield benefits of both pruning and weeding, Minore allowed heavy sheep use of a test plot for three days during mid-August. Because of increased fruit production during the third growing season after treatment he concluded that sheep use reduces tree encroachment, adds significant nitrogen, and increases yield. Unfortunately, among-treatment comparisons were not made and the relative significance of the third season production increase on the control plot was not evaluated. In any case, sustained overgrazing could seriously reduce long term production. Although recovery to pretreatment levels had occurred by the end of the second growing season, V. membranaceum cover was reduced by 50% the first growing season after treatment. In a separate study, plant damage was sustained by pruning to top removal levels of 50% and 80% (Minore et al. 1979, personal communication from Crandall). Although browsing by wildlife is common its magnitude probably does not approach the level of either of these studies (Grier et al. 1981, Reed 1983, Viereck and Little 1972).

Fertilization is a common cultural treatment of commercial Vaccinium fields with yield increases up to 50% reported after addition of ammonium nitrate (Mincre 1972a, Townsend 1966). However, Ingestad (1973) reports that adding effective levels of nitrogen to V. myrtillus and V. vitis-idaea stands may cause excessive soil salt concentration. Nelson (1974) applied three levels--10, 40 and 160 pounds per acre--of ammonium sulfate to an established V. membranaceum field in the southern Washington Cascades. Vegetative responses the following season were greatest, but not significantly different, for the 40 and 160 pound per acre application rates. Foliar nutrient levels were similar for all treatments indicating that increased growth associated with the nitrogen applications was supported by adequate soil levels of other nutrients. Plants grown in native soil under greenhouse conditions demonstrated significantly more growth with 160 than 40 pound per acre equivalencies suggesting that when nitrogen exceeds a threshold level some other growth factor becomes limiting. Nelson (1974) found that growth was strongly inhibited when potassium was elevated, relative to nitrogen, in aquaculture solution. He suggested that V. membranaceum can absorb potassium indiscriminately, resulting in an internal imbalance. For V. angustifolium, increased stem growth was promoted by nitrogen application prior to shoot emergence while application after dieback caused an increase in floral bud density the following year (Trevett 1965). Season of burning, and associated nutrient release, may similarly affect *V. membranaceum* growth.

Cultivated *V. angustifolium* is burned at about 3 year intervals (Chandler and Mason 1943), and the use of prescribed fire in *V. membranaceum* fields of the Cascade Range could similarly incorporate the preceding cultural practices into one operation. Vigorous new growth would replace decadent aerial stems, the preexisting root system would provide a substantial headstart over competitors and a more favorable nutrient regime would result from release of nutrients and increased nitrification. Sprouting is more prolific when stems are killed to below ground level: this stimulates rhizome buds rather than above ground adventitious buds (Miller 1977). Miller (1977) monitored the sprouting response of *V. globulare* to spring and fall understory burning in a western Montana *Pseudotsuga menziesii*/*Larix occidentalis* community. Spring burns were all followed by significant increases in *V. globulare* cover and frequency while 10 of 11 fall burned areas had not recovered to preburn levels by the end of the first growing season after treatment. The unfavorable response to fall burning was apparently a result of heat penetration to mineral soil horizons rather than reduced root carbohydrate levels and physiologic inability to sustain new shoots (Miller 1978). The amount of forest floor debris, and its moisture content, and the moisture content of the upper soil horizons were most strongly correlated with soil heat flux and associated rhizome mortality. Miller concluded that unfavorable sprouting responses are generally inevitable from fall burns. Minore et al. (1979) followed mechanical overstory removal with fire to improve the fruit yield of two V. membranaceum stands experiencing significant tree invasion in the central Cascades. Because V. membranaceum cover and fruit production had not recovered to pretreatment levels by the third and fifth posttreatment growing seasons, respectively, Minore discounts the short term benefits of fire as a tool for V. membranaceum culture. However, he did not measure fire behavior variables objectively and bases his conclusion on what were, in effect fall burns. The response of V. membranaceum to well documented spring and fall burns should be determined.

Cultural practices under nonagricultural conditions are often expected to produce yields as predictably high as those of intensive cultivation. There is no evidence that huckleberry fields used and, allegedly, managed by Indians produced uniformly high yields. In fact, ignition was probably random and resulted in patchy and irregular annual yields, a condition still apparent at the Potato Hill field on the Yakima Indian Reservation (Personal observation). Fluctuations in yield over space and time, due to scarcity of pollinators, weather anomalies, stem decadence, burning pattern, above and below ground competition and other factors, were probably bemoaned in prehistoric times just as they are now.

Late Succession

The magnitude, timing and ecological conditions associated with the successional decline of V. membranaceum productivity are not well understood. The timing of shrub dominance and decline varies among seres and among species, the latter as a function of their relative dominance within a stand (Lyon and Stickney 1974, Oliver 1981, Long 1977). Coverage of the two most dominant shrubs in a chronosequence of 5, 22, 30, 42, and 73 year old Pseudotsuga menziesii /Gaultheria shallon stands was highest in the 22 year old stand and significantly lower in the 30 year old stand. Franklin and Hemstrom (1981) have identified seral cohorts in the western Cascades with a 100 year recruitment period and, citing large and/or repeated wildfire, suggest that reforestation and canopy closure may take more than 40 years. Although floristic composition and rate of change vary among seres, general structural trends are predictable and in the Abies amabilis Zone V. membranaceum will be maintained after canopy closure and into old growth stages (Mueller-Dombois 1965, Franklin and Dyrness 1973, Thornburgh 1969, Long 1976).

The profound influence of the dominant tree canopy is summarized by Horn (1971):

> The most dramatic environmental change from field to forest is the decrease in light intensity near the ground. Light is cut off by progressively more plants of greater height, and only a tiny fraction of the intercepted light is converted to stored energy; the rest must ultimately be dissipated as heat. Thus the distribution of heat varies as succession proceeds. The distributions of heat and of leaves affect evaporation and water balance. Water balance, in turn, affects the supply of nutrients from the soil.

The continued presence of V. membranaceum depends on its ability to photosynthetically fix sufficient carbon to maintain at least vegetative presence in the reduced light conditions imposed by the tree canopy. In general, leaves require at least two percent of full sunlight in order for photosynthesis to balance respiration, and growth rate of several deciduous trees declines dramatically when incident light is less than about 35% of full sunlight (Horn 1971). There is evidence that some Vaccinium species are shade plants, although production may vary among species throughout succession. A model comparing V. vitis-idaea and V. myrtillus predicted greater production by the former for the first 20 years of secondary succession with the latter dominating the next 50 years (Kellomäki et al. 1977). After 70 years their production was nearly identical and less than 5 grams per square meter. They concluded that these Vaccinium species are adapted to low light intensities and therefore able to outcompete other understory species in such conditions. Väisänen et al. (1977) found that productivity of V. vitis-idaea and V. myrtillus peaked when actual photosynthesis was significantly less than potential photosynthesis for those species. Specific light saturation and compensation values for V. membranaceum are not known and, while it may be a facultative shade plant beneath a canopy, its response to open conditions is opportunistic. Although dense shade is detrimental to V. membranaceum, e.g. retarding growing degree accumulation and fruit production, a partial overstory may ameliorate a site that is otherwise too harsh and provide protection against random weather perturbations (Minore et al. 1979).

The shading effect of an overstory, although significant, should not be overrated. Relationships and responses often interpreted as the result of suppression by shading may be the result of unequal competition for soil moisture . Competition for water and nutrients becomes especially intense in the forest floor of maturing A. amabilis forests because of increasing populations of fine and mycorrhizal roots and decomposers (Grier et al. 1981). On the other hand, that Smith (1962) found greater shoot/rhizome ratios in shaded, rather than exposed, environments may indicate that in some environments below ground resources are adequate to support increased leaf surfaces in response to reduced light.

Mature A. amabilis forests are characterized by reduced nutrient availability resulting from their concentration in live and slowly decomposing dead biomass (Grier et al 1981, Vogt et al. 1983). In addition to moisture retention and temperature implications, these detritus accumulations have an effect on mineral nutrition. Many authors report nitrogen mineralization rates in *A. amabilis* forests considerably lower than other, lower elevation, forests (Gessel and Klock 1981, Powers 1978). The forest floor nutrient dynamics of young and mature *A. amabilis* communities were compared by Vogt et al. (1983). They determined that, relative to young forest, the mature stand had one-half the annual organic matter turnover rate and double and treble the forest floor potassium concentration and residence time, respectively. Moreover, their report that foliar potassium in mature-community *V. membranaceum* was nearly twice that of the young stand suggests that the growth inhibiting influence of an internal potassium-nitrogen imbalance (Identified by Nelson 1974) may be a significant factor reducing its fruit and vegetative production in mature *A. amabilis* forests.

The reproductive and survival strategies of *V. membranaceum* are probably a direct response to the *Abies amabilis* Zone fire regime (Rowe 1983). Its clonal habit allows it to persist during unfavorable competitive conditions (Silvertown 1982). However, the presence of *V. membranaceum* may not require the competitive conditions reimposed by fire. Populations of *V. myrtillus* in Sweden have age structures which indicate regular rather than the annually variable recruitment typical of many fire-prone ecosystems (Silvertown 1982). Although dendrochronologic aging of clonal populations is difficult, Vasek (1980) calculated that one clone of Larrea spp. in the Mojave Desert may be 11,700 years old. In spite of the conclusions of Minore et al. (1979), the profoundly clonal habit of V. membranaceum suggests its ability to sprout from rhizomes after fire. While clonal growth may ensure the local survival of V. membranaceum, its appearance on severely disturbed sites and its genetic integrity depend on seedling establishment. Although large buried seed populations are common in nearly all terrestrial ecosystems (Silvertown 1982) the existence and viability of buried V. membranaceum seed is unknown. Its fleshy fruit, containing small seeds, indicates that its primary utility is colonization of new and severely disturbed sites.

The behavior of V. membranaceum also reflects its geographic distribution and the existence of ecotypes. Smith (1962) found naturally occurring Vaccinium species in Alberta predominating under low to moderate overstory conditions rather than the exposed habitats they typically occupy in New Brunswick. Evidently shade mitigates the effects of elevation, intense radiation, and relatively low precipitation of Alberta, creating the microclimatic equivalent of maritime New Brunswick. The wide ecologic amplitude and geographic range of V. membranaceum reported by Minore (1972a) make it a prime candidate for ecotypic variation (Daubenmire 1947, Rowe 1983). Even the alleged Indian burning of huckleberry fields may have allowed the competitive differentiation of clones favored by such treatment (Daubenmire 1947). The clonal habit of *Vaccinium* favors the process of natural selection through prolonged competition among clones and the perpetuation of those most adapted to local conditions. This process would logically result in genetic differences among clones occupying different microenvironments within the same habitat (Silvertown 1982). Although not as tenuous as interspecific comparisons, these processes advise caution when making intraspecific comparisons or extending results from my study area to general sites.

On certain sites, particularly less productive habitats of mesic subalpine forests, *V. membranaceum* can dominate the early stages of succession when appropriate combinations of prefire stand structure and composition and fire intensity and frequency occur. This fortuitous period of floristic dominance and high fruit production depends primarily on appropriate light, temperature and, to a lesser extent, soil conditions. The influence of water relations is indeterminate. Site conditions which favor appearance of a *V. membranaceum* sere may be inferred from cultural manipulations of preexisting fields. However, few studies of the species' behavior over a range of sites have been conducted and the variety of habitats capable of supporting productive populations have not been identified or evaluated. Without the repeated occurrence of fire or some external perturbation, the decline of V. membranaceum through crown closure and late succession is inevitable. Although the species' clonal habit allows its effective dormancy through these unfavorable conditions, continued sexual reproduction has obvious survival and evolutionary benefits. Although fruit and vegetative production declines as above and below ground competition restricts available growth factors, the timing of this decline and its magnitude, relative to the declining availability of growth factors, are not known.

CHAPTER THREE

Study Site

The study was conducted on Round Mountain, near White Pass on the eastern slopes of the Washington Cascade Range. Round Mountain is the eastern terminus of a more or less continuous ridge extending laterally about 4 km from the Cascades Crest, Figure 3.1. Its summit, at 1820 m, is bounded on the north by Clear Creek and on the south by the North Fork of the Tieton River. Elevation of these two river bottoms is about 975 m. The study area consists of about 250 ha on the north and east slopes of Round Mountain in an elevation band from 1400 to 1700 m.

Pleistocene glacial activity was widespread, but occurred as small, local alpine glaciers (Franklin and Dyrness 1973); therefore, landforms generally reflect erosional processes. Extreme topography over much of the area and volcanic ejecta cause considerable mixing of parent materials and may prevent development of mature soil profiles.

The Western Cascades Geologic Unit described by Franklin (1965) includes Round Mountain. Here, soil parent materials consist of colluvial and residual Pleistocene igneous extrusives as well as volcanic ash from that and the Holocene eras (Franklin 1965). Bedrock for the study area is Hogback Mountain Olivine Basalt venting from Hogback

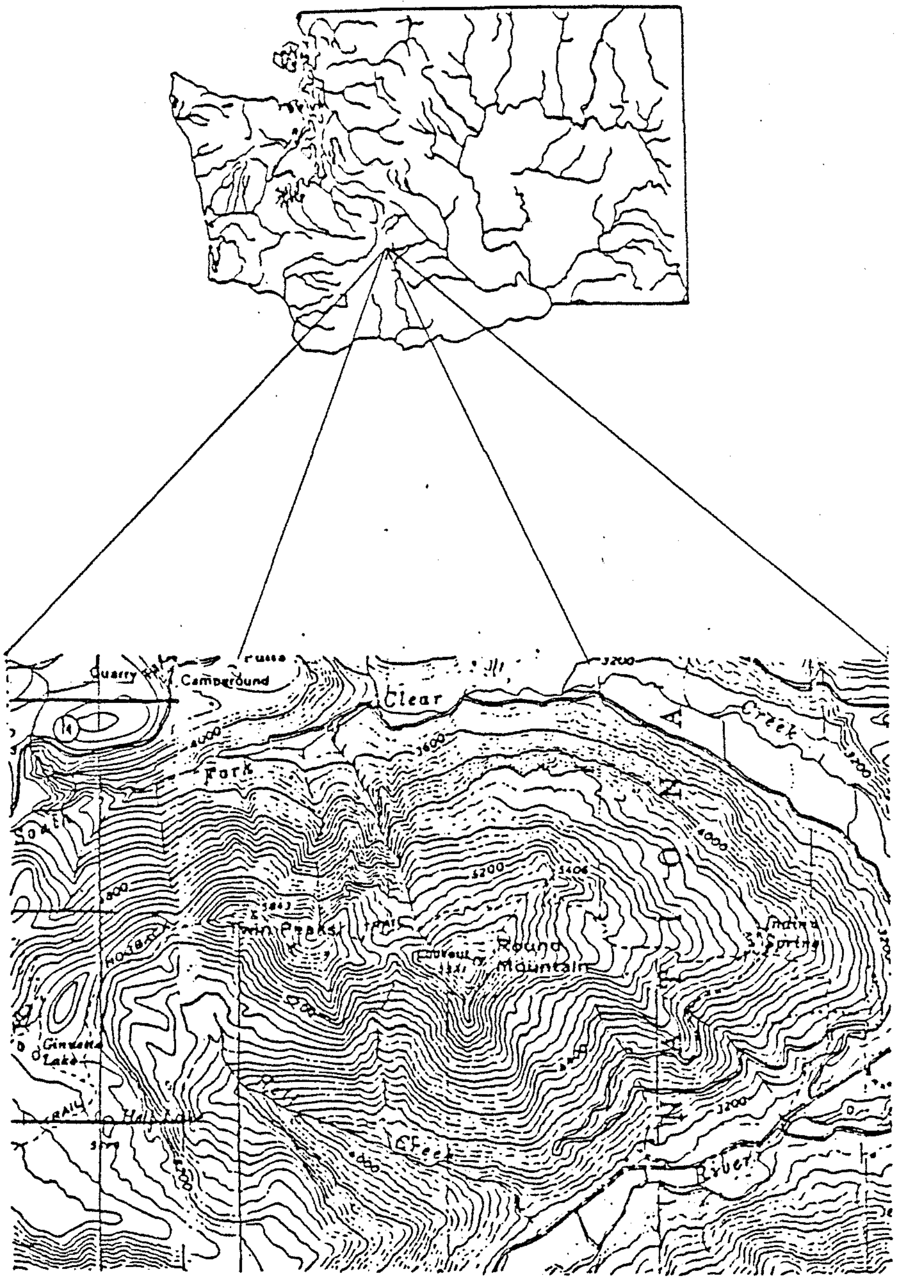


Figure 3.1. Topographic map and geographic location of the study area within the state of Washington. Approximate map scale 1 cm = 3.4 k, contour interval 24.4 m.

Mountain in the Goat Rocks Wilderness. Lower elevation northeast portions of Round Mountain are underlain by Spiral Butte Andesite (Ellingson 1972). The entire area is overlain by volcanic ash originating from Mt. Mazama and Mt. St. Helens (Crandall et al. 1962). The most recent deposition, between 1 and 2 cm, was from the 1980 eruption of Mt. St. Helens.

Spodosols (1967 Soil Classification System) are the predominant soil great group of subalpine elevations in the Round Mountain study area. Franklin (1965) reports greatest development of podzolic A2 and B2ir horizons in midelevation *A. amabilis* forests rather than higher elevations where *T. mertensiana* is present. Cryorthods (podzols according to the 1938 Soil Classification System) develop on the western portions of the study area while reduced precipitation and increased temperatures in the eastern portions limit podzolization to the development of haplorthods (brown podzols according to the 1938 Soil Classification System). Haplorthods are also typical of seral *Abies amabilis* Zone communities east of the Cascade Crest (Franklin 1966). Such communities are common on Round Mountain. Study area soils are typically coarse and well drained, largely due to the presence of coarse volcanic ash. The 1980 ash deposition has not been incorporated into forest floor organic layers and exists as a discrete layer between the preeruption duff layer and subsequent litterfall. The wide range of disturbance history and climate on Round Mountain suggests a variety of local soils.

