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Productivity and taxonomy of the Vaccinium globulare V. membranaceum complex in western Montana

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PRODUCTIVITY AND TAXONOMY OF THE

VACCINIUM _GLOBULARE_, _V._ _MEMBRANACEUM_ COMPLEX

IN WESTERN MONTANA

By

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A ranked set sampling pattern was used to determine the effects of wildfires and logging practices on berry production of globe huckleberry plants (V. globulare) in known grizzly bear habitat in northwestern Montana. Mature stands or stands burned between 60 and 100 years ago were unproductive. Berry production increased if forested areas with some huckleberry plants, on mesic northern or eastern aspects were burned by wildfire 25 to 60 years ago, or were clearcut and broadcast-burned 8 to 15 years ago. Disturbance by either fire or logging on xeric, south and west aspects reduced percent cover and berry production; scarified clearcuts were unproductive on all aspects. Reductions in competition from understory species that accompanied increases in elevation improved berry production within sites, but the increases in environmental stresses reduced the average height of globe huckleberry plants. Berry production in thinned stands was erratic and not related to the parameters considered in this study. Fruit production was limited when the tree canopy cover was greater than 30 percent. The absence of light in old-aged stands limited flower formation and berry maturation. A site's berry production was not related to the percent cover or height of globe huckleberry plants because the species is late-seral or climax, with meso-seral fruit production. Berries from different sites were tested for sugar content. Because all samples were collected at approximately the same stage of fruit maturation, there was no correlation between berry sugar content and date of sample collections, but sugar content increased with elevation. Berry crops of 3 productive areas sampled in 1977 failed in 1978, presumably because of late frosts or snowstorms. Grizzly bears in 1 area did not leave, even though the crop failure was widespread. The failures in the other 2 areas were restricted to microsites or drainages and probably did not limit bear intake of berries. Because evidence from other studies suggests bears prefer older clearcuts with tree or shrub cover and wildfires 25-60 years old, recommendations are made for long-range planning in the manipulation of grizzly habitat to assure the production of huckleberry crops in the future.

Leaves of collected globe huckleberry and thin-leaved huckleberry (V. membranaceum) shrubs were almost all elliptic and half as wide as long, regardless of the region of collection. All the flowers collected in Montana, Idaho, eastern Washington, and Oregon were broader than long, or round. The 2 species were differentiated by the shape of the leaf apices of the second or third leaves on the current annual growth. No new locations of the oval-leaved huckleberry (V. ovalifolium) or the velvet-leaved huckleberry (V. myrtilloides) were found in western Montana.

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CHAPTER I

INTRODUCTION

Seven species of *Vaccinium* occur in western Montana (Stickney 1969). This study is primarily concerned with two, *V. globulare* and *V. membranaceum*. Both species are often referred to as huckleberries. Because of the role they play as a food source for the threatened grizzly (*Ursus arctos horribilis*), this study was undertaken to clarify their status in grizzly range, and to obtain basic data about huckleberry distribution, productivity, physiological requirements, and responses to disturbances such as fire and logging. Information about huckleberry fruit production will benefit not only grizzlies but the many other birds and mammals that rely on the berries for fall sustenance.

Berry Production

Huckleberry distribution and productivity are influenced by the occurrence and periodicity of fire. Light, surface burning at 2- to 3-year intervals is a common management tool used to increase productivity in cultivated eastern North American blueberries (Black 1963). Personal communications with others (Stickney, pers. comm.) and my own preliminary field observations suggest berry production is limited in western Montana *Vaccinium* species for at least several years after a burn. The recovery rate is related to the intensity of the fire and the species involved (Miller 1977), but production eventually increases. In the Pacific Northwest, large fields of huckleberries were once maintained by repeated natural fires. In the absence of fire, other plant species became dominant in many of those fields (Minore 1972).

Vaccinium berry production declines in the absence of fire, but Pfister et al. (1977) list globe huckleberry and grouse whortleberry (V. scoparium) as shrub components of some climax community stands in western Montana. In those communities, Vaccinium may not be dependent on fire for its continued existence in a plant community. But if the general information about the physiological responses of the Vaccinium species of the Pacific Northwest and the eastern United States applies to the huckleberries in Montana, it seems that fires and burns in areas previously occupied by huckleberries will eventually increase berry production.

The effects of common logging practices on Vaccinium species in grizzly range have not been well documented. New huckleberry fields sometimes develop on recent clearcuts, but occurrence and production are erratic (Minore 1972). Moisture conditions and species composition of the site prior to disturbance influence the composition of the resultant community (Miller 1977), as do the type of cut and the post-logging treatment of the site.

Permanent berry production plots that are sampled every year could contribute to an understanding of the factors which influence huckleberry production. Maximum benefits will be derived if the plots are located on sites at different stages of development influenced by varied physical factors, fire, and logging. This study was designed, therefore, to not only meet the needs of my research, but also to provide and add to a basic format for long-term sampling of Vaccinium growth and productivity in the central Rocky Mountain area.

The literature review deals primarily with the eastern lowbush blueberry (V. angustifolium), a member of the subgenus Cyanococcus. V. globulare and V. membranaceum are in the Euvaccinium subgenus. Flowers of the species of the Cyanococcus subgenus are formed in racemes on late wood stems, the anthers are horned or tubed with no awns, and the sepals are persistent and turn blue with the fruit (Stickney, pers. comm.). The Euvacciniaceae have solitary flowers on current wood and the anthers are not horned or tubed. Fruit production and vegetative growth of the lowbush blueberry recover quickly after surface burns, but those of western huckleberries generally do not. Unfortunately, supportive physiological studies of the western huckleberries are limited. Minore (1975a; 1975b) and Nelson (1974) have worked with V. membranaceum in Washington and Oregon, and Miller (1977) has studied certain aspects of V. globulare in western Montana. Their work is cited where it is appropriate. Some of the general information about the eastern blueberries probably applies to the western species of Vaccinium, but the differences between the two subgenera should be kept in mind when extrapolations of physiological information are made.

Taxonomy

In addition to the lack of information about berry production in western Vaccinium species, identification problems have been encountered in western Montana. The variation in the vegetative characteristics of V. globulare and V. membranaceum exceeds that reported by Hitchcock and Cronquist (1973) to the extent that most of the time, differentiating between the two species in the field is difficult. The variation in the leaf shapes could be a response to environmental conditions rather than being indicative of different species or of hybrid plants, although both species are tetraploids so they could hybridize. The problem will not be conclusively resolved without cytological studies, but collections of plants from the type localities and from areas where the more variable plants are found will aid in solving identification problems within the complex.

Another aspect of this study concerns the velvet-leaved huckleberry (V. myrtilloides) and the oval-leaved huckleberry (V. ovalifolium). V. myrtilloides is known from only one location in Montana near West Glacier National Park. No verifiable specimens of V. ovalifolium have been found, but, because it is found in southern British Columbia and in northern Idaho, it could occur in northwestern Montana. An attempt was made to locate both species in the study area, but neither was found.

CHAPTER II

LITERATURE REVIEW

Flowering and Berry Development

Flower development on species of *Vaccinium* is best described by Bell and Burchill (1955). The following is a paraphrased version of their abstract. The dates and length of the required resting stage vary between species and depend on local site conditions, but the sequence of events is similar (Darrow 1942).

> The small epigynous floret of the lowbush blueberry (*V. angustifolium*) is formed by the first of August, during which time, some reproductive tissue is differentiated in both the ovary and the stamen. No development takes place from September through December but some mitosis begins again as early as January. However, definite differentiation does not start until March. Active growth and meiosis are complete in the anthers during the first week in May and about a week later in the ovules. Subsequent development in the ovules is of the Polygonum type. The flower is mature by the last week in May and the floret primordia form from the base of the stem to the apex in June. The carpels are, at first, appendicular and later receptacular.

The flower buds develop in early summer or mid-summer. Flower buds can usually be distinguished from vegetative buds by their much larger size in late September. The ratio of flower buds to vegetative buds is greater on new sprouts than on old twigs, and the buds formed on new shoots are hardier and contain more flower buds (Hall and Aalders 1975). Therefore, the number of flower buds per sprout and the number of sprouts with flower buds can be increased if old stems are periodically removed. Light burning is an effective and economical method of removing old stems in commercial stands. Fields burned in early spring produce the highest flower/vegetative bud ratio. This ratio drops significantly if plots are burned later in the growing season (Eaton and White 1960).

Fruit set is initiated by insect (bee) pollination. If pollination is adequate, fruit set is determined by the amounts of rhizome carbohydrates available to the developing embryo (Aalders et al. 1969). Partial defoliation from diseases or insects reduces leaf area and could lower the carbohydrate reserves and reduce fruit set. Partially defoliated plants have lower percentages of fruit set, a lower average berry weight, a lower seed number per berry, and fewer ripe berries at 2 months than do control plants (Aalders et al. 1969).

Fruit development occurs in 3 stages. Stage I is a period of rapid growth of the pericarp. During Stage II, the embryo develops, but the size of the fruit does not increase. Rapid growth of the pericarp and fruit maturation occur in Stage III (Young 1952).

Sugar content increases in the berries during Stage II. Glucose and fructose are present during all stages in approximately equal concentrations, while trace amounts of sucrose are found only in mature berries (Barker et al. 1963). Lowered light intensity reduces the percentage of berries ripe at harvest, but does not adversely affect the total yield. Although the percentage of reducing sugars is lowered by shade, sugar content is not affected by defoliation (Aalders et al. 1969). The results of Minore and Smart (1975) contrast with these. Sweetness of V. membranaceum berries, measured as content of soluble solids, was not significantly affected by shading in the field. The difference could be that Aalders' experiments were in a laboratory, and some factors such as exposure, were not considered. In that case, the control plants may have had an advantage the exposed ones in the field lacked.

Rainfall variation can influence the size of the fruit, but it does not influence the duration of Stages II and III in fruit development (Young 1952). On the other hand, temperature differences have little effect on the percent fruit set and ultimate berry size, but they do increase the number of days required for the fruit to reach maturity (Hall and Aalders 1968).

The physiology of flowering and berry development in eastern *Vaccinium* species is well documented, but the influences that combinations of physical or environmental factors have on these processes in the field have not been reported.

Physical Variables

Environmental Influences on Growth

In the year of a burn, the spring growth of the lowbush blueberry consists of vegetative development of buds as unbranched sprouts. Later, the vegetative shoots stop elongating when the apical meristem dies. The more proximal buds differentiate as flower buds while the distal buds remain vegetative (Barker and Collins 1963). From October to December some growth occurs, but it proceeds slowly and a period of minimum activity or dormancy takes place, again, from December through February (Bell 1953). The year after a burn, the shoots that developed the previous year grow by development of axillary branches. Each branch reduces the number of flower buds in those axils close to the apices. This cycle continues each year, producing an increasingly branched system.

Bell (1953) said the growth cycle of V. angustifolium was essentially unaltered by environmental factors. Pruning or burning delayed the spring developments, and latitude or weather retarded them, but by fall, all the plants were at about the same stage. Barker and Collins (1963) did not agree. In their studies, although the shoots that formed by the development of axillary buds were morphologically identical to shoots formed from burned aerial shoots, the lateral shoots on year-old burns were more vigorous than those on a recently burned area. The older shoots also grew, had at least 50 percent apical abortion, and had floral buds approximately 1 month before the newer shoots. The latter investigators attributed the difference in vigor to the top/root or rhizome ratio, and the difference in chronology to variations in soil and air temperatures. Therefore, the cycle is altered by certain environmental factors. Barker and Collins do not, however, feel that the control of apical abortion is environmental. They believe it to be inherent and related to auxin levels.

I could not find evidence to support Barker and Collins' findings, but the growth pattern of western species of Vaccinium is probably similar to that described for the lowbush blueberry. The timing of events may vary with temperature, altitude, etc., but the sequence of events should be similar.

Photoperiod and Temperature

The lowbush blueberry is a short-day plant that produces flower buds with no new vegetative growth during short days (less than 12 hours daylight) and grows vegetatively during long days (more than 12 hours daylight). The vegetative growth at 21°C is significantly greater than that at 10°C and the differences are accentuated by the lengths of the days (Hall and Ludwig 1961). Flower buds form during both 11- and 13-hour photoperiods but more form when the temperature is 21°C than when it is 10°C.

Lowbush blueberries must be exposed to short days for 6 weeks and then exposed to long days before normal flowering racemes will form (Hall and Ludwig 1961). Plants exposed to short days for less than 6 weeks will not flower normally. Limited lowbush blueberry production in northern Canadian areas could be the result of inhibited flower bud formation during long days in a short growing season. By the time day length shortens sufficiently to induce flower bud formation, temperatures are often cold enough to limit growth (Hall et al. 1964).

Once the flowers are formed, fruit maturation time is determined by temperature. Hall and Aalders (1968) contrasted the effects of temperatures of 21°C light and 16°C dark with 16°C light and 10°C dark during 16-hour photoperiods. Berries under the warm conditions were all ripe before any of those in the cool treatment were. Temperature did not affect the percent fruit set or the ultimate berry size, but did affect the number of days required for the fruit to reach maturity. Therefore, lowbush blueberries will grow vegetatively and produce flower buds and fruit of normal size at temperatures as low as 10°C if short- and long-day periods are sufficient. However, temperature determines the number of flower buds formed and the time required for fruit maturation.

Light Intensity

The effects of different light intensities on lowbush blueberry growth and production have been studied sufficiently to produce general conclusions. In laboratory experiments, Hall and Ludwig (1961) found that one or two layers of cheese cloth used to cover lowbush blueberry plants produced no significant differences in stem diameters, but plants grown under two layers produced significantly fewer flower buds.

In field experiments plants under shade screens with low light intensities produced short stems with small diameters and were more branched than control plants (Hall 1958). The natural light under the screens varied from 11 to 100 percent. The number of flower buds declined with decreased light so Hall concluded "shade was detrimental to blueberry growth and production, particularly the latter."