The climate of Round Mountain is neither maritime or continental. Table 3.1 presents a summary of climatic data for Bumping Lake, representative of the east-of-crest study area, and Stampede Pass, representative of a more strongly maritime Abies amabilis community. Study area summers are warm, although temperatures rarely exceed 20° C, and their characteristic drought is mitigated by the occasional presence of a cloud bank extending from west of the Cascade Crest. Summer showers are frequent but account for less than 15% of about 115 to 140 cm of annual precipitation. A winter snowpack of about 2-3 m develops in late October or early November and persists until mid-June at higher elevations on north slopes. Steep elevation and maritime/continental gradients across the study area are reflected in the plant communities.

The strength of maritime climatic influences is apparent in the major climax species, A. amabilis, as well as seral T. heterophylla and T. mertensiana. Several other seral species are more typical of interior environments; A. lasiocarpa, L. occidentalis, P. contorta, P. monticola, P. menziesii. The most conspicuous understory species is V. membranaceum. Other significant understory species are V. scoparium, R. albiflorum, R. lasiococcus, P. secunda, L. borealis and C. umbellata. Franklin (1966) reports that

TABLE 3.1

Climatic data representative of the study area (Bumping Lake station) and a more maritime environment (Stampede Pass station) for the years 1956 through 1965 (snowfall 1931 - 1965). Source: Pacific Northwest River Basins Commission, Climatological Handbook.

				Temperature					Precipitation		
Station	Elevation	Latitude	Longitude	Average Annual	Average January	Average January Minimum	Average July	Average July Maximum	Average Annual	Average June - August	Average Annual Snowfall
	Meters			Degrees C					Millimeters		Centimeters
Bumping Lake	1048	46° 52'	121° 18'	5.1	-4.2	-9.2	15.2	24.3	1214	70	576
Stampede Pass	1206	47° 17'	121° 20'	4.2	-4.3	-6.5	13.8	18.9	2342	193	1138

X. tenax and *V. membranaceum* codominate the understories of many *Abies/Tsuga* communities in the southern Washington Cascades. On Round Mountain however, *X. tenax* is more common on treeless xeric sites and rarely occurs in understories with *V. membranaceum*. Franklin (1965) includes the east slopes of the Washington Cascades, south to Klickitat Meadows, in the Wenatchee Ecological Province; where *A. amabilis* and *Tsuga* spp. are minor species. He thus includes Round Mountain in the province most compositionally similar to the *Picea-Abies* forests of the northern Rocky Mountains. Such classification is justified if only seral species, characteristic of interior climates, are considered.

Seral forests dominated by *A. amabilis*, *L. occidentalis/P. contorta*, and *A. lasiocarpa/T. mertensiana* at low, middle, and high elevations, respectively, cover much of the study area. Relict specimens of *L. occidentalis* and *P. menziesii* occur sporadically throughout the low and midelevation forests. These stands are from 55 to 65 years old and may have originated during the same fire period that devastated much of northern Idaho during the early 1900s. In the scattered, unburned patches of mature forest a 300 to 400 year-old cohort of seral intolerants is very conspicuous, although *A. amabilis* is asserting codominance. Hemstrom (1979) reports a natural fire rotation of 453 years for the

A. amabilis forests of Mt. Rainier National Park. Fire frequency in the less maritime A. amabilis forests east of the Cascade Crest was probably intermediate between this and the 70 to 150 year mean fire free interval reported for similar forests of northern Idaho (Arno and Davis 1980).

CHAPTER FOUR

Methods

Study Site Selection and Plot Location

The east slopes of the Cascade Range in Yakima County, Washington were extensively reconnoitered for *V. membranaceum* communities. Round Mountain was chosen as the study site because nearly all communities thus identified were included within a manageable geographic area. Homogeneous communities on Round Mountain are mapped and sample plots are located in Figure 4.1. Plant communities in which *V. membranaceum* was an understory dominant were subjectively selected to represent their entire range of disturbance history and environment. These communities will be referred to as stands. Eight stands were selected. In each stand, two plots were established so as to represent the stand. Plots were located far enough inside the stand boundary to avoid edge effects and were separated by a distance of 15 to 30 m. Mueller-Dombois and Ellenburg (1974) report that sampling efficiency is greatest for plots transverse to the slope. In this study, plots were oriented with their long axis at 240° or 330°, whichever approached transverse. Plot geometry, Figure 4.2, was similar to that described by Daubenmire and Daubenmire (1968) in which a macroplot encloses a series of quadrats located at 1 m intervals along two longitudinal transects.

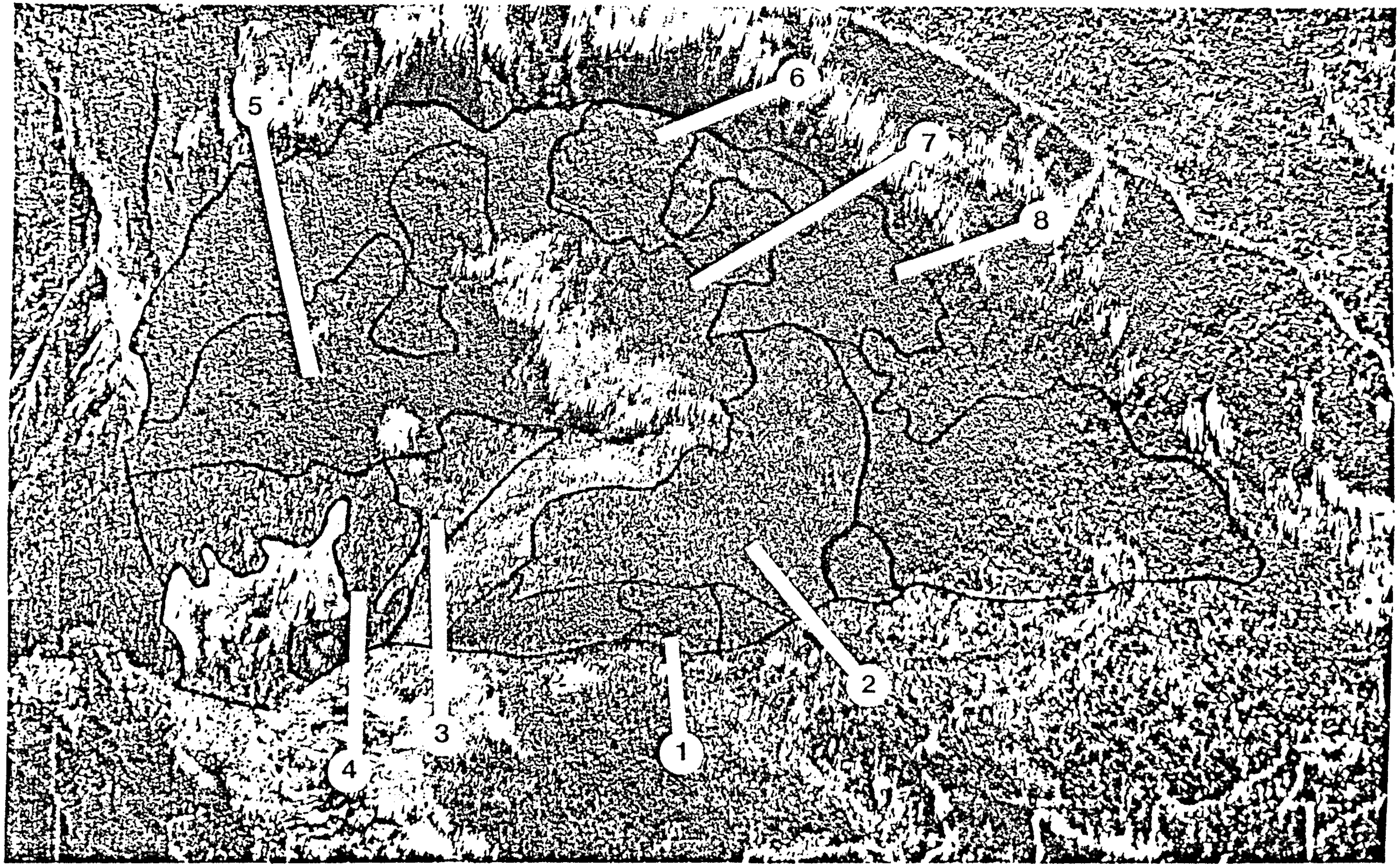


Figure 4.1. Aerial photograph of study area showing boundaries and identifying sampled stands. Approximate scale 1:15840.

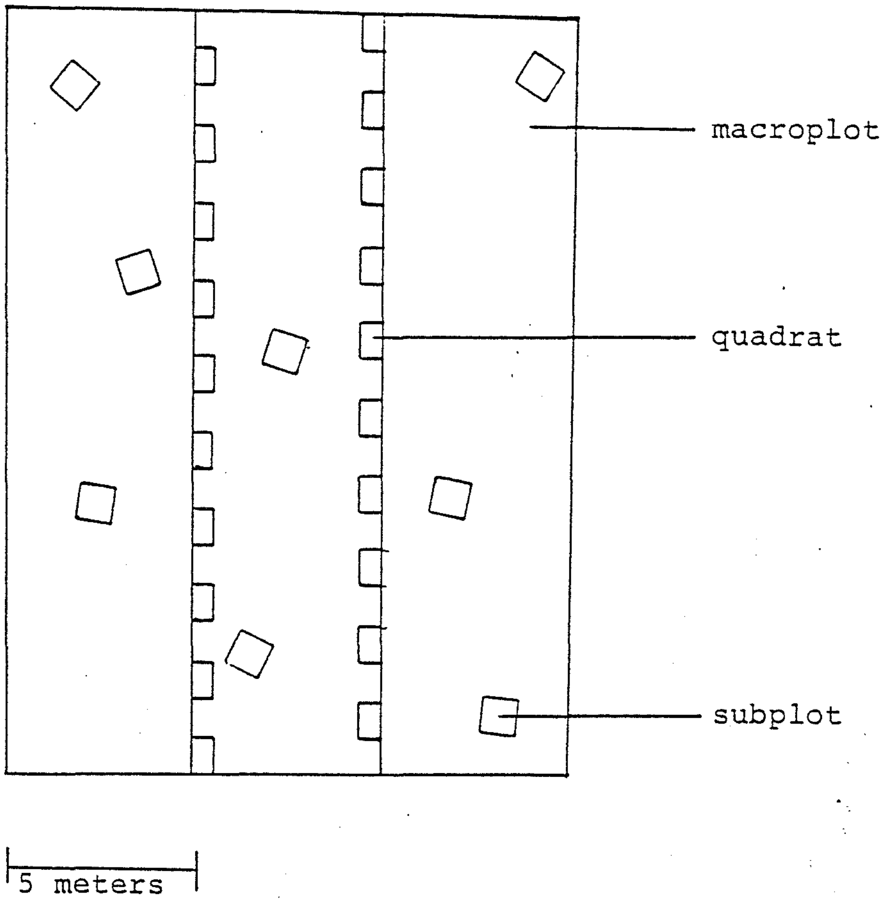


Figure 4.2. Illustration of macroplot with quadrats located at intervals along two longitudinal transects as well as one possible outcome of subplot location.

Data were collected for each of these 16 plots, two in each of eight stands.

From July 1 through September 30, hygrothermographs in instrument shelters at 1.5 m above ground level monitored temperature and relative humidity in stands 2 and 3, low and high elevation stands, respectively, within the study site.

Data Collection

Vegetation

Measured on each of the 20 quadrats within one plot were; percent cover and rooted occurrence for herb and shrub species; tree seedling occurrence; percent cover and soundness of down large logs; and moss occurrence. Plot values for angiosperms were calculated as the arithmetic mean of percent cover for all quadrats. Percent frequency was calculated as the proportion of quadrats occupied. For the entire macroplot, all trees were tallied by species and the diameter of those taller than 1.37 m was measured. Trees under 1.37 m in height were tallied into 2.54 cm diameter classes up to 7.62 cm. For tree species, relative frequency was determined and relative basal area was calculated from diameter measurements and class midpoint values. Plant species present in the stand but absent from the quadrats were noted. The following topographic variables were also measured; percent slope, aspect, and elevation.

V. membranaceum production

Each plot's production was sampled on eight subplots one square meter in size and consisting exclusively of *V. membranaceum* vegetation. Subplots were separated by at least 3 m in order to maximize the probability that each subplot consisted of stems of a unique clone. The uneven coverage and erratic production of *V. membranaceum* further complicated this selection procedure. Random sampling was too inefficient; instead, a method designed to sample the extremes of fruit production was chosen. The four most- and four least- productive subplots on each plot were selected for sampling after flower corollas had abscised and before fruit had matured. Figure 4.2 presents one possible outcome for location of a plot's subplots.

Percent tree canopy density above each subplot was measured with a spherical densiometer (Lemmon 1956) mounted on a platform 30 cm above ground level. The arithmetic mean of canopy densities on all eight subplots was taken as density of tree canopy for the plot. Annual potential solar radiation for various combinations of slope and aspect are provided by Buffo and Fritschen (1972). The fraction of this potential radiation incident at the plot understory was determined as:

adjusted solar radiation = (100-plot canopy density) (annual potential solar radiation).

To minimize losses from predation, fruit harvest began as soon as maturation was apparent. Because phenologic development and fruit maturation were not uniform within or among plots, several collections were required to harvest the entire crop from all subplots. To reduce respiratory weight loss, berries on each subplot were collected in separate plastic bags for transport and dried within 6 hours of harvest at 60° C for 24 hours. Fruit production for each subplot was expressed two ways: as the total number of harvested berries, and their dry weight to the nearest .1 g.

Immediately following final harvest of a stand's fruit production, each subplot's V. membranaceum biomass was collected by clipping at ground level. Samples of the largest portions of the root/rhizome system were also gathered for each subplot and, with its above-ground vegetation, transported from the field in plastic bags.

Shoot and leaf growth for the current growing season were clipped, air dried for 48 hours and weighed to the nearest 0.1 g. Leaf abscission on some plots had begun prior to final leaf harvest. Its magnitude was estimated in the field and a percentage adjustment made to the air dry weight of affected plants. During clipping, the magnitude of aborted, parasitized and molded fruit and occurrence of stem fungal infection was recorded.

The largest stem and rhizome sections collected for each subplot were sampled to determine maximum

V. membranaceum age for each plot. The cut end of the stem or rhizome was shaved with a scalpel, wetted with water and the growth rings were counted with the aid of a dissecting microscope.

Fruit development (ie., failure to initiate fruit; aborted, molded and parasitized fruit; matured fruit) of four clones at each instrument shelter in stands 2 and 3 was monitored throughout the growing season. Five *V. membranaceum* stems in each cardinal direction 10 m from the instrument shelter were selected from the same clone and their flowers counted. A prolifically flowering clone was found in stand 2 and its fruit development was recorded as well.

CHAPTER FIVE

Results: Vegetation

Results of the vegetation survey for herb and shrub, as well as tree species are shown in Tables 5.1 and 5.2, respectively. Plot environmental data are presented in Appendix B. For all plots, *V. membranaceum* and *R. lasiococcus* are the most conspicuous shrub and herb species. With the exception of stands 6 and 8, *V. membranaceum* cover and frequency values are within 50% of one another for both plots of a stand. Stands 3 and 4 are most flowering-species rich while stand 2 is most conifer-species rich. All stands have a component of both *A. amabilis* and *T. mertensiana*. Although the former species is least conspicuous in stand 2, it is very conspicuous in adjacent stand 1.

TABLE 5.1

Percent cover and frequency of herb and shrub species on the 16 study plots.

Number to left of dot is percent cover where value exceeded 0.5% + indicated cover less than 0.5%; number to right of dot is percent frequency; X indicates presence in stand but outside the plot.

Stand	1		2		3		4		5		6		7		8	
Plot	1	1B	2	2B	3	3B	4	4B	5	5B	6	6B	7	7B	8	8B
SHRUBS																
Arctostaphylos uva-ursi			+.5	+.15												
Juniperus communis					3.15											
Pachistima myrsinites				1.20	+.10	1.10	+.5	1.10					3.55	2.30	1.20	6.11
Rhododendron albiflorum	1.15	2.20		+.10					25.85	14.55		17.35				
Ribes viscosissimum															1.20	
Vaccinium membranaceum	6.80	9.80	20.95	15.55	5.30	18.55	48.100	35.80	11.100	13.85	12.60	27.100	37.90	41.90	31.100	59.27
Vaccinium scoparium	1.15	+.25	18.95	12.85	2.15		7.55	5.40			+.5		1.5	2.20	8.35	6.5
HERBS																
Achillea millefolium					1.50	1.25	+.10	+.5								
Anaphalis margaritacea					1.25	+.15								+.5		
Arnica cordifolia					6.55	5.55	1.45	1.30					+.10	1.25		+.2
Berberidaceae achlys													+.5			
Carex spp.			+.5		12.90	4.65	7.90	4.85								

TABLE 5.1 (Continued)

Stand	1		2		3		4		5		6		7		8	
Plot	1	1B	2	2B	3	3B	4	4B	5	5B	6	6B	7	7B	8	8B
<u>Calamagrostis</u> spp.				+.10		+.10										
<u>Castillega</u> spp.					1.20		+.10									
<u>Chimaphila umbellata</u>		+.10									+.25	1.15	1.25	+.5	1.20	6.7
<u>Epilobium angustifolium</u>														+.5		
<u>Goodyera oblongifolia</u>											+.5	+.15			+.5	
<u>Agoseris aurantiaca</u>					1.25	2.45	+.5									
<u>Hieracium scouleri</u>			+.5		3.60	2.50	2.45	1.35					+.20	+.20	+.5	
<u>Linnaea borealis</u>												+.5	10.30	16.80	7.80	18.25
<u>Lupinus polyphyllus</u>	+.15		10.100	23.100	26.100	14.85	12.85	14.90					4.70	3.60	1.45	
<u>Penstemon</u> spp.				+.15	+.5		1.20						+.5	+.15		
<u>Polemonium pulcherrimum</u>					4.5											
<u>Pyrola secunda</u>	+.15	+.25			1.10	1.15	1.25	+.10	+.10		+.5	+.15	1.50	1.30	+.15	+.5
<u>Valeriana sitchensis</u>							x	x								
<u>Viola</u> spp.	+.5	+.10			4.50	2.45	6.75	2.75	+.10			+.30	1.30	+.5	+.10	+.2
<u>Rubus lasiococcus</u>	1.25	+.10	2.20	1.20	8.75	6.70	12.95	6.95	3.65	3.50			8.100	7.90	1.50	+.11
<u>Xerophyllum tenax</u>			2.40	2.25		+.10						+.5		+.5	1.10	6.5

TABLE 5.2

Relative basal area (m2) and density of tree species on the 16 study plots.