In Washington, Minore and Smart (1975) thought spring snow melt patterns might obscure the effects of shade on berry production. Snow under isolated groups of trees melted faster than that in the open, thin-leaved huckleberry stands, and plants in the former areas had green leaves while those in the fields were still dormant and bare. Minore and Smart did not discuss whether production differed between the 2 areas, but they did find that berry sweetness, measured in the field with a refractometer, was not affected by the shade. Aalders et al. (1969) found that lowered light intensity reduced the percent of fruit set, fruit ripe at harvest, and total yield of the lowbush blueberry. They were working in open fields where snow was probably more evenly distributed than in Minore and Smart's plots (1975). If other factors such as snow pack are controlled, shade does slow vegetative growth, inhibit flower and bud formation and fruit set, and decrease total yield of the *Vaccinium* species studied.

Soil Composition and Type

Under natural conditions, species of *Vaccinium* are restricted to acidic soils. Optimum growth of lowbush blueberries occurs in soils with a pH of 4.2-5.2 (Hall et al. 1964) and acidity is more important than soil texture (Minore 1972) or clay content (Johnston 1942). Blueberry plants most frequently occur on light, well-drained podzols (Hall and Aalders 1975).

Nitrogen is the limiting nutrient in the growth of most cultivated blueberry plants and the ammonium form of nitrogen is used more readily than the nitrate form (Minore 1972). This is important in sandy soils where nitrates are easily leached (Hall et al. 1964). Cain (1952) suggested that nitrates may even by harmful to blueberries in basic soils because they tend to concentrate, but ammonium nitrogen is short-lived in those soils. In acidic soils, nitrates are quickly converted into the ammonium form so concentrations are low. However, Oertli (1963) could not confirm Cain's hypothesis.

Lowbush blueberries grow in low nutrient soils. They can tolerate very high levels of manganese and grow well even if phosphorus levels are low (Hall et al. 1964). In western species, growth is correlated with the amounts of extractable iron, magnesium and aluminum in the soil; the presence of acetate-extractable iron is an excellent indicator of potential blueberry soils (Minore 1972).

Wildfire and Prescribed Burns

Three methods are used to burn the eastern blueberry fields. Some farmers spread straw over the fields before they ignite them. Others with large farms use oil burners to flame the fields; gas burners are used for small fields (Hall and Aalders 1975). Repeated burning, especially with flame throwers, could be detrimental to long-term production because each burn destroys some of the upper soil (Minore 1972), but Black (1963) found no evidence that flash burning seriously affected the rhizomes or the reserves of plant food in the soil.

The role of fire in establishing new populations of western species, or in maintaining old ones, is not well documented. The first year after spring experimental burns in a western Montana larch-fir (*Larix occidentalis*/*Abies lasiocarpa*) forest, globe huckleberry plants occurred in the same, or in an increased number of quadrats than they were found in before the burn; the total number of globe huckleberry stems on the site also increased. The year after fall burns, the total number of globe huckleberry stems often decreased and the plants were not found in as many quadrats as they were before the burn. The increase in numbers on spring burn plots was significant on 4 of 11 plots and the decrease on fall burns was significant on 2 of 11 plots. The second year after the burns, significant increases in the numbers of globe huckleberry stems were still occurring on 8 of 20 spring plots, but the increases were not as highly significant as those from the prefire to the first year after the fire. No increases occurred in the number of stems on the fall burn plots the second year (Miller 1977).

The effect of fall fires was often more severe than that of spring fires and Miller (1977) concluded that plant responses to the fires were related to moisture conditions at the time of plot ignition. Soil moisture content was important in relation to the extent of rhizome destruction, and duff moisture was an important regulator of heat penetration during the fire. "Differences in plant response were probably caused by different temperature regimes created at the ground level and within the rhizome network." Fall moisture levels were generally lower than spring levels and, therefore, heat penetrated to greater depths and destroyed the rhizomes rather than stimulating them (Miller 1977).

Lyon's research (1976) on the Sleeping Child burn in western Montana was the only study that documented a western *Vaccinium* species recovery after a natural fire. No records of berry production were kept, and the use of herbicides, cattle grazing, etc., obscured the results of the recovery.

Post-burn Sprouting

Sprouts from blueberry rhizomes produce most of the new growth after both light and heavy burns (Brayton and Woodwell 1966). Stems that emerge from the underground portion of rhizomes are the most vigorous, and those that emerge from partially burnt, above-ground stubs are shorter and have fewer flower buds per stem (Trevett 1962). Shoots emerge from burnt stubs rapidly and emergence is progressively slower in buds farther and farther removed from the tip of the rhizome. Therefore, the severity of the burn can determine the time required for post-burn shoot emergence. If the severity is controlled, the date of the burn determines emergence time. Emergence of lowbush blueberry shoots in fields burned during April requires 40-50 days, but shoots in fields burned on 1 June emerge in only 15 days. Therefore, the number of days between burning and stem emergence is determined by the rhizome location from which the new stem develops and by the date of burning (Trevett 1962). However, the length and number of sprouts is greater when burning is done in early spring than when it is done later in the season (Eaton and White 1960); the later the date of emergence, the fewer the average number of flowers per shoot (Eggert 1956). Thus, spring burns increase lowbush blueberry production more than later ones.

The timing of top removal in relation to the reserve requirements of the plant affects the vigor of the sprouts initiated because the sprouts are dependent on carbohydrate reserves for growth, and the combined effect of stored carbohydrates and hormones probably controls the amount of sprouting (Miller 1977). No sprouts in eastern blueberries are produced after burns in August, September, October, or November until the following year (Eaton and White 1960).

Clipping the top from blueberry plants does not increase shoot density or fruit production like burning does. The stimulative effects of the nutrients released in the ash with burning, along with other microclimate changes, are more important than the pruning action of a burn for eastern blueberries (Smith and Hilton 1971). But western Vaccinium species do not recover from fire as quickly as their eastern counterparts, so they would not benefit as much from the higher nutrient levels present immediately after a burn. The western species probably benefit more from the increase in light and decrease in competition from trees, shrubs, and herbaceous plants that accompany wildfires or prescribed burns, than from changes in nutrient levels.

All the factors involved in a burn are probably influential in increasing the production of blueberries. The important points are that prescribed burns in commerical fields increase production by increasing soil fertility and the number of flowering shoots in a stand, and that early spring burns are the most effective way to achieve the increased production.

Plant Variables

Rhizomes

Carbohydrates, nutrients, and organic fractions are stored in rhizomes (Townsend et al. 1969). These compounds or elements generally decrease in the rhizomes of lowbush blueberries during the growing season, then increase in the fall. A rapid decrease takes place during the early spring when the meristematic tissue resumes growth, so any reduction in the amounts of carbohydrates stored in the rhizomes during fall will be reflected in poorer shoot growth the following spring (Aalders and Hall 1964).

Rhizomes also function in the spread of species of *Vaccinium*. When trying to establish stands of blueberries, hastening or improving rhizome growth and development is important (Hall 1971). High temperatures and long photoperiods increase the growth of rhizomes (Kender 1967) and the soil or growth medium is very important in the regulation of underground stem growth (Kender and Eggert 1966). Mulching and applications of sawdust, peat, etc., are common in eastern North America. Mulching increases aeration and moisture in the soil, while added organic matter decreases resistance to rhizome growth (Kender 1967).

Several other methods for increasing lowbush blueberry production have been tested. Disking followed by burning increased the number of new, upright shoots, but produced such a high mortality in the living plants that it was not considered practical (Hitz 1949).

Burns alone are used to increase blueberry production by increasing the number of new sprouts from the rhizomes. The effect of the intensity of fires on rhizomes is a direct one. More rhizomes are destroyed as the temperature and the depth of heat penetration increase. Those two factors appear more important to the blueberry rhizomes than frequency of burning. Evidence does not exist that flash burning at 2- or 3-year intervals seriously affects blueberry rhizomes (Black 1963). No studies of critical heat depths or temperatures for *Vaccinium* rhizomes were found, but after a burn in

Maine, sprouting occurred from rhizomes at depths up to 5 centimeters (Brayton and Woodwell 1966). Smith (1968) reported a decrease in sprouting response of *V. myrtilloides* (subgenus *Cyanococcus*) on high intensity burns and Miller (1977) said that decrease might have been "due to a greater heat penetration into duff layers under intense fires, which increased the amount of sprouting site destruction." Thus, the depth of heat penetration and the intensity of the fire, together with the amount of stored carbohydrates at the time of the burn will play the major roles in determining the number of sprouts that will emerge after a burn.

Interspecific Competition

Wild huckleberry stands in Oregon and Washington are dwindling rapidly as the density of the tree canopy increases in the absence of fires (Minore 1972). That is also probably the case in the Rocky Mountains where fire has been controlled. The decline takes place as invading trees and shrubs crowd out the huckleberry plants. Lodgepole pine (*Pinus contorta*), mountain ash (*Sorbus* spp.), and beargrass (*Xerophyllum tenax*) are the most serious competitors in Washington (Minore 1972). Spiraea (*Spiraea latifolia*) competes with lowbush blueberries in eastern Canada for land space (Jackson and Hall 1975). Menziesia (*Menziesia ferruginea*) competed with *V. globulare* plants on undisturbed sites in the subalpine fir/queencup beadlily-menziesia and subalpine fir/menziesia habitat types (Pfister et al. 1977) in this study.

Fire increases production in old fields but may not be beneficial in establishing new blueberry stands. When Hall (1955) cut and burned a woodlot in New Brunswick, rushes, ferns, and other vegetation occupied the site but blueberries did not. Hall concluded that the cutting and burning in one year was too drastic a treatment for survival and development of repressed plants of Vaccinium. He recommended a gradual opening of the canopy to allow vigorous blueberry rhizomes to become established. Minore (1972) speculated that the reason the lowbush blueberries did not grow on the woodlot was because the pH of the soil was raised by the fire. Even though more nitrogen was available, the blueberries could not compete with the other species on a less acidic soil.

To test methods of controlling invasion of wild huckleberry stands by other species, Minore (1975a) compared the tolerances of lodgepole pine and thin-leaved huckleberry to boron and manganese. Huckleberry was less tolerant of excess boron than lodgepole pine. Both species tolerated excess manganese. He did not recommend further study of either micronutrient for purposes of eliminating lodgepole in favor of huckleberries. Other studies of tolerances were not related to competition.

Insect Pollination and Plant Destruction

The flowers of blueberries need to be pollinated by insects. Bees (honey and bumblebees) are the usual pollinators (Hall and Aalders 1975). Wind and rain pollinate some flowers but are inefficient. Aalders et al. (1969) discovered that partial, experimental defoliation of plants that had just been pollinated resulted in a decrease in percent fruit set, percent of fruit ripe at harvest, and a decrease in total yield. Partial defoliation by insects and diseases occurs occasionally on wild huckleberries, and probably has the same effect on berry production.

CHAPTER III

STUDY AREA

Most of the berry plots were sampled in known grizzly habitat in western Montana, primarily in the North Fork and South Fork Drainages of the Flathead River (Joslin et al. 1976). The distribution of the plots is listed in Table 1 and pictured in Figure 1.

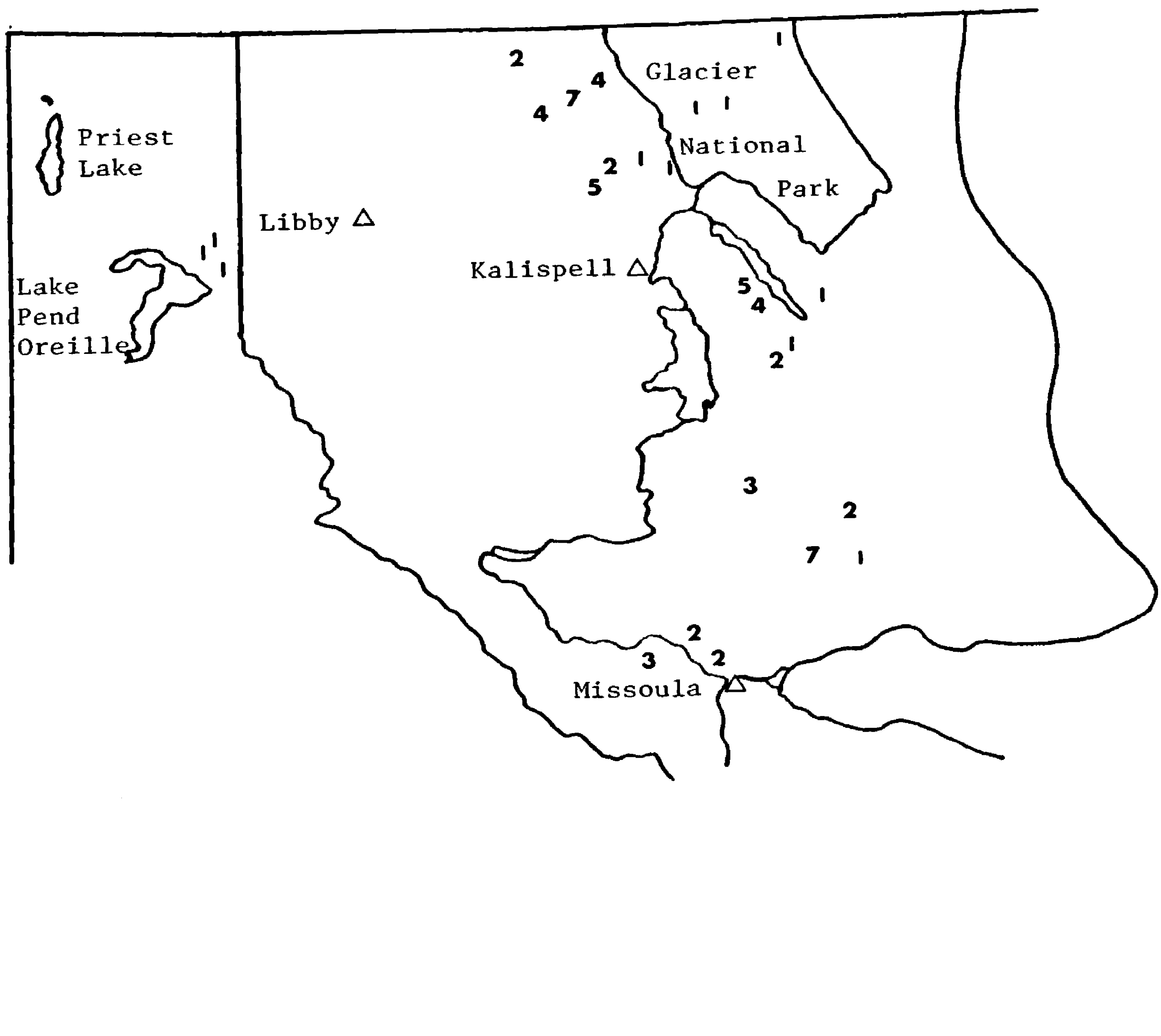
The geology of the North Fork Drainage was reviewed by Jonkel (1966) and Tisch (1961). Antos (1977) extensively reviewed the climate and geology of the Swan Valley, and to some extent, that of the Mission Mountains. Perry (1962) discussed the general geology and climate of Montana. Information from these papers will not be repeated here.