Number to left of dot is basal area; number to right of dot is density; X indicates presence in stand but outside the plot.

Stand	1		2		3		4		5		6		7		8	
Plot	1	1B	2	2B	3	3B	4	4B	5	5B	6	6B	7	7B	8	8B
Abies amabilis	20.95	36.92	1.8	1.2		17.1	2.1	5.4	99.98	99.97	6.93	10.92	2.25	1.17	67.80	62.84
Abies lasiocarpa	4.01			3.4	36.88	63.92	71.91	61.82					1.1			2.6
Abies procera			1.1												1.3	
Chamaecyparis nootkatensis			X	X					X	X						
Larix occidentalis	22.01	11.1	65.41	60.32		5.1						33.1	88.41	74.40	26.5	9.1
Picea engelmannii					1.1		2.1									
Pinus contorta		3.1	13.12	11.11	1.1		2.3									
Pinus monticola				1.2							26.1			1.2		
Pinus ponderosa				6.6	24.2											
Pinus albicaulis			13.6	12.25	4.3		8.1	1.1								
Pseudotsuga menziesii			2.3	1.2	21.3	11.1		5.1					6.14	19.27		
Thuja plicata	10.01	9.4														
Tsuga heterophylla											68.6	55.2	1.1			
Tsuga mertensiana	48.03	44.3	4.22	6.8	12.2	4.2	15.2	29.13	1.2	1.3		2.3	2.12	7.14	6.12	6.2

CHAPTER SIX

Discussion: Vegetation

Tabulated vegetation data (Tables 5.1 and 5.2) are often evaluated for ecological relationships but their interpretation requires much experience and enlightened subjectivity. Quantitative methods of vegetation analysis exist which increase objectivity, reveal otherwise obscure relationships and help generate testable hypotheses (Pfister and Arno 1980, Long 1976). However, caution should be exercised in their application because actual relationships may be obscured and spurious results obtained, depending on the nature of vegetation parameters employed and their subsequent mathematic manipulation (Daubenmire 1968, Pfister and Arno 1980).

Ordination is one such procedure in which sample plots are located as points in an n-dimensional coordinate system where the graphic distance between any two plots, or groups of plots, represents their relative similarity. Similar plots are relatively close together and more dissimilar plots are relatively further apart. Polar ordination, first described by Bray and Curtis (1957) and modified by Beals (1960), was selected for this study because it reliably provides undistorted representations of environmental relationships and is the least arcane of several methods (Del Moral and Watson 1978, Long 1976, Whittaker 1973, Whittaker and Gauch 1973). Indirect ordination arrays sample plots along axes defined by the collective gradient of plot vegetation characteristics, axes which may subsequently be correlated with actual single- or multiple-factor environmental gradients. Such correlation with physical environment is by no means assured. Whittaker (1973) indicates that floristically defined axes may represent disturbance or successional, rather than environmental, gradients.

Two ordination graphs were constructed; one based on herb and shrub species, the other based on trees as well as herbs and shrubs. Preliminary steps included evaluating each species' significance on each plot and subsequently quantifying the vegetative similarity between plots.

Two or more quantitative parameters may be combined as a species' importance value (IV) to arrive at a summary measure of its significance on a plot (Daubenmire 1968). Although traditional importance values have been determined from relative measures of such parameters (Beals 1960), absolute cover may be a more accurate indicator of an environment's productive capacity and improve among plot comparisons (Daubenmire 1968, Beals 1960). For these reasons, absolute cover was used to calculate herb and shrub importance values. Because frequency may poorly express the ecologic importance of a species (Daubenmire 1968) and because stand selection was based on <u>V. membranaceum</u>

frequency, calculations of herb and shrub importance values were weighted in favor of cover by:

$$\text{species IV} = .5(F) + 2(C)$$

where F is frequency and C is cover. Importance values for each tree species were computed as the sum of their relative frequency and relative basal area.

The relative similarity between plots was expressed using Sorensen's index of similarity (IS_{mo}) as modified for use with quantitative values such as species IV and was calculated for each plot pair following Mueller-Dombois and Ellenburg (1974). Expressed as percent similarity:

$$IS_{mo} = ((2Mw)/(MA+MB)) \text{ X } 100$$

where Mw is the sum of the lower of the two IVs for each species common to both plots; MA is the sum of IVs for all species in plot A; MB is the sum of all IVs for all species in plot B. In other words, IS_{mo} is the fraction of the average floristic characteristics of two plots common to both plots, i.e.,

$$IS_{mo} = \frac{\text{common floristic characteristics X 100}}{\text{average floristic characteristics}}$$

In theory, these values may range from 0% for plots with no common vegetation characteristics, to 100% for an identical pair of plots. However, Beals (1960) calculated an average IS_{mo} of 85% for replicate sampling of the same community and recommends that plot pairs with IS_{mo} greater than 85% be considered identical. To provide a measure of the relative dissimilarity between plots, an index of dissimilarity (ID) for each plot pair was defined as the complement of IS_{mo}:

$$ID = 100 - IS_{mo}$$

Values for IS_{mo} and ID were entered in the lower left and upper right, respectively, of a similarity matrix. Two similarity matrices were constructed; one comparing plots on the basis of herb and shrub IVs, the other including tree IVs in the comparison.

Indirect polar ordinations of sample plots were constructed following the computational procedures of Mueller-Dombois and Ellenburg (1974) and are based on the vegetative relationships summarized in the similarity matrices. That plot most different from the others was selected as origin (original reference plot) of the ordination diagram. Index of dissimilarity values were then scanned and the plot most different (highest ID) from the previously selected plot became the terminus (terminal reference plot) of the X-axis. Computational safeguards ensured that neither reference plot was so different from the others as to skew subsequent placement of the remaining plots (Beals 1960). Selection of reference plot pairs which potentially represented extremes of two different environmental gradients, e.g. a warm-dry plot and a cold-wet plot, was avoided. Pfister and Arno (1980) report that such discrimination aids plot separation and expression of environmental gradients along subsequent axes. The length of the axis defined by these reference plots is equal to their ID value. In other words, the X coordinates of the original and terminal reference plots are 0 and their ID, respectively. The X coordinates of the remaining plots were determined trigonometrically, Figure 6.1, as a function of their dissimilarity to the two reference plots according to:

$$X = \frac{L^2 + Da^2 - Db^2}{2L}$$

Similar separation of the sample plots in a second dimension, Y-axis, was performed. The plot with the poorest fit to the X-axis, e.g. most dissimilar to the two X-axis reference plots, and its most dissimilar cohort became the origin and terminus, respectively, of the Y-axis with length equal to their ID. Y coordinates for the remaining plots were determined according to:

$$Y = \frac{L^2 + Da^2 - Db^2}{2L}$$

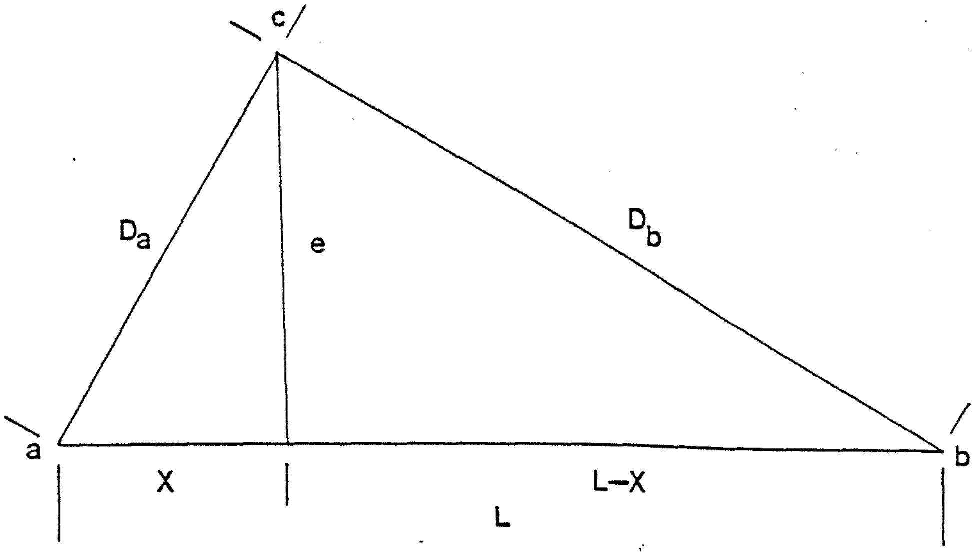


Figure 6.1. Trigonometric basis of the procedure for locating plots on the ordination graph (from Beals 1960).

a and b are reference plots.

c is any other plot.

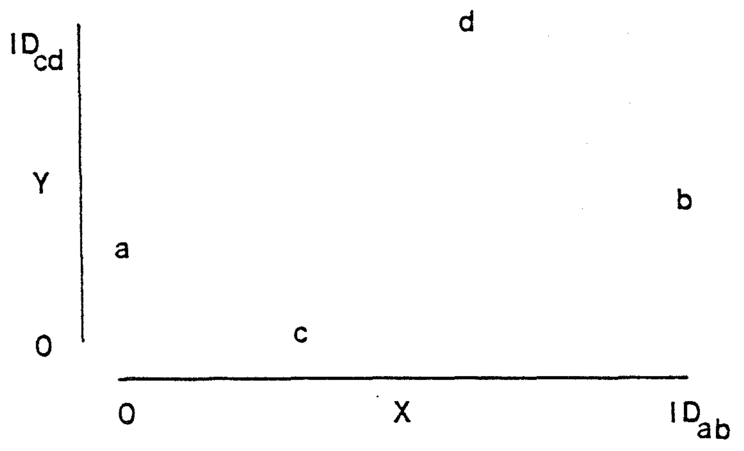
L is the ID between plots a and b. i.e., length of the X-axis.

Da and Db are the IDs between a third plot, c, and plots a and b.

X is the location of plot c along the X-axis.

The magnitude of e represents the magnitude of the dissimilarity between plot c and the two X-axis reference plots.

Plots were then located within an X-Y coordinate system, e.g. below:



In each of the two-dimensional ordinations thus constructed some plots were located close together which, in reality, were quite dissimilar. In such cases, Cottam et al. (1973) recommend further separation to identify a third direction of community variation. A third axis of ordination was constructed which arrayed the plots similarly to the X-axis. Calculation and testing of the correlation coefficient, r, between the X and Z ordination values revealed that these two axes of ordination were not significantly different (herb/shrub X-Z ordination values $r=.86$, $P<.001$; herb/shrub/tree X-Z ordination values $r=-.94$, $P<.001$) and the Z-axis was abandoned.

Because the representation of ID values in an ordination graph is subject to error, particularly from the selection of reference plots, its accuracy should be tested (Gauch 1977, Mueller-Dombois and Ellenburg 1974). For each ordination ten plot pairs were randomly selected and their graphic separation calculated. The correlation coefficient between these distances and the ID values they theoretically represented was calculated and tested for its statistical significance: a significant result indicating that if the similarity matrices based on species' importance values are ecologically meaningful, then the ordination graphs based on those similarity matrices are ecologically meaningful. Each ordination faithfully represented the relationships summarized in its similarity matrix, herb/shrub ordination $r=.89$ with $P<.001$ and herb/shrub/tree ordination $r=.86$ with $P<.002$.

Four potential climax associations described by Franklin (1966) are represented by stands evaluated for this study (Table 6.1). Because these associations were more discreetly represented, and understory influences more accurately reflected, by the herb/shrub ordination than the combined herb/shrub/tree ordination, the latter was rejected. The herb/shrub ordination graph is presented in Figure 6.2 where the three outlined plot groups represent seral communities of a unique habitat type and potential climax association. Refer to Tables 5.1 and 5.2 and Figure 6.2 for the following discussion.

Stands 3 and 4 are closely related to the Abies amabilis/Veratrum viride Association. They were the

TABLE 6.1

Climax plant associations of the southern Washington Cascades described by Franklin (1966) and represented by stands evaluated in this study.

Stand	Association Represented
1	*A. amabilis - T. mertensiana*/*V. membranaceum*
2	*A. amabilis - T. mertensiana*/*V. membranaceum*
3	*A. amabilis*/*V. viride*
4	*A. amabilis*/*V. viride*
5	*A. amabilis*/*M. ferruginea*
6	*A. amabilis - T. heterophylla*/*V. membranaceum*
7	*A. amabilis - T. mertensiana*/*V. membranaceum*
8	*A. amabilis - T. mertensiana*/*V. membranaceum*

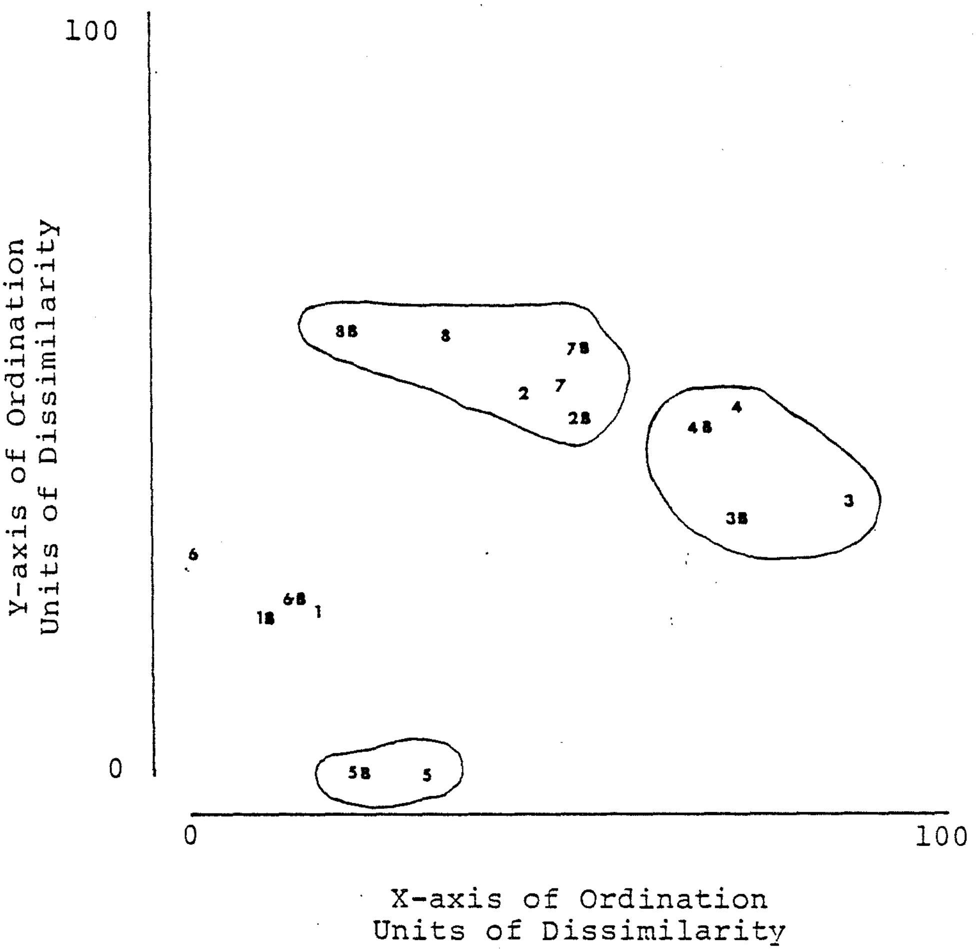


Figure 6.2. Polar ordination graph of sample plots based on herb and shrub vegetation. Outlined plot groups represent seral communities of climax plant associations described by Franklin (1966) for the southern Washington Cascades.

highest stands studied and, occurring on the windward side of a major ridge, are fully exposed to weather conditions originating west of the Cascade Crest. In fact, this ridgetop is frequently cloud shrouded earlier and later than the rest of Round Mountain. This conforms to the association's status as a topoedaphic climax on moist sites (Franklin 1966). Although plot 3 had one of the most diverse tree populations of the study area, stands 3 and 4 were dominated by A. lasiocarpa. On some A. amabilis habitats, A. lasiocarpa dominated stands are seral to a very delayed A. amabilis climax forest (Henderson 1981). Franklin (1966) reports that an herb rich understory is the most distinctive feature of the Abies amabilis/Veratrum viride Association. These stands experienced greater diversity and dominance of shrub and herb species than all other stands. Additionally, they supported the only conspicuous population of Carex spp. A notable difference between stands 3 and 4 is the greater dominance of both V. membranaceum and V. scoparium in the latter giving it a much more luxuriant understory. While stand 3 was more species rich than stand 4, its total coverage was less, possibly because of reduced soil water due to coarser soil and a more exposed ridgetop location. Canopy closure has not occurred in either stand.

The Abies amabilis-T. mertensiana/V. membranaceum Association is represented by seral stands 2,7 and 8, and old growth stand 1. There are, however, some significant physiographic and floristic differences among the seral stands. The old growth stand will be discussed later. Occurring at the eastern boundary of the study site in a deep basin on the lee side of Round Mountain, stand 2 is probably at the xeric limit of the Abies amabilis Zone. Its understory, dominated by Vaccinium spp. and L. polyphyllus supports the only conspicuous populations of X. tenax and A. uva-ursi (typical dry site species), in the study area. Reflecting this stand's early seral status, A. amabilis is not a significant component of the overstory nor is it well represented among understory regeneration. The four most dominant overstory tree species are L. occidentalis, T. mertensiana, P. contorta, and P. albicaulis. The latter two species are more conspicuous in this and stands 3 and 4, than in the others. Relative to stand 2, stands 7 and 8 are more mesic, have greater dominance and diversity of angiosperms and lower conifer diversity. The two are adjacent to one another, stand 8 lying about 100 m above stand 7, but their floristic boundary is very abrupt. In spite of their physiographic and age similarities there is a profound difference in overstory composition between these two stands. Stand 7 is dominated almost exclusively by L. occidentalis with a relatively minor component of A. amabilis. The situation is reversed in stand 8 where a more dense all size stand of A. amabilis occurs. Both have a significant T. mertensiana component. In stand 7, there are scattered old growth (greater than 300 years old) L. occidentalis and P. menziesii which probably account for this stand's present composition. Large L. occidentalis snags are abundant in stand 8 and were probably contemporary with the relict trees in stand 7 which survived the stand initiating fire. The former dominance of L. occidentalis in stand 8 and the present shrub/herb similarities argue that habitat type for the two stands is the same and that floristic dissimilarities are due to chance factors, i.e., previous fire patterns. This argument is bolstered by Ellingson's (1972) report indicating only one potential soil parent material for the entire study area, olivine basalt. Canopy closure has occurred in all three stands with lower tree density in stands 2 and 7 than in stand 8. Additionally, the abundance of L. occidentalis in the overstory of the two former stands contributes to their relatively light and airy understory.