The general geology of the Pacific Northwest is an important determinate in the distribution of the *Vaccinium* species and is reviewed in the Taxonomy Discussion section. In an effort to differentiate *V. globulare* and *V. membranaceum*, many globe huckleberry plants were collected in northwestern Montana. For comparisons, collecting trips were made into northern Idaho, eastern Washington, and northern Oregon. I also reviewed the *Vaccinium* collections at the University of Montana and the Forestry Sciences Laboratory in Missoula, and the collection at Oregon State University in Corvallis.

Table 1. Geographic distribution of the sampled berry plots in western Montana and northern Idaho.

	Number of Plots	
	1977	1978
North Fork Flathead River	7	26
South Fork Flathead River	4	13
Swan Valley	-	10
Lolo National Forest-Surveyor Creek Drainage	2	7
Glacier National Park	4	3
Mission Mountains-North Crow Drainage	3	3
Kaniksu National Forest-Lightning Creek Drainage	1	2
	21	64

Fig. 1. Distribution of the sampled berry plots in western Montana and northern Idaho in 1978.


Priest Lake
Lake Pend Oreille
Libby
Kalispell
Glacier National Park
Missoula

CHAPTER IV

MATERIALS AND METHODS

Berry Production

The sampling method was based on the ranked-set sampling pattern developed by Halls and Dell (1966) for sampling range forage. Sites were chosen so that at least 3 samples from all aspects, elevations, topographic positions, and site conditions were obtained; as many different slopes, habitat types (Pfister et al. 1977), and percentages of tree, shrub, and herbaceous cover as possible were represented. Most of the samples were in known grizzly habitat defined by personnel of the Border Grizzly Project (Joslin et al. 1976).

At each site, 9 plots 2.25 m^2, arranged in a square with 3 plots per side and 10 paces between adjacent plots, were sampled (Fig. 2). A random digit table was used to assign each plot a low, medium, or high ranking so that there were 3 high, 3 medium, and 3 low plots per site. Each plot was divided into 9 sections 0.25 m^2 (Fig. 3). Three of the 9 sections in each plot were randomly chosen and also ranked low, medium, or high, based on the amount of fruit in each section. If the 2.25 m^2 plot was ranked high, I picked all the fruit in the highest ranked of the 3 sections 0.25 m^2; if it was ranked medium, I picked the fruit in the section that was ranked medium, and if it was low, I picked the least prolific section.

Fig. 2. Site sampling pattern with 9 plots 2.25 m^2 per site.

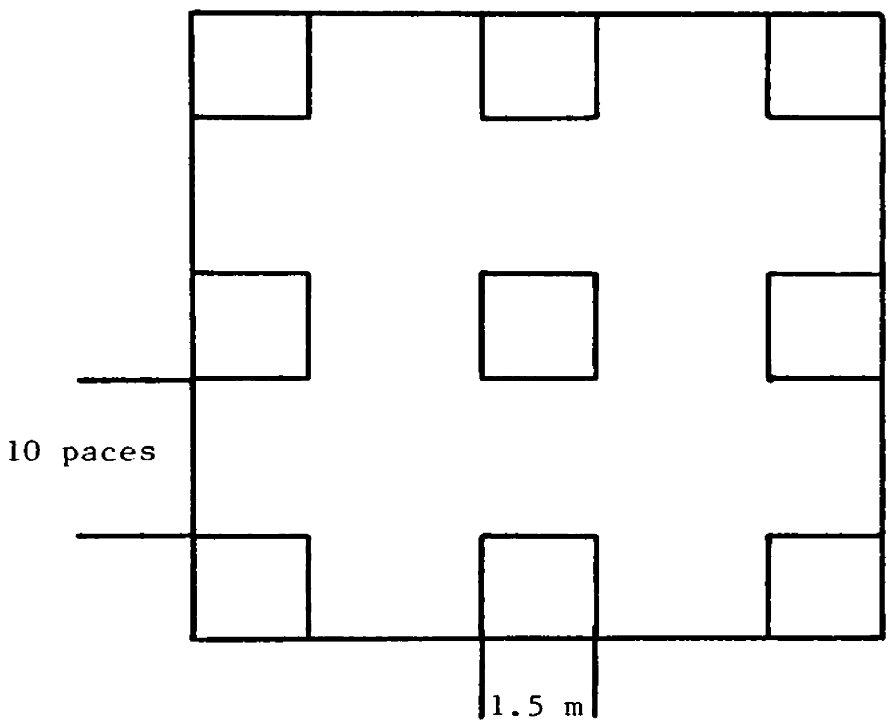
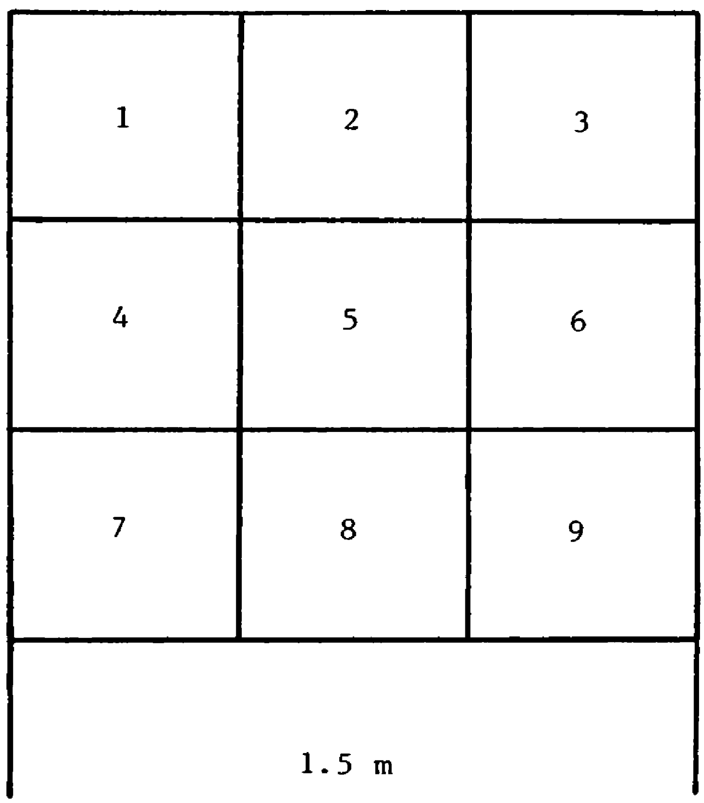

10 paces
1.5 m

Fig. 3. Division of 2.25 m^2 plot into 9 sections .25 m^2.