Located on a steep north slope at the west boundary of the study area, the vegetation of stand 5 is characteristic of the A. amabilis/M. ferruginea Association. Its overstory is dominated by A. amabilis with a minor component of T. mertensiana, and, at higher elevations, C. nootkatensis. All sized A. amabilis regeneration and a tangle of about 2 m tall R. albiflorum and V. membranaceum dominate the understory of this coldest and wettest stand. Franklin

(1966) indicates the absence of M. ferruginea is not unusual for such high elevation communities.

The proximity of stands 1 and 6 on the ordination graph reflects old growth floristic rather than habitat similarities. Stand 6, located at the lower west (warm and wet) boundary of the study area, is a nearly typical member of the A. amabilis-T. heterophylla/V. membranaceum Association. This association is comparable to that considered transitional between western Cascades P. menziesii/T. heterophylla and A. amabilis forests by Zobel et al. (1976). While A. amabilis regeneration is present in this stand, its most notable feature is an overstory dominated by classic old growth P. monticola, L. occidentalis and T. heterophylla. In contrast to stand 6, stand 1 is located near the dry east boundary of the study area. It is adjacent to stand 2 and represents the same association, A. amabilis-T. mertensiana/V. membranaceum. Structurally, it resembles stand 6 except that its understory is less parklike. In addition, T. heterophylla is replaced by T. mertensiana, and A. amabilis is better represented in all size and age classes.

Moisture and temperature are the environmental gradients most often associated with axes of ordination, either by direct measurement or indirectly inferred from vegetation. Complete measurements of these factors were not made.

When the magnitude of percent overstory density and adjusted solar radiation for each plot are superimposed on that plot's ordination position (Figures 6.3 and 6.4, respectively), the X-axis trend is obvious. With increasing distance from the X-axis origin, percent overstory density decreases or conversely, adjusted solar radiation increases. Neither of these variables represent intrinsic environmental gradients. Rather, they represent the competitive regime, affected by overstory plants, which impacts the understory. Because it integrates topographic and solar radiation factors, as well as biotic competition, into a more quantitative measure of the understory light regime, adjusted solar radiation is preferable to percent overstory density. In fact, the correlation between adjusted solar radiation and X-axis position for each stand is very strong, $r=.89$ and p .001, and this axis is taken to represent a gradient of potential solar radiation incident at the understory.

Even though temperature regime is related to adjusted solar radiation, the arrangement of stands along the X-axis is not consistent with temperature trends. However, those temperature data gathered for stands 2 and 3, along with stand ordination location and stand topography, indicate a gradient of increasing temperature from the Y-axis origin, Figure 6.4. The old growth stands are arrayed at the coolest end of the gradient, near stand 5, because of the moderating influence of their tree canopies. Although there

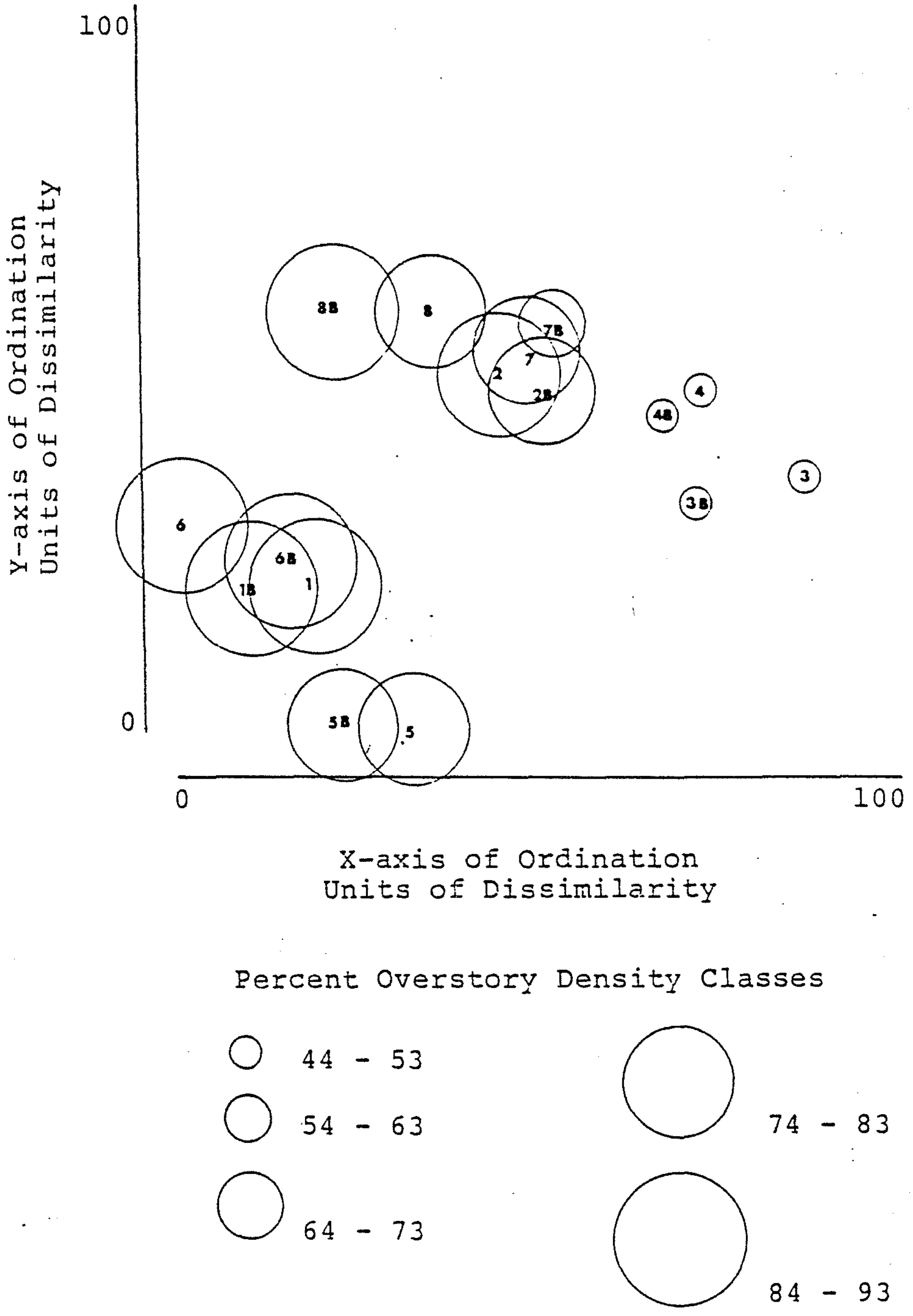


Figure 6.3. Magnitude of percent overstory density for each plot, superimposed on its ordination position. Circle size is proportional to percent overstory density.

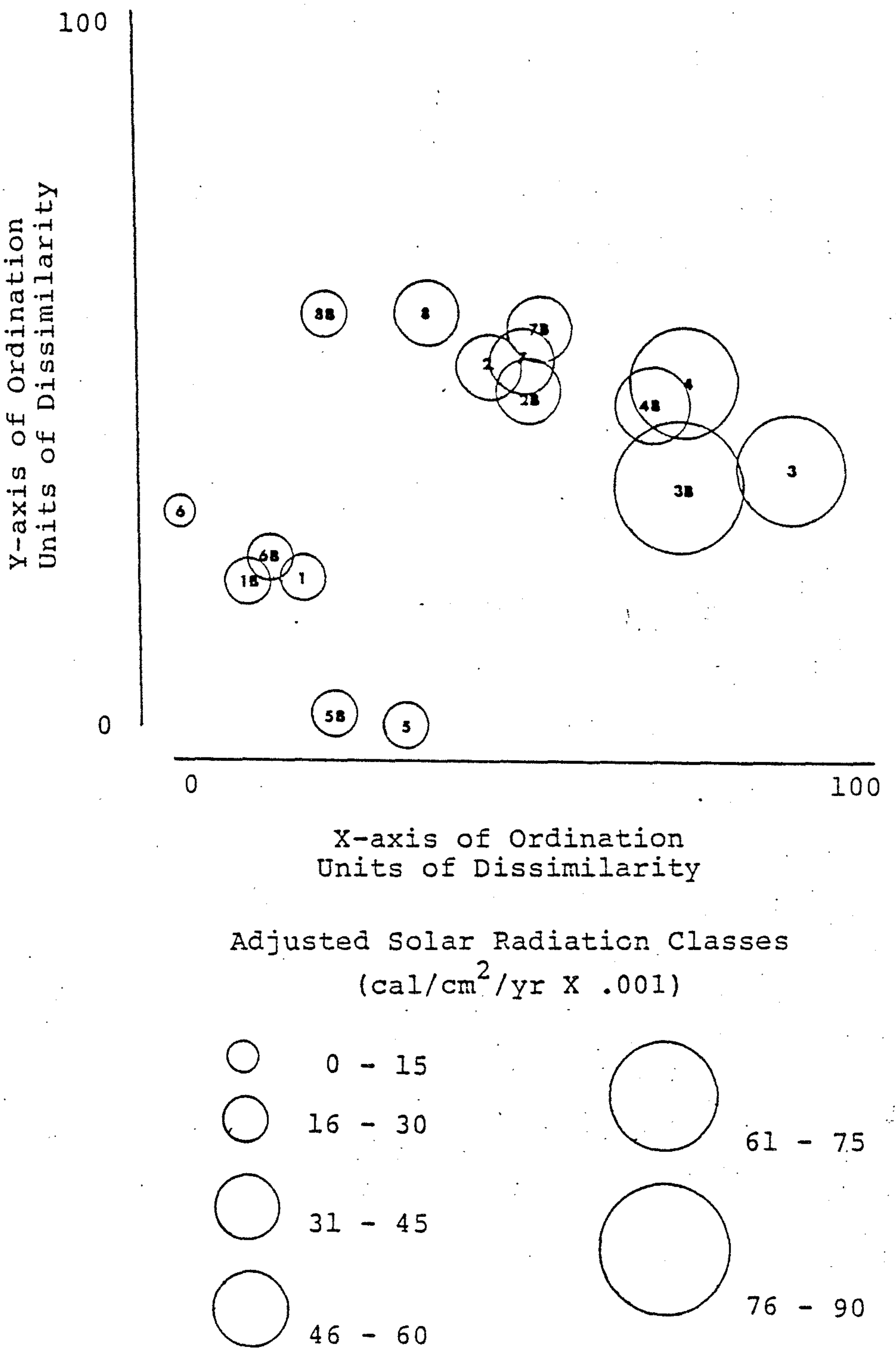


Figure 6.4. Magnitude of adjusted solar radiation for each plot, superimposed on its ordination position. Circle size is proportional to adjusted solar radiation.

are smaller graphic separations among the warmer stands, meaningful differences do exist. For the 1982 growing season, average July temperatures for stands 2 and 3 were 15° C and 12° C, respectively. These results are consistent with the generalization that A. amabilis/V. viride is a higher elevation association than A. amabilis-T. mertensiana/V. membranaceum. In fact, with the exception of stand 4, the trend of decreasing stand elevation with increasing distance along the Y-axis is consistent for the 5 seral stands. The influence of converging maritime and continental climates and the lack of temperature data for each stand preclude statistical correlation of the Y-axis with temperature regime. In spite of this, the Y-axis is considered a gradient of increasing temperature.

Even for deliberately selected stands, random disturbance and colonization factors confound chronosequential interpretation of successional trends, e.g. stand 7 vis-a-vis stand 8. It is even more difficult in this study because many of the stands represent different habitats. In fact, microsite factors which spared stand 1 from the fire that consumed the adjacent stand 2 may affect their comparison as mid and late seres of the same association. The general trend of V. membranaceum production as a function of successional time may be inferred from these two stands, the specific form of the relationship may not.

Although the inferred environmental gradients represent transitory successional conditions they do not represent the dynamic successional environment of a unique habitat type. However, in terms of current conditions, relative comparisons among the eight stands and 16 plots are valid. Thus, their V. membranaceum populations may be evaluated in terms of environment, certain growth factors and associated plants; and conclusions may be communicated in terms of generalized forest habitats.

CHAPTER SEVEN

Results: V. membranaceum Production

The following three production statistics were defined for each plot as the arithmetic mean of the production variables of its eight subplots (Table 7.1):

N_{fruit} = mean number of berries per subplot
W_{fruit} = mean weight of berries per subplot
W_{plant} = mean weight of vegetation per subplot.

In addition, the total number of aborted or parasitized berries and fungus infected stems are reported for each plot. Vegetative production was apparent in all stands. However, fruit production in stands 1, 5, and 6 was negligible. Although area-wide fruit production may vary considerably from year to year, relative production among stands is expected to be consistent.

To account for relative differences in V. membranaceum biomass and distribution within a stand, three indirect expressions of plant production were defined (Table 7.2).

Neither of the two statistics summarizing fruit yield account for differences in the vegetative system supporting that yield, e.g. if subplot A and subplot B each produce 100 berries from 5 and 10 dry grams of vegetation, respectively, number of berries per subplot indicates they are equally productive when, in fact, the former is twice as

TABLE 7.1

Plot means and standard deviations of subplot *V. membranaceum* production as well as total number of aborted or parasitized berries and fungus infected stems.

Stand	Plot	N_{fruit}		W_{fruit}(g)		W_{plant}(g)		Aborted/ Parasitized	Fungus Infected
		$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	n	n
1	1	1	<1	0.1	0.1	44.6	2.4	6	0
	1B	1	<1	0.1	0.2	11.5	1.0	2	0
2	2	122	44	7.0	2.8	36.2	2.7	7	0
	2B	78	24	3.0	1.0	33.7	0.7	9	0
3	3	114	57	4.8	1.2	52.8	4.7	48	7
	3B	182	36	9.6	2.2	79.5	2.0	31	6
4	4	244	61	10.0	3.2	70.2	1.5	37	6
	4B	124	52	5.7	2.4	68.1	0.6	44	4
5	5	3	1	0.2	0.1	19.3	2.1	3	0
	5B	3	1	0.3	0.1	12.0	1.0	1	2
6	6	5	2	0.4	0.1	12.5	1.2	1	0
	6B	16	7	1.0	0.4	28.8	0.1	6	0
7	7	226	71	12.0	4.0	72.2	8.7	19	2
	7B	309	79	15.8	4.3	75.5	5.3	34	1
8	8	69	27	3.4	1.3	51.7	6.1	7	1
	8B	36	17	2.0	0.9	32.2	0.9	4	2

TABLE 7.2

Plot means and standard deviations of expected *V. membranaceum* production for randomly selected subplots.

Stand	Plot	N_{fruit}/W_{plant} (n/g)		EN_{fruit} (g)		EW_{plant} (g)	
		$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
1	1	0.2	0.09	<1	<1	2.7	0.1
	1B	0.1	0.03	<1	<1	1.0	0.1
2	2	4.5	1.82	24	9	7.3	0.5
	2B	2.3	0.64	12	4	5.1	0.1
3	3	2.2	0.42	6	3	2.6	0.2
	3B	2.3	0.46	33	6	14.3	0.4
4	4	3.6	0.89	117	29	33.7	0.7
	4B	2.1	0.89	43	18	23.8	0.2
5	5	0.1	0.69	<1	<1	2.1	0.2
	5B	0.2	0.94	<1	<1	1.6	0.1
6	6	0.3	0.13	<1	<1	1.5	0.1
	6B	0.6	0.22	4	2	7.8	0.01
7	7	2.9	0.63	83	26	26.7	3.2
	7B	4.0	0.79	127	32	30.1	2.2
8	8	1.2	0.44	21	8	16.0	1.9
	8B	1.1	0.47	21	10	19.0	0.5

productive as the latter in terms of photosynthetic area. To improve among plot comparisons of subplots, a standardized expression of fruit production, representing a subplot's photosynthetic efficiency, was calculated as:

N_{fruit}/W_{plant} = fruit production per unit of vegetation per subplot.

The above production statistics apply to individual clones, represented by subplots. They do not represent the expected production of a randomly selected square meter of plot: this requires the use of V. membranaceum average cover values for each plot. The following production statistics express the expected production of a randomly selected square meter of plot, referred to as a random subplot

$EN_{fruit} = N_{fruit}$ X V. membranaceum cover

$EW_{plant} = W_{plant}$ X V. membranaceum cover.

CHAPTER EIGHT

Discussion: V. membranaceum Production

Production statistics were compared among the 16 plots by one-way analysis of variance (ANOVA). When ANOVA indicated at least one significant difference among the compared means, subsequent Student-Newman-Keuls (SNK) multiple comparisons revealed the means among which these differences occurred. All statistical tests were conducted at significance level of .05.

Because extremes of production were sampled for each plot, traditional calculation of the sample variance by mean sums of squared deviations overestimated the population variance. Similarly, standard calculations of the F-test statistic for ANOVA were inappropriate. Assuming however, that V. membranaceum production is normally distributed, a relatively accurate estimate of sample variance, via sample standard deviation, is possible. This assumption was made and sample variance was estimated by the following argument:

> the means of the 4 most- and 4 least- productive subplots accurately represent the extremes of plot production and enclose at least 95%, i.e. two standard deviations, of its production distribution:

and $U \pm 2O$ includes 95.46% of the population distribution

$\bar{X}_i \pm 2S_i$ includes 95% of the sampling distribution

$$4S_i = \bar{X}_{Mi} - \bar{X}_{Li}$$

$$S_i = (\bar{X}_{Mi} - \bar{X}_{Li})/4$$

i = plot 1 through plot i

$\bar{X}_M$ = mean of the most productive subplots

$\bar{X}_L$ = mean of the least productive subplots

$\bar{X}_G$ = overall plot mean

This estimate of subplot production variance was then used to calculate the within groups (error) sum of squares for ANOVA and SNK tests.