1
2
3
4
5
6
7
8
9
1.5 m

For each plot, I counted the number of berries picked, measured the height of the globe huckleberry shrubs, and estimated the percent of globe huckleberry, shrub (other than globe huckleberry), and herbaceous cover. The productivity of the site was determined by measuring the total volume of fruit by water displacement. Often, all of the fruit was not ripe, so I converted the volume of the sample to ripe volume with the following formulas from Minore et al. (1978):

1. $\frac{\text{Volume of 100 ripe berries}}{100} = \text{Volume per ripe berry}$

2. $\frac{\text{Volume of 100 random berries}}{100} = \text{Volume per berry in sample}$

3. $\frac{\text{Volume per ripe berry}}{\text{Volume per berry in sample}} \times \text{Total volume of picked sample} =$ Ripe volume of berry sample (ml)

The ripe volume was converted to liters per hectare (l/ha) as follows:

$$\frac{\text{Total ripe volume (ml)}}{1000} \times 4444.4 \text{ plots per ha} = \text{l/ha}$$

or:

$$\text{Total ripe volume (ml)} \times 4.444 = \text{l/ha}$$

At each site, I recorded the date, township, range, section, major drainage, aspect, percent slope, elevation, site history, habitat type, primary and secondary understory components, the dominant tree species in the overstory, topographic position, pH, and the age of the tree stand (measured with an increment borer). The moisture conditions, percentages of canopy and ground cover, the condition or vigor of the globe huckleberry shrubs, the number of berries per plant, and the average berry size were estimated. I also noted whether the globe huckleberry shrubs were clumped or scattered and picked 250 ml of berries at most sites to dry and test for sugar content. The sugar samples were analyzed by T. Bumgarner with spectrophotometry (Hodge and Hofreiter 1962).

The data were analyzed with the University of Montana DECSYSTEM-20 computer and statistical programs in the Statistical Package for the Social Sciences (SPSS, Nie et al. 1975).

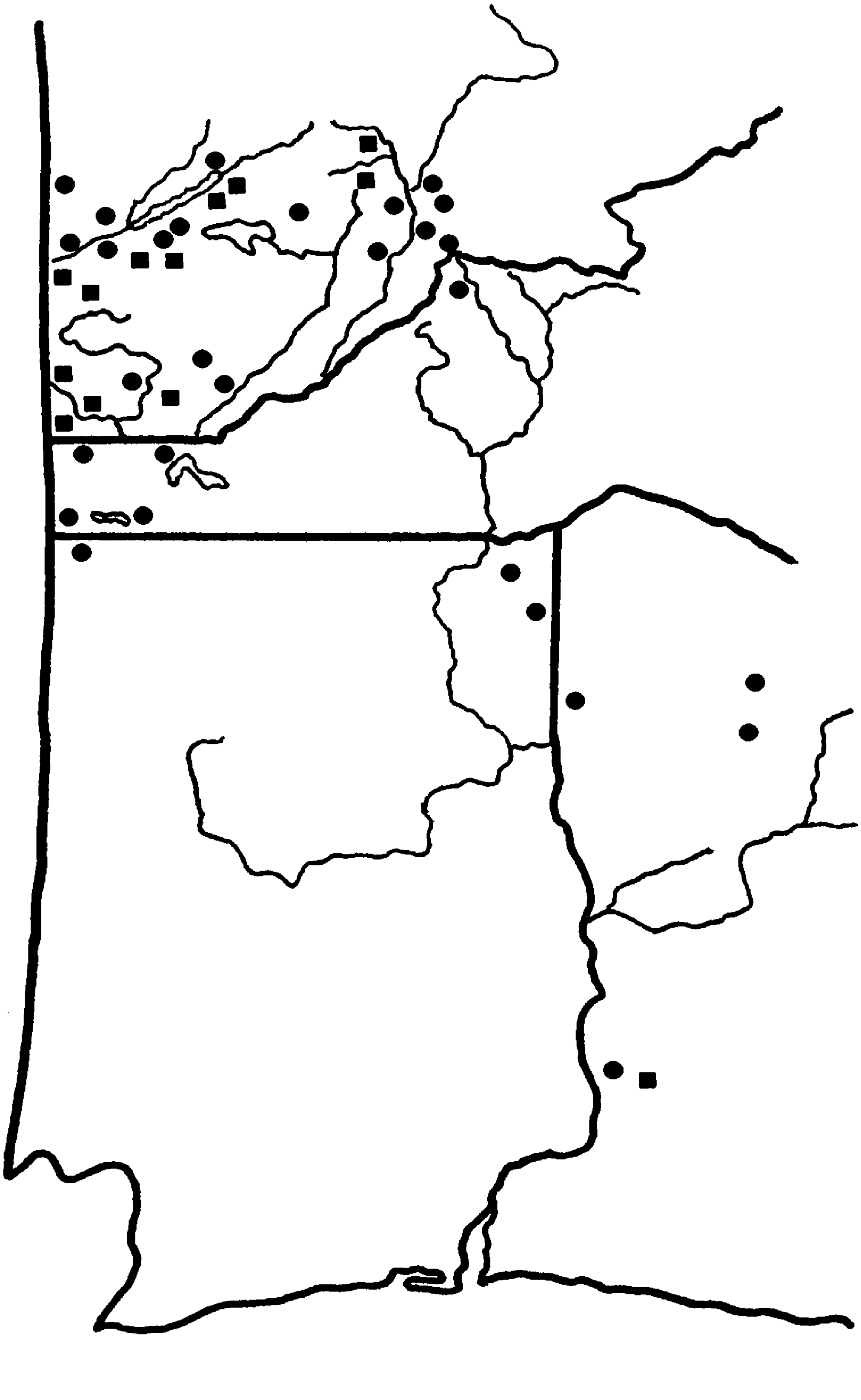
Taxonomy

Two hundred eight-three pressed voucher specimens of *Vaccinium* from western Montana, Idaho, Washington, and Oregon were made (Fig. 4). Fresh flowers were preserved in a 10 percent alcohol solution and their lengths and widths were later measured. Duplicate collections of the specimens will be placed in the University of Montana and the Forestry Sciences Laboratory in Missoula, Montana.

To determine leaf shape, I measured the length, width, and distance from the apex to the widest point of 3 sets of the terminal, second, third, and fourth leaves of each collected plant. Some plants from the herbaria at Oregon State University in Corvallis, the Forestry Sciences Laboratory and the University of Montana in Missoula, were also measured. The measurements were converted to ratios of width/length and distance from the apex to the widest point/length. Using the two ratios as axes, the plants were graphed in a scatter diagram.

Fig. 4. Huckleberry plant collection sites of Idaho, northern Oregon, eastern Washington, and western Montana.

●= 1-10 collections
■= 10 or more collections



CHAPTER V

RESULTS AND DISCUSSION

Statistical analyses of the data revealed significant trends in berry production, percent cover, and average height of the huckleberry shrubs, but the coefficients of linear correlation (r^2) for individual variables with the huckleberry characteristics were usually less than 0.30. The reasons for the low r^2 values were that berry production, cover, and height were the result of physical and vegetative site characteristics' interactions with site histories. No single factors had constant, regular effects on production, regardless of other site characteristics. Combinations of factors or regressions with several variables did not improve the r^2 values because many relationships were non-linear.

The site characteristics and histories are interpreted individually to clarify their importance. The r^2 values are reported for comparisons, and as reminders of the complexity of interactions between measurable variables and their combined effects on berry production, cover, and height of the huckleberry shrubs. Where not noted in the text, "production" refers to huckleberry fruit production, "cover" to percent cover of huckleberry plants, "canopy cover" to tree overstory, and "height" to average height of the huckleberry shrubs. Common plant names are used in the text. Scientific names are listed in Table 2. Nomenclature follows that of Hitchcock and Cronquist (1973).

Table 2. Specific names and common names for the species of Vaccinium, the trees, shrubs, and forbs mentioned in the text.

Scientific name	Common name
Vaccinium angustifolium	eastern lowbush blueberry
V. caespitosum	dwarf huckleberry
V. deliciosum	blue-leaf huckleberry
V. globulare	globe huckleberry
V. membranaceum	thin-leaved huckleberry
V. myrtilloides	velvet-leaved huckleberry
V. myrtillus	dwarf-bilberry
V. ovalifolium	oval-leaved huckleberry
V. scoparium	grouseberry, whortleberry
Abies lasiocarpa	subalpine fir
Larix occidentalis	western larch
Picea engelmanii	white spruce
Picea glauca	cat spruce
Pinus contorta	lodgepole
Pseudotsuga menziesia	Douglas-fir
Tsuga mertensiana	mountain hemlock
Menziesia ferruginea	menziesia
Pachistima myrsinities	pachistima
Sorbus spp.	mountain ash
Spiraea latifolia	spiraea
Clintonia uniflora	queencup beadlilly
Xerophyllum tenax	beargrass

Berry Production

Physical Site Characteristics

Table 3 summarizes the effects of the physical and vegetative site characteristics on total volume of berries produced, estimated number of berries per plant, average berry size per site, and heights and percent cover of globe huckleberry shrubs.

Aspect. Of the physical site characteristics considered, aspect had the strongest, single influence on berry production. Fruit production decreased as aspect changed from northwest through east to west. The effect was significant in 1977 and 1978, but the coefficient of linear correlation (r^2) was very low in 1978 (Fig. 5, 6). However, with one exception, the plotted mean productivities for each aspect were very close to the mathematically determined regression line and, as such, were closely related to the aspect of the plot. The number of plots and the mean productivities for each aspect are listed in Table 4.

The mean productivity for the eastern aspect plots in 1978 was not near the regression line. It was elevated by the 2 most productive plots in the sample (Plots 64 and 70), which respectively produced 1.8 times and 1.4 times as much fruit as the third-most productive plot. If they were not included in the computation, the mean of 167 l/ha for eastern-aspect sites fell just slightly above the regression line. Most of the site characteristics on those 2 plots tended to increase berry production on the other plots, such as being

Table 3. Factors affecting the mean percent cover, average height, total volume, number of berries per plant, and average berry volume for a site on the sampled plots in 1978. (Codes from Arno, pers. comm.)

	Average cover of huckle-berry plants	Average height	Total volume produced per site	Number of berries per plant	Average berry volume
Aspect					
NW-E-W	-	-	D	-	D
N+E vs. S+W	D	D	D	-	-
Canopy cover = 0%	D	D	D	--	--
Elevation	-	-	-	-	-
Percent slope	-	-	I-D	-	-
Moisture conditions	-	I	-	-	-
Tree canopy cover					
0-30%	I	I	d	-	I
30-90%	D	I	d	D	D
Shrub cover	D	--	d	--	-
Herbaceous cover	D	--	d	-	-
Total understory cover	d	--	d	-	-
Not burned in 50 years to burned in 50 years	D	D	I	I	I

I = significant with increase in variable
i = insignificant increase with increase in variable

D = significant decrease with decrease in variable
d = insignificant decrease with decrease in variable

- = no predictable effect on huckleberry characteristics

I-D = significant increase, then significant with changes in variable

Fig. 5. Productivity for each plot, mean production (▲) for each aspect, and general regression line for the 1977 berry plot samples.