For each V. membranaceum production statistic, ANOVA revealed at least one significant difference among the 16 plot means, Table 8.1. Subsequent SNK tests indicated where, among the ranked means, those differences were located, Table 8.2. Groups of means which are not statistically different are underlined, unique means are not. Plots underlined more than once could not be unambiguously placed in a single group. These tests identified

TABLE 8.1

Results of analysis of variance comparing mean subplot V. membranaceum production among 16 plots.

Statistic Compared	Source of Variation	SS	DF	MSS	$F_{statistic}$	$F_{critical}$	Probability
N_{fruit}	error	1.82E5	112	1.63E3	48.47	1.75	<.001
	groups	11.84E5	15	78.94E3			
	total	13.66E5	127				
N_{fruit}/W_{plant}	error	50.72	112	0.45	77.01	1.75	<.001
	groups	523.17	15	34.88			
	total	573.90	127				
EN_{fruit}	error	2.29E4	112	0.20E3	68.27	1.75	<.001
	groups	20.96E4	15	13.97E3			
	total	23.25E4	127				
W_{plant}	error	1.34E3	112	0.12E2	384.04	1.75	<.001
	groups	69.18E3	15	46.12E2			
	total	70.53E3	127				
EW_{plant}	error	0.14E3	112	0.01E2	813.99	1.75	<.001
	groups	15.38E3	15	10.26E2			
	total	15.52E3	127				

TABLE 8.2

Results of Student-Newman-Keuls multiple comparisons of plot means of subplot *V. membranaceum* production.

N_{fruit}	1	1	3	3	5	16	36	69	78	114	122	124	182	226	244	309
coefficient of variation %	50	50	50	42	41	40	47	40	32	50	36	42	20	32	25	26
ranked plots	1	1B	5	5B	6	6B	8B	8	2B	3	2	4B	3B	7	4	7B
N_{fruit}/W_{plant}	0.1	0.1	0.2	0.2	0.3	0.6	1.1	1.2	2.1	2.2	2.3	2.3	2.9	3.6	4.0	4.5
coefficient of variation %	50	50	50	39	39	41	44	36	43	19	20	27	22	25	20	41
ranked plots	1B	5	1	5B	6	6B	8B	8	4B	3	3B	2B	7	4	7B	2
EN_{fruit}	1	1	1	1	1	4	6	12	21	21	24	33	43	83	117	127
coefficient of variation %	50	50	50	42	41	40	50	32	47	40	36	20	42	32	25	26
ranked plots	1B	1	5	5B	6	6B	3	2B	8B	8	2	3B	4B	7	4	7B
W_{plant}	11.5	12.0	12.5	19.3	28.8	32.2	33.7	36.2	44.6	51.7	52.8	68.1	70.2	72.2	75.2	79.5
coefficient of variation %	5	8	9	11	1	3	2	7	5	12	9	1	2	12	7	3
ranked plots	1B	5B	6	5	6B	8B	2B	2	1	8	3	4B	4	7	7B	3B
EW_{plant}	1.0	1.5	1.6	2.1	2.6	2.7	5.1	7.3	7.8	14.3	16.0	19.0	23.8	26.7	30.1	33.7
coefficient of variation %	8	9	8	11	9	5	2	7	1	3	12	3	1	12	7	2
ranked plots	1B	6	5B	5	3	1	2B	2	6B	3B	8	8B	4B	7	7B	4

production differences among stands and between plots within a stand. Variation within a plot was quantified by coefficient of variation for the production variable being considered. Refer to Table 8.2 for the following discussion.

Because N_{fruit} provided less ambiguous results than W_{fruit} and the two were strongly correlated ($r = .98$ and $P<.001$) all analyses of fruit production are based on the former statistic.

When subplot productivity is compared among the 16 plots, via N_{fruit}, the three least productive stands; 1, 5 and 6; are not significantly different. All are equally unproductive. Among the remaining stands, as productivity increases, its variation among plots increases and variation within plots, i.e., among subplots, decreases. Generally, variation within a stand is as apparent as that among stands. In fact, of the five most productive stands, only one stand (stand 2) had equivalent production from both plots. The stands can be stratified into three productivity groups: an unproductive group (stands 1, 5 and 6), an intermediate group (stands 2, 3 and 8), and a productive group (stands 4 and 7).

These production groups are apparent when comparing photosynthetic efficiency, N_{fruit}/W_{plant}. Both plots of stand 8 are statistically removed from the intermediately productive group. However, the SNK test lacked the power to unambiguously place them in the unproductive group. Of the remaining plots, at least one of each stand pair remains in its previous production category. Rank ordering is the same as for N_{fruit} with the following exceptions. Plots 2 and 2B show relative increases in production, the former by virtue of two exceptionally productive subplots. Plot 3B now appears with its cohort in the intermediate group and plot 4B, formerly first in the intermediate group, is now last.

When each plot's subplot production is scaled by its V. membranaceum cover, EN_{fruit}, only the unproductive and productive groups are unambiguously differentiated. The statistical difference between production of the unproductive and intermediately productive stands is indeterminate. Empirically, however, the latter is distinct. Other than the occurrence of plot 3B in the intermediate group, there are no significant changes in rank ordering, relative to N_{fruit}.

Only the productive group, stands 4 and 7, described for N_{fruit} is statistically differentiated for its vegetative corollary, W_{plant}. Two exceptionally productive plants caused plot 3B to be ranked first. The remaining plots are characterized by considerable differences in production. As with fruit production on the more productive plots, within stand variation is more conspicuous than among stand variation. The unproductive group is statistically differentiated in the results for EW_{plant}. Again, variation among the remaining plots is very significant. Although all three production categories are not apparent in each SNK test they may be inferred from the rank ordering of the two vegatative production statistics. However, only the extremes of production are consistently located and variation patterns are most ambiguous for stands of the intermediate group. Variation among subplots within a plot is small for either expression of vegetative productivity and no trend is apparent.

Aborted and molded fruit represent a considerable crop reduction (Table 7.1). Aborted fruit appeared in every stand and in the poor-producing and late-maturing stands represented a greater proportion of the total crop. The proportion of the potential fruit crop successfully developing from flower to fruit may depend considerably on conditions preceding pollination. Table 8.3 summarizes the magnitude of crop failure in stands 2 and 3. Fruit initiation was not apparent in over two thirds of the flowers of either stand. Possible explanations are failed pollination and/or weather factors. Subfreezing temperatures occurred only at stand 3 (-1° C on July 13 and August 18) and were probably not low enough to cause flower abscission. Additionally, similar failure rates for each stand indicate that similar factors were effective in each stand. Temperatures in the V. membranaceum canopy, lower than those in the instrument shelter, may have been lethal to their flowers. In any case, inefficient pollination is a

TABLE 8.3

Percentages of flowers maturing to fruit, failing to initiate fruit and aborted or parasitized fruit at the hygrothermograph shelters in stands 2 and 3 and a subjective location in stand 2.

	Stand 3 Hygrothermograph Shelter	Stand 2 Hygrothermograph Shelter	Stand 2 Subjective Location
Maturing to Fruit	10	20	50
Aborted-parasitized	15	12	20
Failing to Initiate Fruit	75	68	30

more plausible explanation for the large proportion of failed flowers. No explanation is offered for the considerably greater fruit maturation rate of the prolifically flowering plant, located subjectively in stand 2.

Berry gatherers often report that berries from their preferred patch are the biggest they've seen. Tests comparing berry size, N_{fruit}/W_{fruit}, indicate that there is a difference among the 16 plots, Table 8.4. However, this difference is significant only between the extremes of the plots ranked by berry size. No one stand produces significantly larger berries.

Several berries harvested after September 15 had been parasitized by larvae of a species of sawfly (family Tenthredinidae), which had by then eaten the seeds and fruit pulp. This was most conspicuous in stands 1, 4 and 5, which generally reached peak fruit maturity later in the season, thus providing the only firm berries for egg deposition.

Ordination graphs of statistically significant relationships among plots for each production variable are shown in Figures 8.1 through 8.5. Similarly productive plots have their ordination positions superimposed by equivalent circles with size proportional to production. Where SNK tests failed to unambiguously differentiate them, plots were subjectively placed in the most reasonable production group to clarify relationships. Two features are readily apparent: production declines with decreasing

TABLE 8.4

Analysis of variance and Student-Newman-Keuls multiple comparisons of berry size (expressed as number of berries per dry gram of berries) among the 16 plots.

Source of Variation	SS	DF	MSS	$F_{statistic}$	$F_{critical}$	Probability
error	6.44E3	92	69.97	3.61	1.75	.001
groups	3.79E3	15	252.52			
total	10.22E3	107				

N_{fruit}/W_{fruit}	9	12	15	16	19	19	20	20	20	22	23	23	23	29	30	37
coefficient of variation %	36	32	38	38	26	31	14	14	12	20	17	11	37	49	26	100
ranked plots	5B	6	1B	8B	5	6B	8	7B	7	3B	4B	3	2	2B	4	1

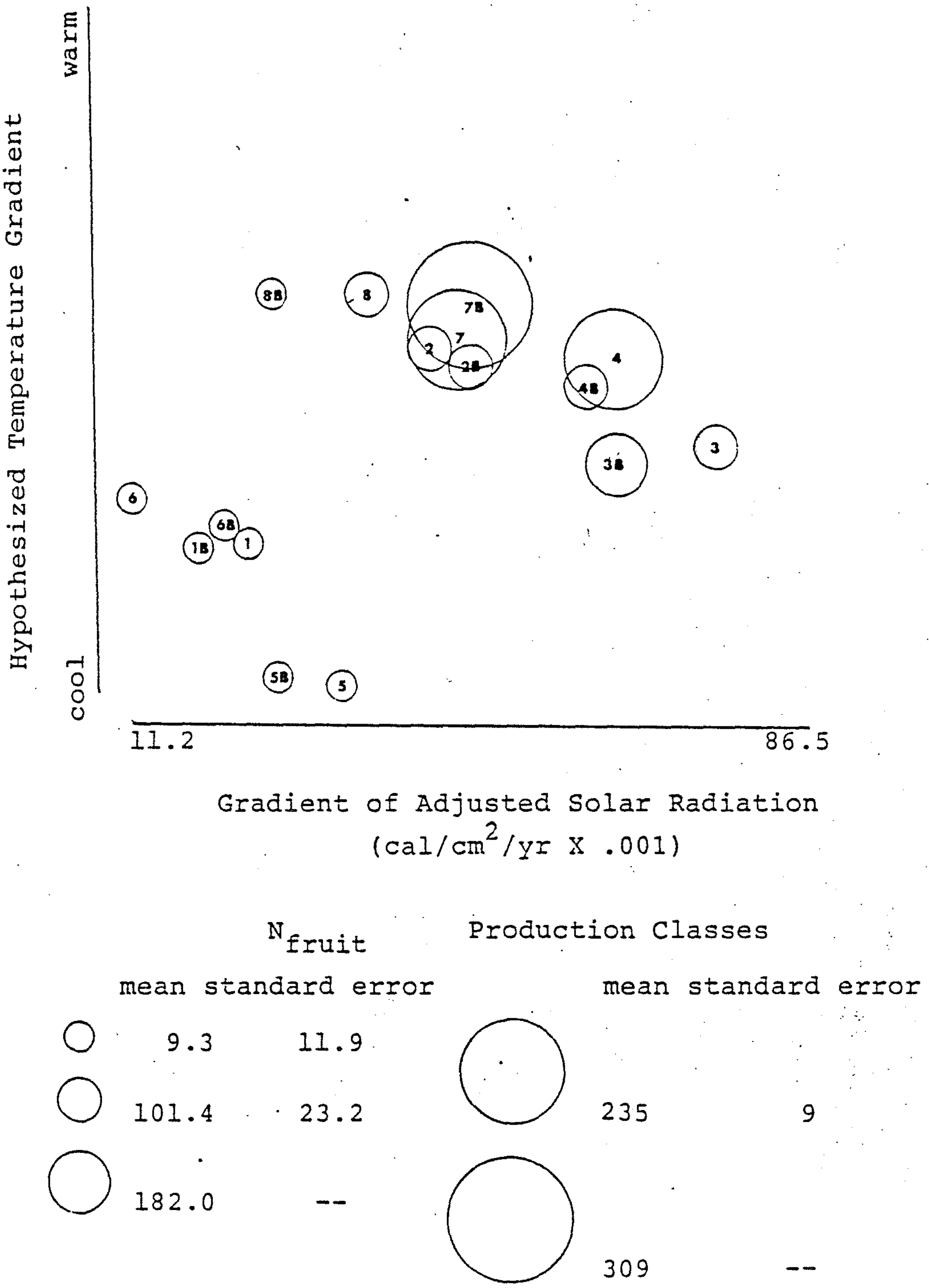


Figure 8.1. Ordination graph with environmental gradients indicated and the magnitude of N_{fruit} production for each plot superimposed on its ordination position. Circle size is proportional to production.

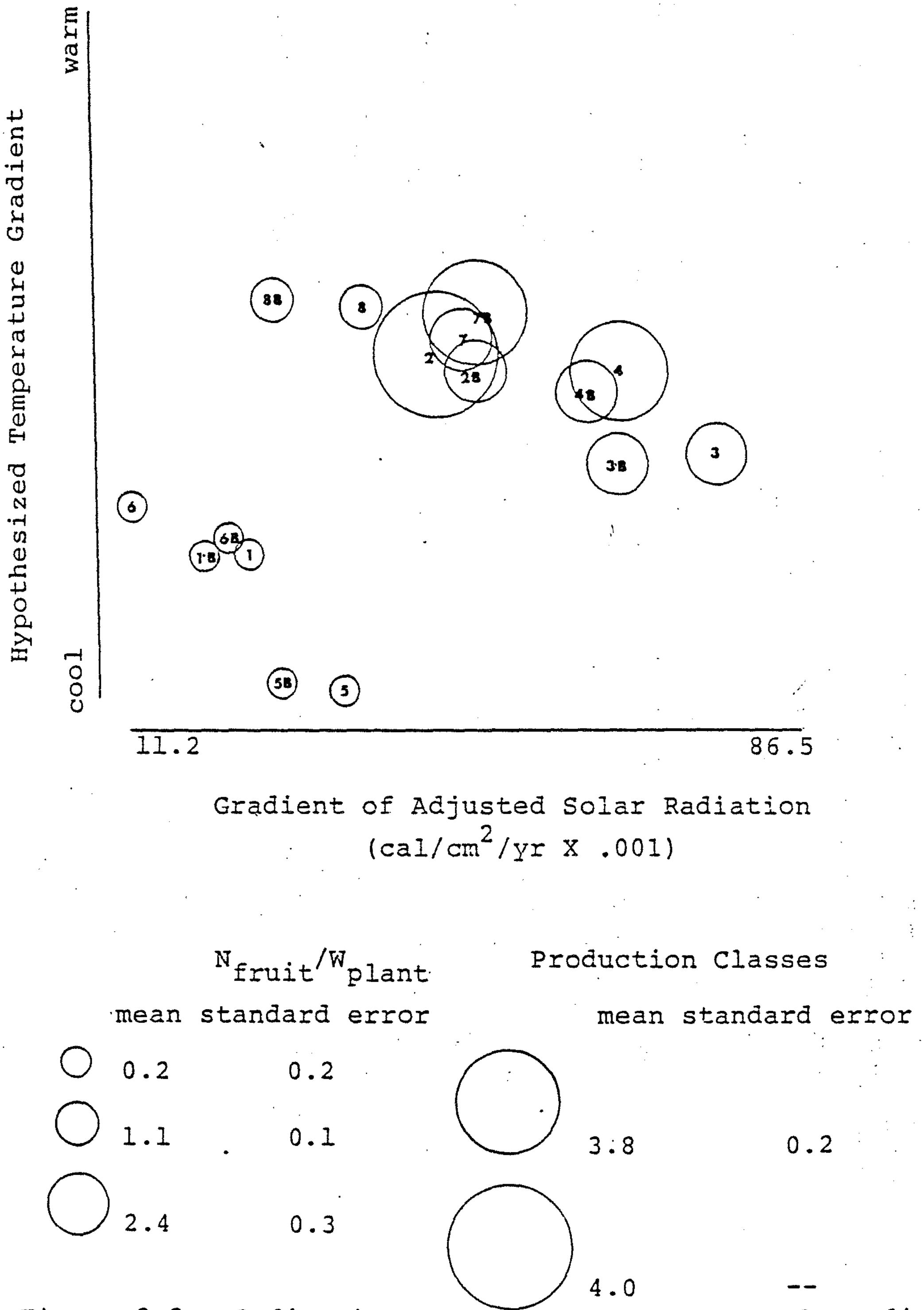


Figure 8.2. Ordination graph with environmental gradients indicated and the magnitude of N_{fruit}/W_{plant} production for each plot superimposed on its ordination position. Circle size is proportional to production.

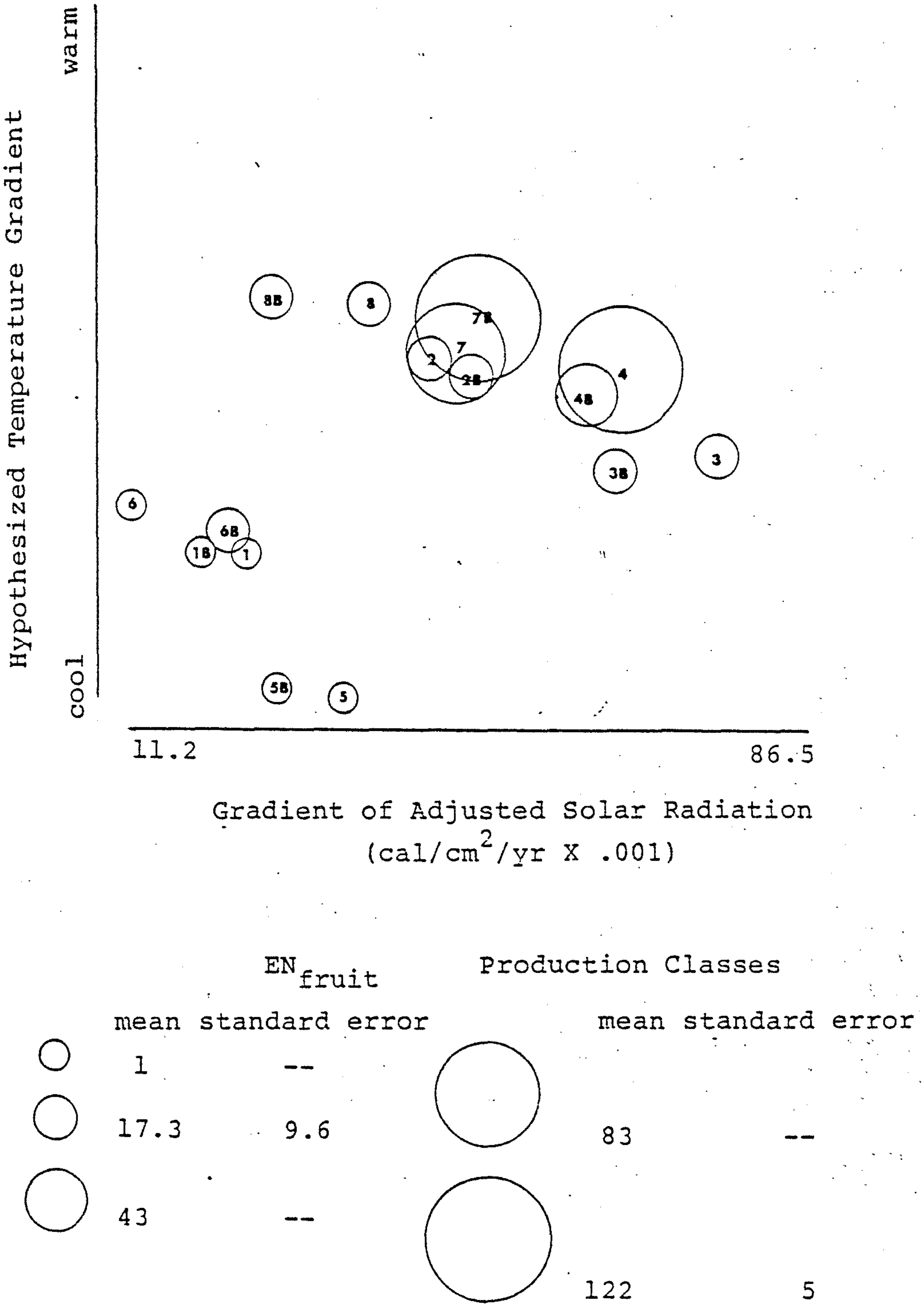


Figure 8.3. Ordination graph with environmental gradients indicated and the magnitude of EN_{fruit} production for each plot superimposed on its ordination position. Circle size is proportional to production.

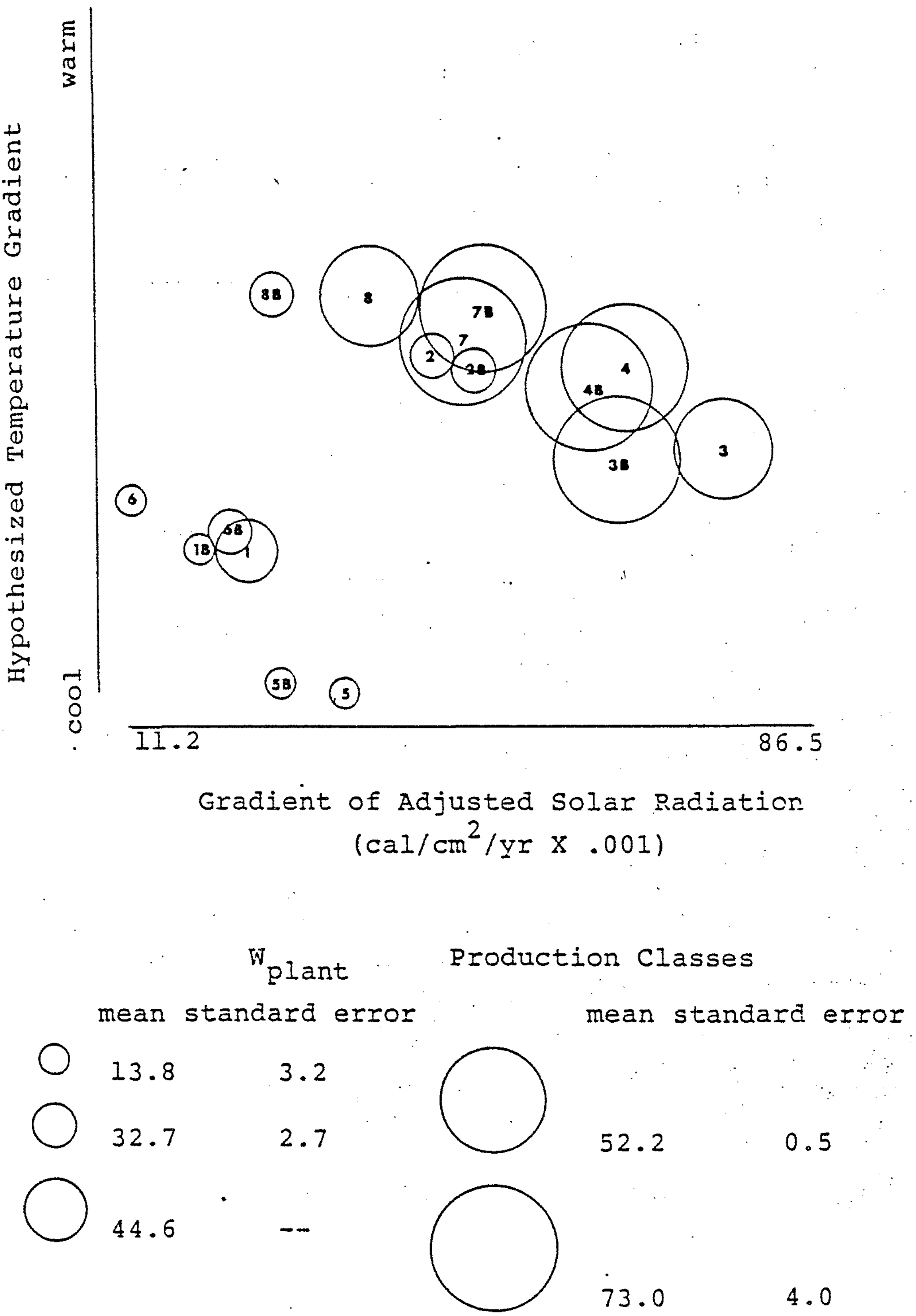


Figure 8.4. Ordination graph with environmental gradients indicated and the magnitude of W_{plant} production for each plot superimposed on its ordination position. Circle size is proportional to production.

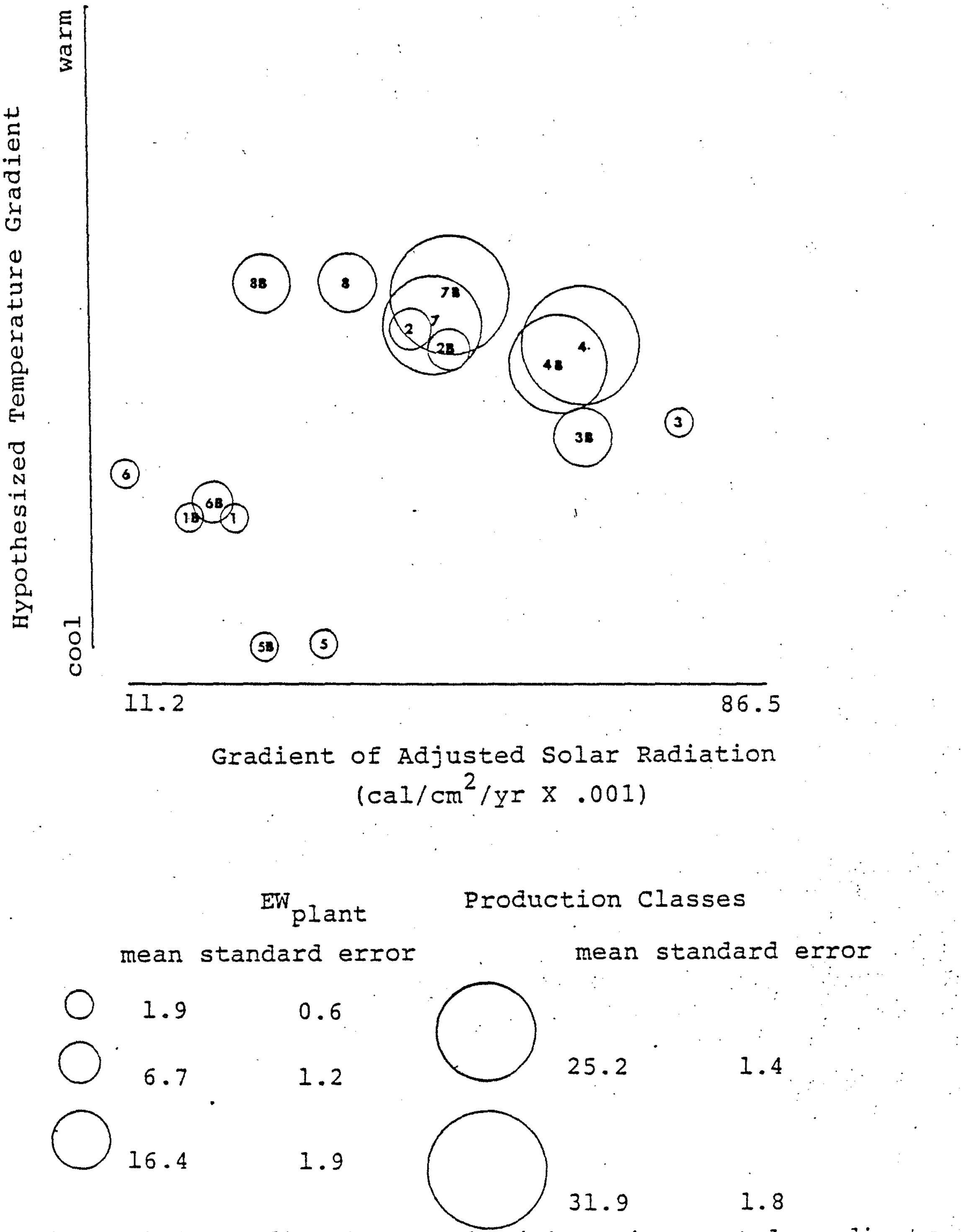


Figure 8.5. Ordination graph with environmental gradients indicated and the magnitude of EW$_{plant}$ production for each plot superimposed on its ordination position. Circle size is proportional to production.

adjusted solar radiation along the X-axis and increases along the hypothesized temperature gradient, Y-axis.

The relationship between production and adjusted solar radiation was evaluated by simple linear regression of logarithmic transformations of these variables. Power, exponential, and logarithmic functions were tested. The latter provided the best fit (Figures 8.6 through 8.10). Although all five relationships are significant, the strength of the relationship is not as great for random subplot production (Figures 8.8 and 8.10). Vegetative production, W_{plant} is the variable most strongly correlated with adjusted solar radiation. Because of the large component of L. occidentalis in stands 2 and 7, their understories' actual solar radiation is greater than that presented here which has been adjusted only by tree canopy outline. Lacking equations to predict leaf area index for this species, no method was available for objective estimation of adjusted solar radiation for these stands. Subjective adjustments were not made. Thus, the nonlinear response of fruit production to adjusted solar radiation should be interpreted conservatively. Within most stands, an increase in adjusted solar radiation is associated with an increase in production. Notable exceptions are stands 3 and 8 (Table 7.1 and Appendix B). The failure of subplots in these stands to respond photosynthetically to increased light suggests that some other factor may be limiting fruit

$y = 24.35 + 2.66x$

$r = .74$

$.002 > p > .001$

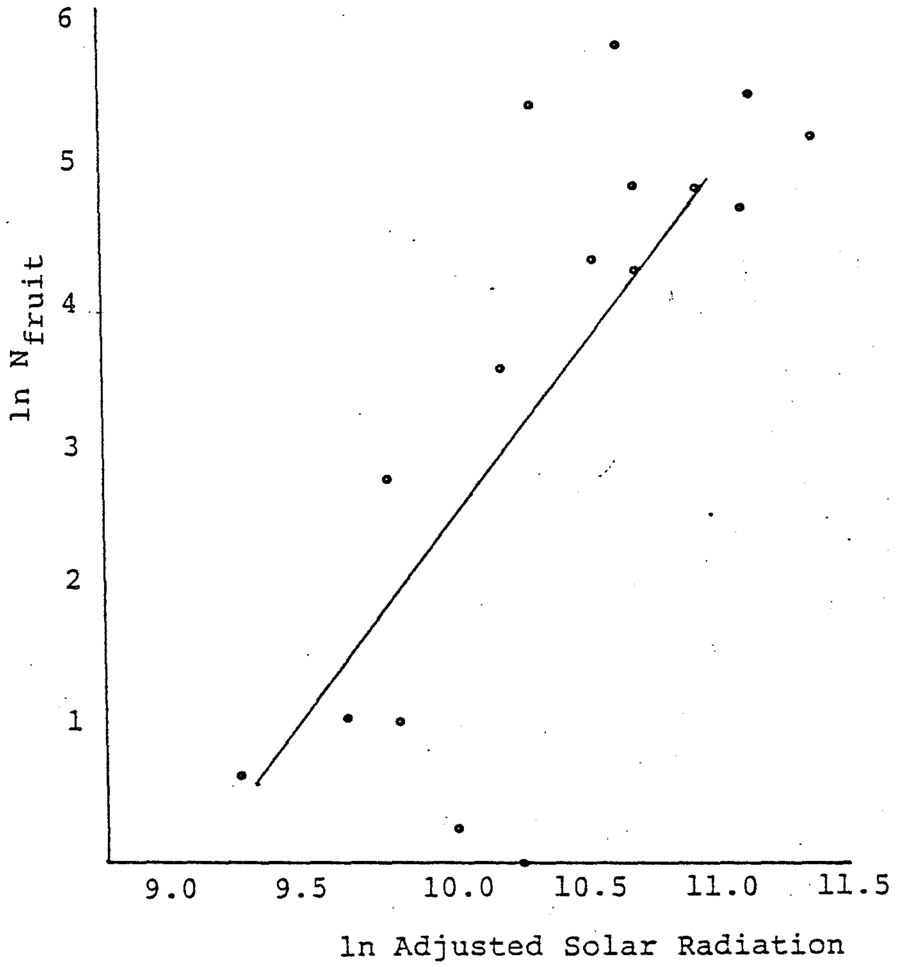


Figure 8.6. Regression of ln N_{fruit} with ln adjusted solar radiation.

$y = -18.06 + 1.72\ X$

$r = .72$

$.002 > p > .001$

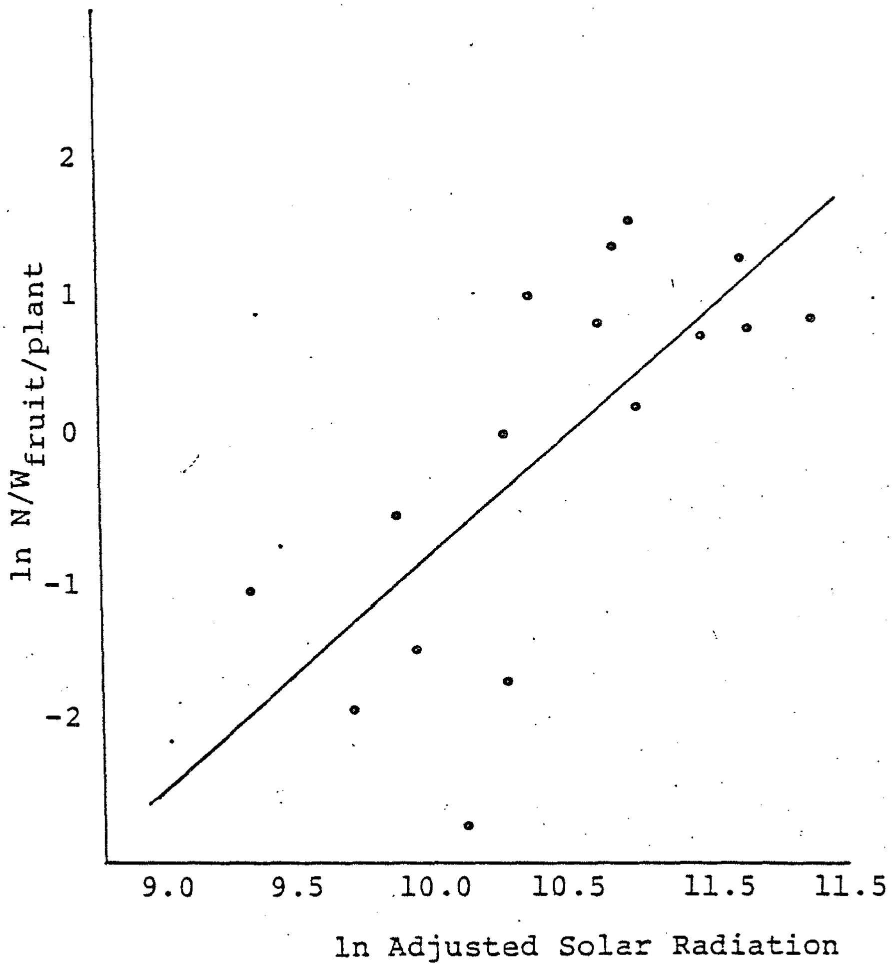


Figure 8.7. Regression of ln N_{fruit}/W_{plant} with ln adjusted solar radiation.

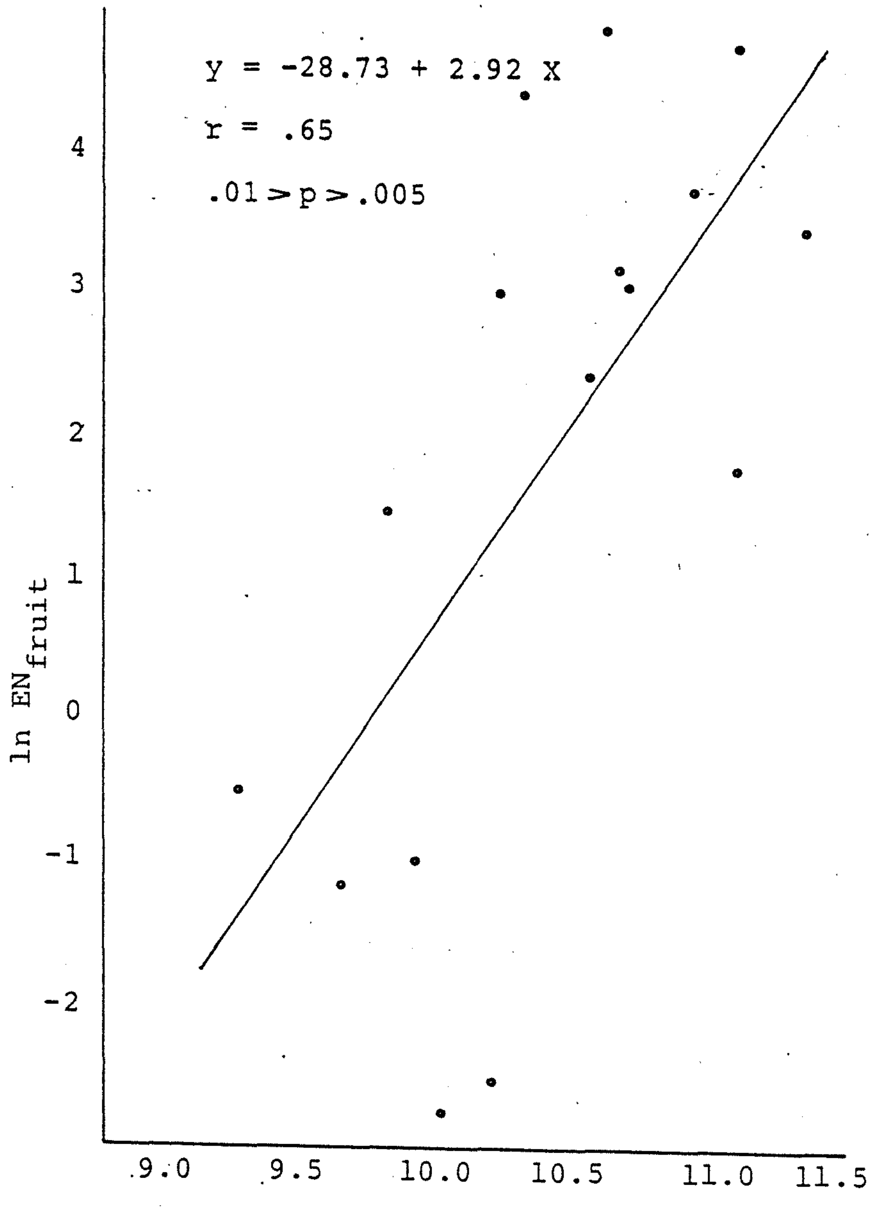


Figure 8.8. Regression of ln EN_{fruit} with ln adjusted solar radiation.

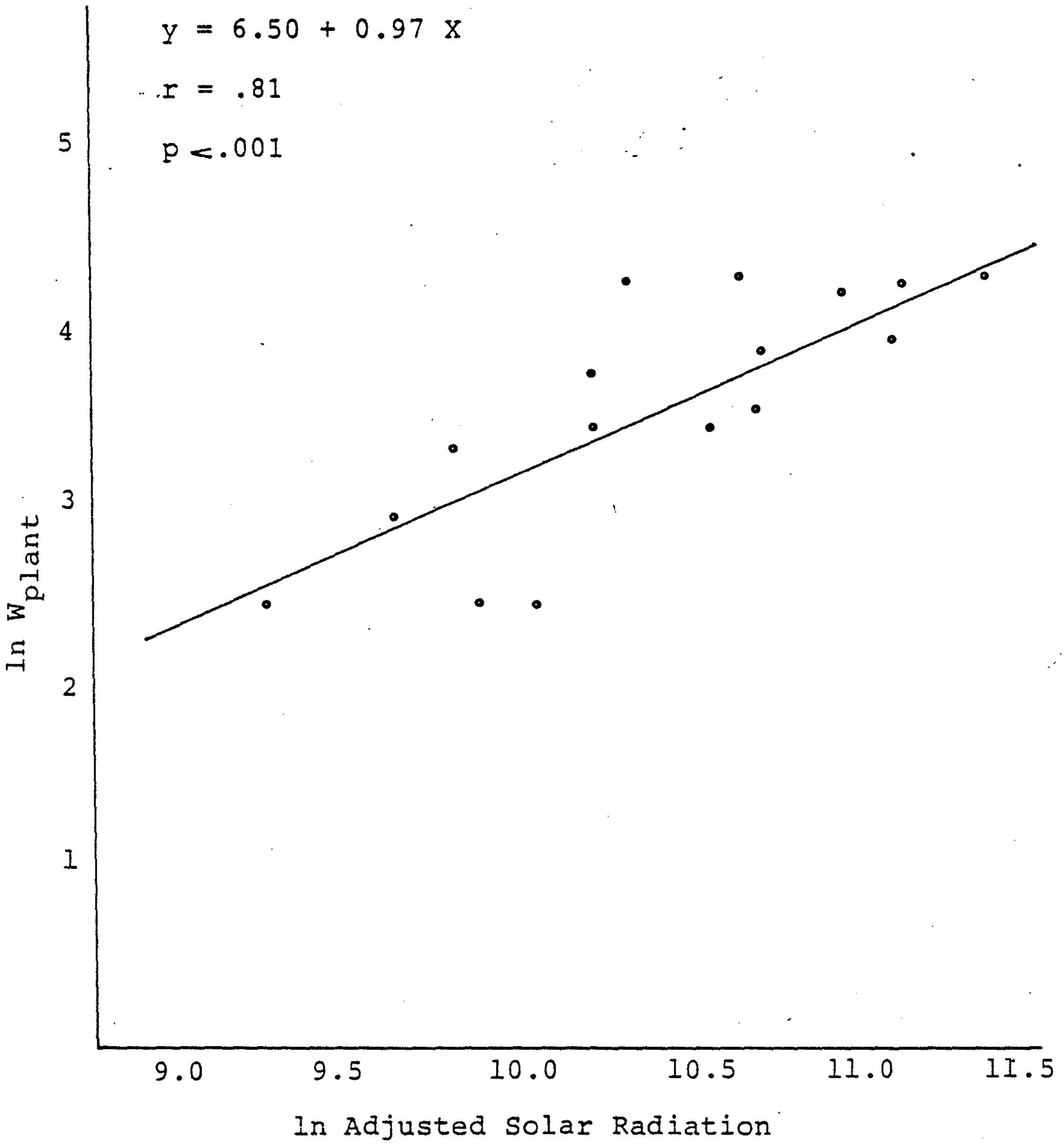


Figure 8.9. Regression of ln W_{plant} with ln adjusted solar radiation.

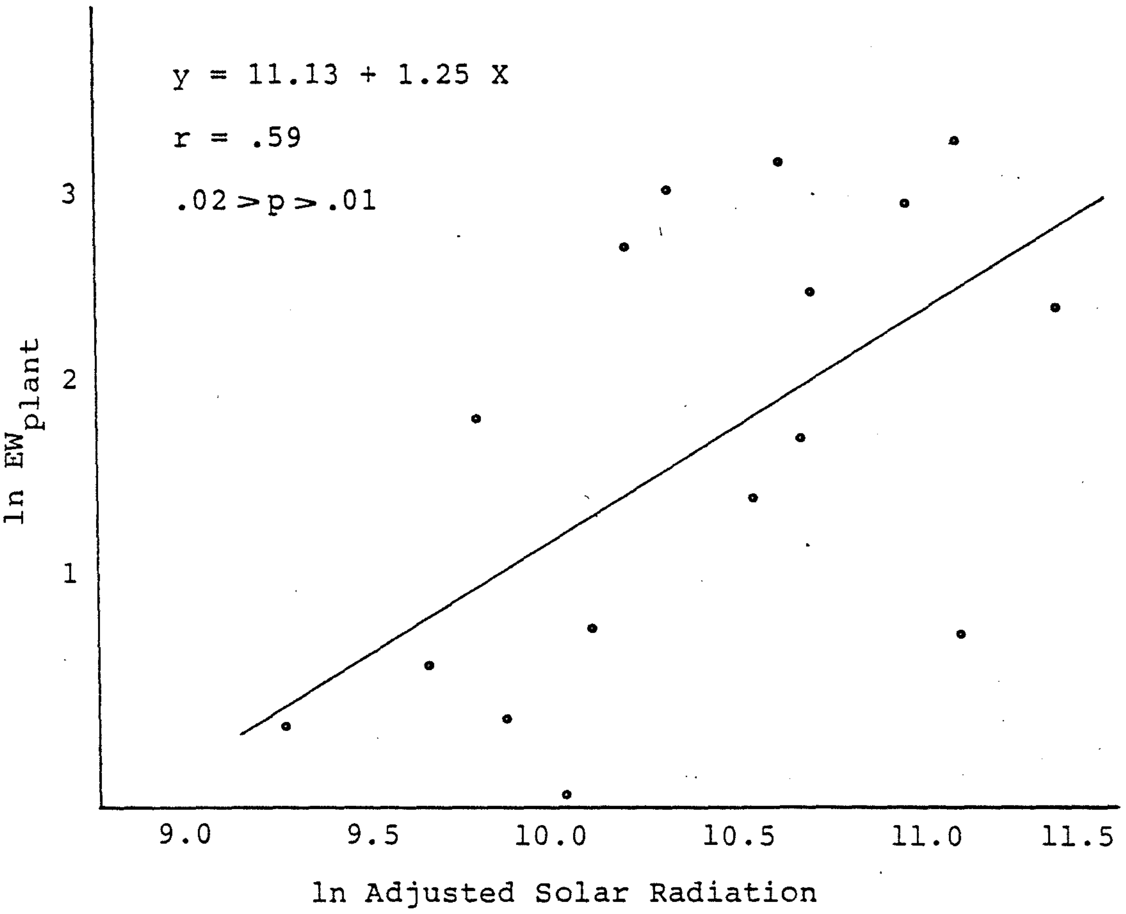


Figure 8.10. Regression of ln EW_{plant} with ln adjusted solar radiation.

production. A similar response by stand 8 for $EN_{production}$ is attributed to successional changes in stand structure to be discussed later.

Comparisons of slopes and correlation coefficients from the regressions (Figures 8.6 through 8.10) indicated whether relationships between adjusted solar radiation and production were statistically similar within each of the following response pairs: subplot fruit/subplot vegetative; subplot fruit/subplot photosynthetic efficiency; subplot fruit/random subplot fruit; subplot vegetation/random subplot vegetation (Table 8.5). For all pairs of relationships compared, strength of the association between adjusted solar radiation and production was not significantly different. Subplot and random subplot responses to increasing adjusted solar radiation were not significantly different. The sensitivity of fruit production to adjusted solar radiation is greater than either photosynthetic response or vegetative production. Slower vegetative and photosynthetic response rates suggest that V. membranaceum is a shade plant, that is, its leaves are light saturated at relatively low intensities. In addition, the elevated response of fruit production relative to vegetative production may be related to stem morphology. Stem elongation generally produced two or three nodes during a single growing season, each node capable of producing one berry.

TABLE 8.5

Results of pairwise comparisons of relationships between various production variables and adjusted solar radiation.

Production comparison	Production variable pair compared	Does production show a similar rate of response to increasing adjusted solar radiation for each of the variables?*	Is the strength of the association between production and adjusted solar radiation similar for each of the variables?**
Subplot fruit - Subplot vegetative	$W_{fruit} - W_{plant}$	No $P < .05$ W_{fruit} response $>$ W_{plant} response	Yes $P > .30$
Subplot vegetative - Random subplot vegetative	$W_{plant} - EW_{plant}$	Yes $P > .05$	Yes $P > .34$
Subplot fruit - Random subplot fruit	$N_{fruit} - EN_{fruit}$	Yes $P > .05$	Yes $P > .30$
Subplot fruit - Subplot photosynthetic Efficiency	$N_{fruit} - N_{fruit}/W_{plant}$	No $P < .05$ N_{fruit} response $>$ N/W_{fruit} response	Yes $P > .30$

*From comparison of the slopes of their two regressions.

**From comparison of the correlation coefficient of their two regressions.

Once this elongation limit is reached, additional resources may be allocated to developing additional sexual primordia. On the other hand, occasional stems producing from five to seven barren nodes were observed. These may have represented internal dysfunction and investment of resources in vegetative rather than sexual structures.

Production among the three productivity groups suggested by the ANOVA and SNK tests (Table 8.2) increases with increasing adjusted solar radiation and temperature (Figure 8.11). The following hypothesis is suggested: V. membranaceum production is sensitive to both adjusted solar radiation and heat and strongly influenced by the interaction between these factors. Stands of the unproductive group have inadequate levels of either growth factor for notable fruit or vegetative production. The interaction effect is most apparent in the depressed response of the intermediately productive group. Stand 3, with abundant levels of light, lacks adequate heat. While stands 8 and 2 approach threshold levels of light and heat, neither are abundant enough for notable fruit production. Stands of the productive group, with at least minimal levels of each growth factor, have fruit yields significantly greater than all other stands or groups of stands. If, in fact, such a scenario holds, given adequate levels of light, production is very sensitive to heat. This is apparent in the reduced production of stand 2 relative to stand 7. The

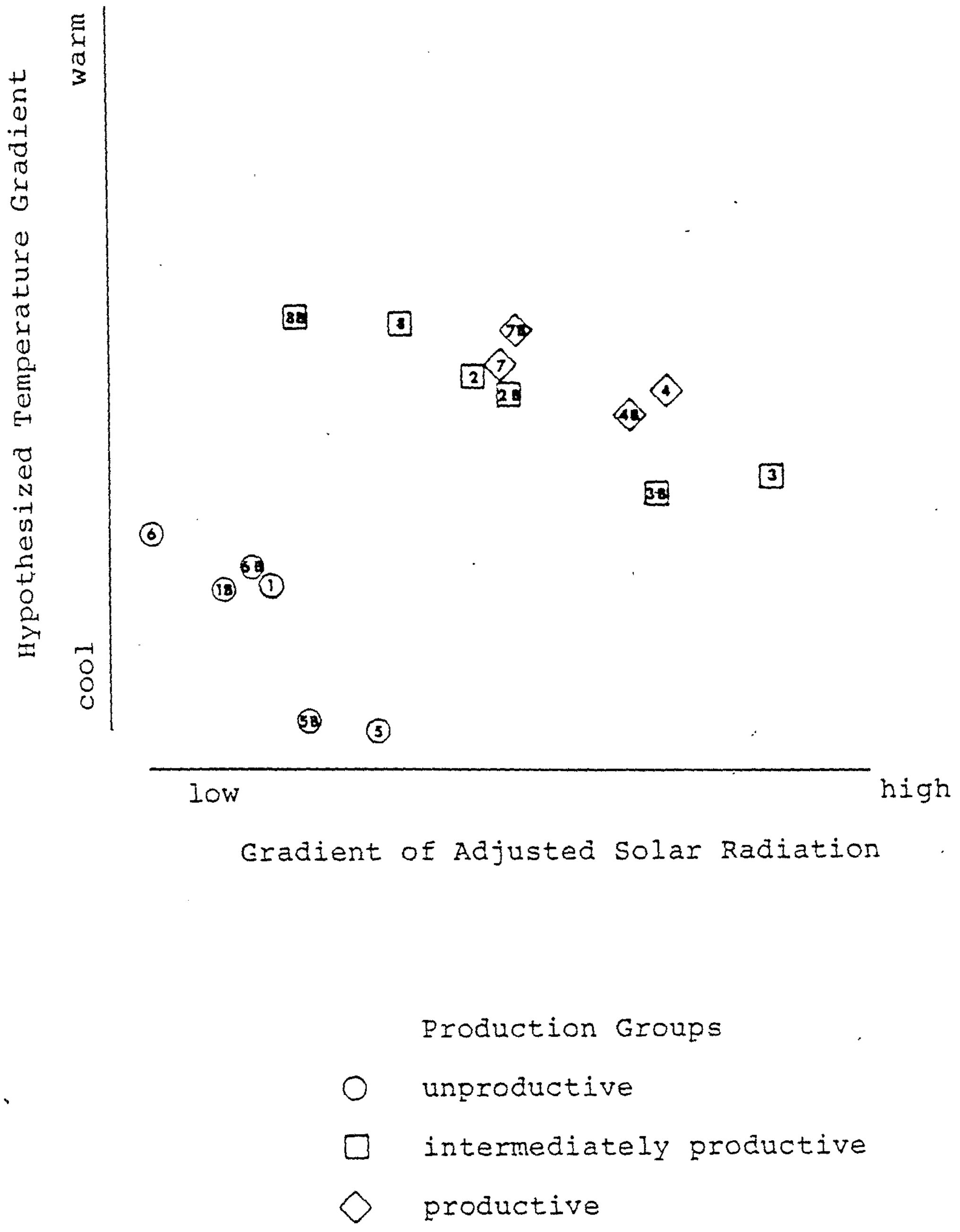


Figure 8.11. Ordination graph with the three production groups indicated with respect to the environmental gradients.

elevated production of stand 4, relative to the equally warm stand 2, is likely due to its compensatingly high level of light.

The two most productive stands and their neighbors were infected by a rust, *Pucciniastrum* spp. (Table 7.1). The sensitivity of many such fungi to microsite factors may have implications for *V. membranaceum* production (Driver 1983, personal communication). However, rust infection in stands 3 and 8 obscures relationships.

Results of the stand ordination/classification and *V. membranaceum* production analysis have shown that good yields, although more dependent on extrinsic biotic than intrinsic site factors, may occur on at least two habitat types; *A. amabilis-T. mertensiana*/*V. membranaceum* and *A. amabilis*/*V. viride*. However, production within a habitat may vary significantly and gross community features often are not ideal predictors. Importance values (IV) of plants that appeared to be promising indicators of *V. membranaceum* production, when the two occurred together, were correlated with *V. membranaceum* production to evaluate their predictive ability (Table 8.6).

R. albiflorum and *L. occidentalis* were not included in these analyses because individuals were not consistently present throughout the study area. *R. albiflorum*, which was strongly associated with poor fruit production, is more competitive than *V. membranaceum* on cold, wet sites.

TABLE 8.6

Results of the regressions between various production variables and importance values of plants that appeared to be promising indicators of <u>V. membranaceum</u> production.

Indicator Plant \ Production Variable	N_{fruit}	EN_{fruit}	N_{fruit}/W_{plant}	W_{plant}	EN_{plant}
<u>V. membranaceum</u>	$r = .52$ $P < .05$ s *	$r = .28$ $.50 > P > .20$	$r = .42$ $.20 > P > .10$	$r = .44$ $.10 > P > .05$	$r = .48$ $.10 > P > .05$
<u>R. lasiococcus</u>	$r = .78$ $P < .001$ s	$r = .73$ $P < .001$ s	$r = .55$ $P < .05$ s	$r = .78$ $P < .001$ s	$r = .68$ $P < .01$ s
<u>A. amabilis</u>	$r = -.73$ $P < .001$ s	$r = -.54$ $P < .05$ s	$r = -.81$ $P < .001$ s	$r = -.69$ $P < .01$ s	$r = -.45$ $.10 > P > .05$
<u>T. mertensiana</u>	$r = 0$ $P > .99$	$r = -.01$ $P > .50$	$r = .04$ $P > .50$	$r = .15$ $P > .50$	$r = .04$ $P > .50$

* s indicates a significant correlation.

Although all stands with significant L. occidentalis were productive, not all productive stands contained conspicuous L. occidentalis, e.g. stand 4.

Of the species evaluated, R. lasiococcus was most strongly correlated with all V. membranaceum fruit production statistics except N_{fruit}/W_{plant}. The strong inverse relationship between production and the IV of A. amabilis reflects the latter species' closed canopy status in stands, 1, 5, 6 and 8: the former three as late seral stands, the latter stand by virtue of disturbance intensity and subsequent colonization. The only significant correlation between the IV of V. membranaceum and its production was for subplot fruit production, N_{fruit}. These results for V. membranaceum reflect the sensitivity of its production to competition and stand development factors.

The importance value of V. membranaceum on each plot is shown symbolically in Figure 8.12. With some exceptions, these importance values fit the three production categories described earlier, Table 8.2 and Figure 8.11. The dominance of V. membranaceum on plot 6B, relative to plot 6 and its other cohorts in the unproductive group, is the result of its location beneath an overstory gap. This suggests that overstory competition is the primary factor depressing V. membranaceum production. The relative importance of above ground versus below ground competition is not certain. Production on plot 6B was negligible even though

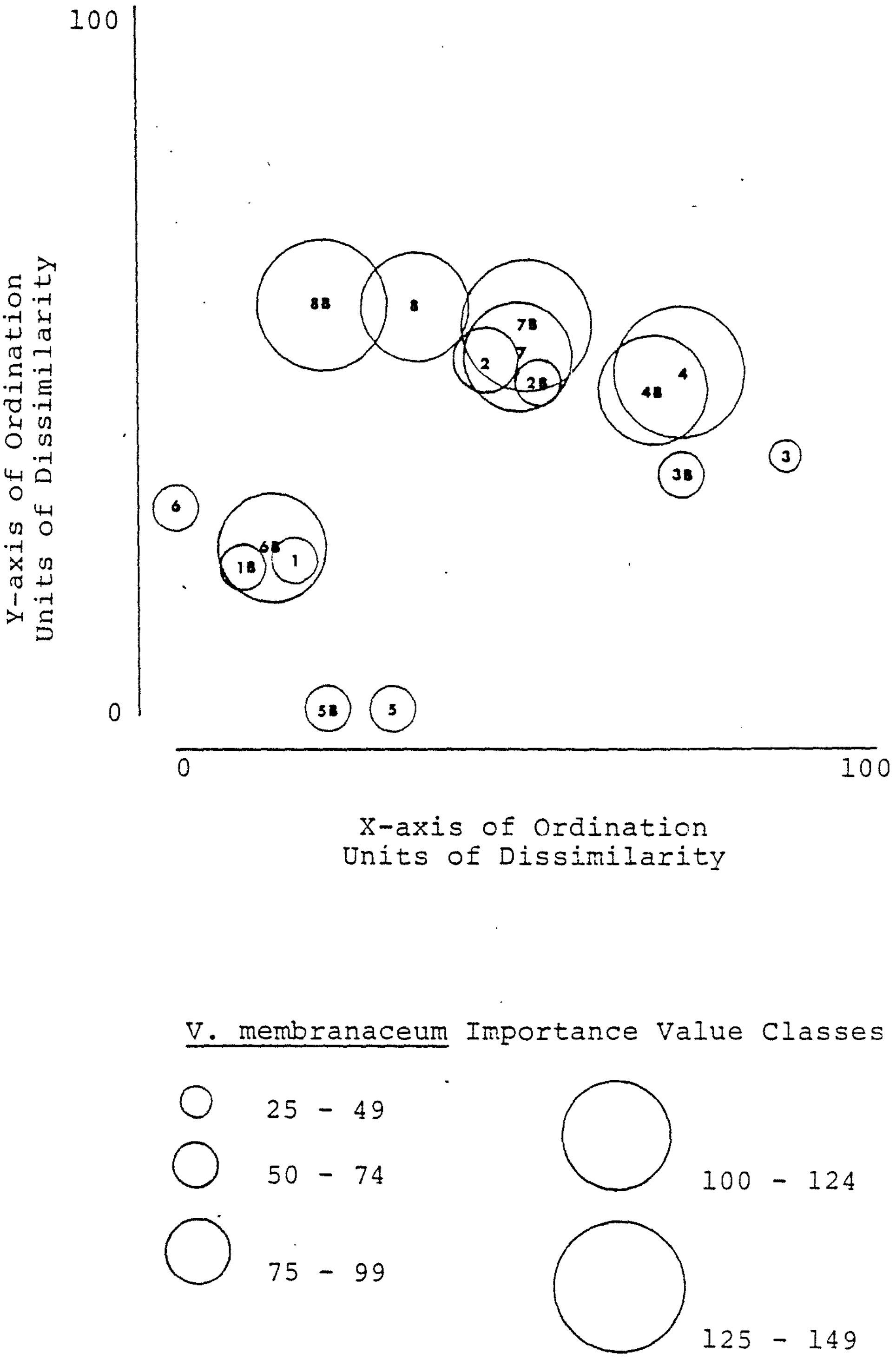


Figure 8.12. Polar ordination of sample plots with the importance value of <u>V. membranaceum</u> for each plot superimposed on its ordination position.

V. membranaceum was dominant on the plot. Advanced *A. amabilis* regeneration has asserted dominance, suggesting that the overstory opening is several years old. Perhaps production was higher shortly after the canopy opened.

The moderately productive stand 8 is the other notable deviation from the production categories. Even though this stand is more completely dominated by dense-crowned *A. amabilis* than stand 7, it supports a comparable *V. membranaceum* population. The two stands are the same age and probably equivalent in terms of intrinsic growth factors. Their different production is probably a result of canopy restricted light and heat in stand 8. Zamora (1982) reports that shrub vigor remains high in the short term following canopy closure. Because of its overstory of *A. amabilis*, stand 8 experienced canopy closure before stand 7. The dominant *V. membranaceum* population of stand 8 reflects conditions earlier in succession and, although its less light-sensitive vegetation retains moderate vegetative productivity, its fruit production has declined considerably.

Fruit yield of the most productive stand, 7, was 117 kg/ha (ripe weight) in 1982 (tree canopy densities of stands in this study are presented in Appendix B). Minore and Dubrasich (1978) measured fruit production over a range of environments and for several plant communities southwest of Mt. Adams, Washington. They report that for

A. amabilis/*V. membranaceum-R. lasiococcus* communities, with tree canopy densities ranging from four to 91%, 1976 fruit yield averaged 231 kg/ha. At the nearby Sawtooth huckleberry field, fruit production ranged from 0 to 137 kg/ha between 1972 and 1975 and in 1977 (Minore et al. 1979). This field is experiencing tree invasion, predominantly *A. lasiocarpa*, and had tree canopy densities of 31% in 1972 and 38% in 1977. Direct comparisons of these yields are unreliable because of annual variation and site differences. However, these data indicate that *V. membranaceum* populations beneath a significant tree overstory are capable of fruit production comparable to that of more open and renowned fields.

The age of *V. membranaceum* stems or rhizomes may be correlated with fruit and vegetative production. The average maximum age of stems and rhizomes were 14 and 18 years, respectively, for the study area as a whole. Comparable stem ages for *V. myrtillus* in Sweden were 18 years (Silvertown 1982). While the ANOVA comparing average maximum stem age among the 16 plots indicated at least one significant inequality, the SNK test located it only between the extremes. There was no significant difference in average maximum rhizome age among the 16 plots (Table 8.7). These data indicate only that an individual stem has the potential to produce fruit for about 14 years, not that there is or is not some productivity trend through those years.

TABLE 8.7

Analysis of variance and Student-Newman-Keuls multiple comparison for mean *V. membranaceum* subplot stem age and analysis of variance comparing mean subplot rhizome age among 16 plots.

ANOVA for stem age	Source of Variation	SS	DF	MSS	$F_{statistic}$	$F_{critical}$	Probability
	error	14.31E2	112	12.77	2.21	1.75	.01
	groups	4.25E2	15	28.34			
	total	18.55E2	127				

mean stem age	11	11	12	12	12	12	13	13	13	14	14	15	15	16	16	18
coefficient of variation %	23	22	15	23	24	21	24	34	22	22	15	28	26	33	39	22
ranked plots	3	5	6B	5B	6	2B	1	8B	2	1B	3B	8	7	4	7B	4B

ANOVA for rhizome age	Source of Variation	SS	DF	MSS	$F_{statistic}$	$F_{critical}$	Probability
	error	34.24E2	112	30.57	1.03	1.75	.40
	groups	4.73E2	15	31.54			
	total	34.87E2	127				

CHAPTER NINE

Summary and Conclusions

Following is a summary of the results of this study:

1. Stands located in different environments fell into the categories of fruit production: productive, intermediate, and unproductive. Among unproductive stands, fruit production was not significantly different. Within and among the more productive stands, differences in fruit production were significant and more profound with increasing production. Conversely, variation among clones decreased with increasing production among stands. This pattern of variation holds for the measured production of V. membranaceum subplots and the expected production of random subplots.

In general, differences among plots were more significant for vegetative than fruit production. The vegetative production of a measured subplot of V. membranaceum was less variable among the unproductive than productive plots. Conversely, the expected production of a random subplot was more variable among the productive than unproductive plots. Variation within plots was low for either variable expressing vegetative production.

2. The success rate for development of flowers to fruit was less than 25% for four plants in each of two

stands. For a subjectively selected plant, this rate was 50%.

3. Fruit and vegetative production appear to increase logarithmically with light and indeterminately with temperature. These relationships are empirically and statistically significant.

4. For both V. membranaceum subplots and random subplots, the relationship between production and light is not significantly different. However, fruit production is significantly more sensitive to light than are vegetative production or photosynthetic response.

5. A less dense L. occidentalis canopy may account in part for the elevated production of one of the two most productive stands. However, such an effect in one intermediately productive stand was not apparent.

6. Analyses suggest that some factor other than light may limit fruit production in plots in each of two intermediately productive stands.

7. Preliminary reconnaissance and the literature both suggest that significant fruit production may be consistently expected only on subalpine sites capable of supporting closed A. amabilis forests. Of such sites, the best development of V. membranaceum occurs on cool, moist habitats: intermediate between cold and dry sites characterized by R. albiflorum and X. tenax, respectively. Of those evaluated in this study, significantly high yields

occurred in A. amabilis/V. viride and A. amabilis-T. mertensiana/V. membranaceum habitats. The A. amabilis-T. heterophylla/V. membranaceum habitat type was represented by an old growth stand with insignificant V. membranaceum, no inference is made concerning its early seral potential. On an A. amabilis/M. ferruginea habitat, R. albiflorum occurred with and dominated V. membranaceum.

8. There is a general trend of declining production as a function of successional time. The rate of decline is variable. Although vegetative vigor remains high in the short term following canopy closure, fruit production appears to decline soon after closure. However, a comparison of the study area and a renowned berry field suggests that V. membranaceum populations beneath a significant tree overstudy are capable of fruit production comparable to that of open grown stands.

9. Of those plants occurring with V. membranaceum, R. lasiococcus was most strongly correlated with production by the former species.

10. An individual stem of a V. membranaceum clone has the potential to produce fruit for about 14 years.

Although V. membranaceum production unarguably declines after crown closure, the variability of the latter makes it unrealistic to predict the former. However, the relationship between fire and those factors contributing to the appearance of a V. membranaceum dominated sere may not be so obscure. The response of V. membranaceum to scheduled prescribed fire as well as unscheduled wildfire should be evaluated. At the same time, the physiologic factors influencing production and its variation could be evaluated. Although the importance of abundant light is most obvious, other factors should not be overlooked: e.g. the light intensity at which leaves become saturated; moisture and temperature and their distribution; soil and nutrition factors, particularly the possible successional relationship between potassium and growth. Other useful areas of research are: the nature of seed in the forest floor and the significance of seedlings; pollination efficiency and the potential self sterility of V. membranaceum clones.

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Appendix A

Scientific and Common Plant Names

TREES

Abies amabilis (Dougl.) Forbes	silver fir
Abies grandis (Dougl.) Forbes	grand fir
Abies lasiocarpa (Hook.) Nutt.	subalpine fir
Chamaecyparis nootkatensis (D. Don) Spach.	yellow cedar
Larrea cav.	creosote bush
Larix occidentalis Nutt.	western larch
Picea engelmannii Parry	Engelmann spruce
Pinus albicaulis Engelm.	white bark pine
Pinus contorta Dougl.	lodgepole pine
Pinus monticola Dougl.	western white pine
Pinus ponderosa Dougl.	ponderosa pine
Pseudotsuga menziesii (Mirbel) Franco.	Douglas fir
Thuja plicata Donn.	western red cedar
Tsuga heterophylla (Raf.) Sarg.	western hemlock
Tsuga mertensiana (Bong.) Carr.	mountain hemlock

SHRUBS

Arctostaphylos uva-ursi (L.) Spreng.	kinnikinnick
Ceanothus sanguineus Pursh	redstem ceanothus
Gaultheria shallon Pursh	salal
Juniperus communis L.	mountain juniper
Menziesia ferruginea Smith	fool's huckleberry
Pachistima myrsinites (Pursh) Raf.	pachistima
Rhododendron albiflorum Hook.	Cascade azalea
Ribes viscosissimum Pursh	sticky currant
Spiraea betulifolia Pall.	shiny leaf spiraea
Vaccinium alaskaense Howell	Alaska huckleberry
Vaccinium angustifolium	lowbush blueberry
Vaccinium caespitosum Michx.	dwarf huckleberry
Vaccinium corymbosum	highbush blueberry
Vaccinium deliciosum Piper	Cascade huckleberry
Vaccinium globulare Rydb.	globe huckleberry
Vaccinium macrocarpon Ait	cultivated cranberry
Vaccinium membranaceum Dougl.	big huckleberry
Vaccinium myrtillus L.	dwarf bilberry
Vaccinium occidentale Gray	western huckleberry
Vaccinium ovalifolium Smith	oval-leaf huckleberry
Vaccinium ovatum Pursh	shot huckleberry
Vaccinium oxycoccos L.	swamp cranberry
Vaccinium scoparium Leiberg	grouse whortleberry
Vaccinium vitis-idaea L.	
Vaccinium uliginosum L.	bog bilberry

HERBS

Achillea millefolium L.	common yarrow
Agoseris aurantiaca (Hook.) Greene	orange agoseris
Anaphalis margaritacea DC.	pearly everlasting
Arnica cordifolia	heart-leaf arnica
Achlys triphylla (Smith) DC.	vanillaleaf
Calamagrostis Adans.	reedgrass
Carex L.	sedge
Castillega Mutis ex L.F.	Indian-paintbrush
Chimaphila umbellata (L.) Bart.	Prince's-pine
Epilobium augustifolium L.	fireweed
Euphorbia serpyllifolia Pers.	spurge
Goodyera oblongifolia Raf.	Rattlesnake-plantain
Hieracium scouleri Hook.	woolly-weed
Linnaea borealis L.	twinflower
Lupinus polyphyllus Lindl.	bigleaf lupine
Penstemon Mitch.	penstemon
Polemonium pulcherrimum Hook.	polemonium
Pyrola secunda L.	one-sided wintergreen
Rubus lasiococcus Gray	dwarf bramble
Senecio vulgaris L.	common groundsel
Valeriana sitchensis Bong	Sitka valerian
Veratrum viride Ait.	false hellebore
Xerophyllum tenax (Pursh) Nutt.	beargrass

APPENDIX B

Plot Environmental Data

Stand	1		2		3		4		5		6		7		8	
Plot	1	1B	2	2B	3	3B	4	4B	5	5B	6	6B	7	7B	8	8B
Percent slope	20	3	10	5	28	28	27	30	51	35	13	12	29	22	25	30
Aspect (azimuth)	110	140	130	112	316	316	325	335	5	350	60	60	60	60	90	70
Elevation (m)	1560		1580		1660		1680		1580		1390		1460		1410	
Adjusted solar radiation ($cal/cm^2/yr$)	24860	24212	44792	39565	66212	86481	67217	57771	16409	20429	11259	19302	31345	41698	44864	28109
Percent overstudy density	84	86	75	77	51	44	51	53	82	82	93	88	79	73	73	81