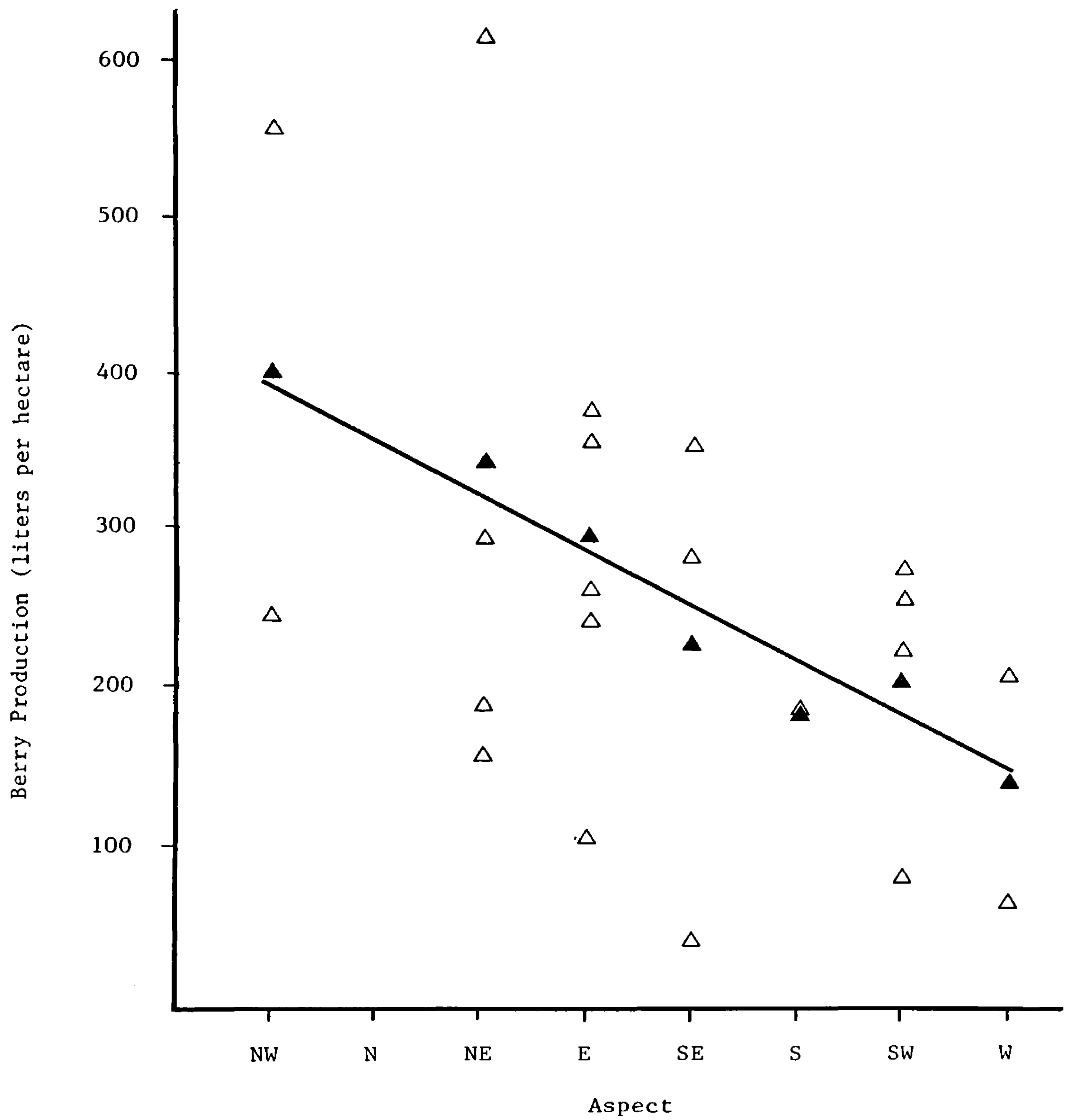
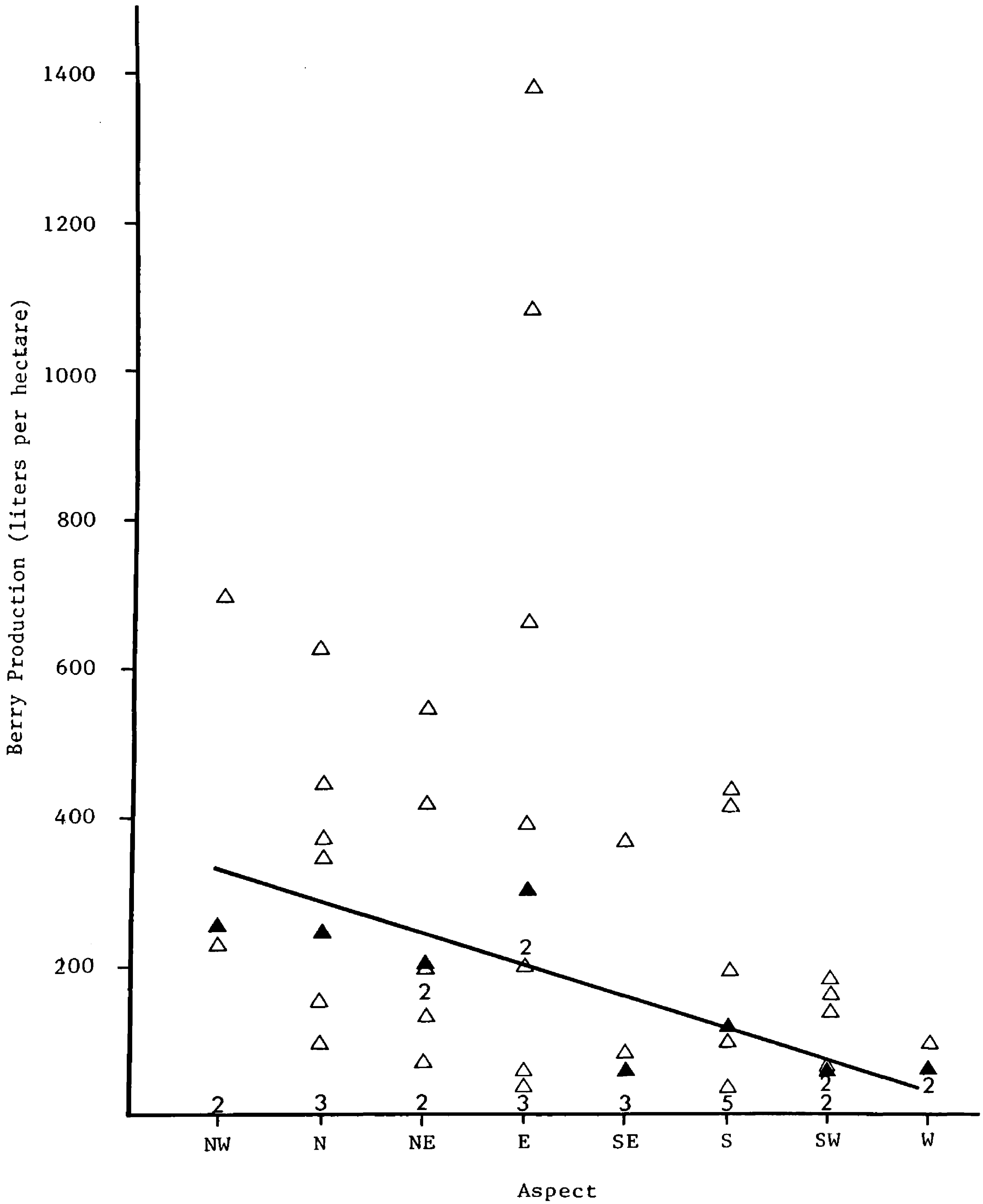

600
500
400
300
200
100
Berry Production (liters per hectare)
NW
N
NE
E
SE
S
SW
W
Aspect

Fig. 6. Productivity for each plot, mean production for each aspect (▲), and general regression line for the 1978 berry plots.



Berry Production (liters per hectare)
1400
1200
1000
800
600
400
200
NW
N
NE
E
SE
S
SW
W
Aspect

Table 4. Number of plots and mean productivity (l/ha) for each aspect in 1977 and 1978.

	1977		1978	
Aspect (^{o})	Number of plots	Mean	Number of plots	Mean
NW (291-335)	2	391	4	226
N (336-360) (0-20)	0	-	9	223
NE (21-65)	4	312	9	180
E (66-110)	5	272	13	337
SE (111-155)	3	218	5	83
S (156-200)	1	178	10	124
SW (210-245)	4	212	8	74
W (246-290)	2	137	3	64
Benches	0	-	3	216
	21		64	

at a high elevation on sites burned by wildfire 25-60 years ago. The sites also had little or no tree canopy, were on east aspects and had low shrub or herbaceous coverages. A combination of positive factors on those sites was apparently responsible for the high productivities.

The mean productivities of the combined northern and eastern aspect plots was significantly higher than the mean of the combined southern and western aspect plots in both years. The absence of a tree canopy accentuated the aspect differences. Four of 5 plots on southern or western aspects without a tree canopy did not produce any fruit. The significant difference between the combined mesic-slope mean, and the combined xeric-slope mean for groups with tree canopies and without tree canopies suggests that moisture, and perhaps daily temperature, are important in the production of fruit.

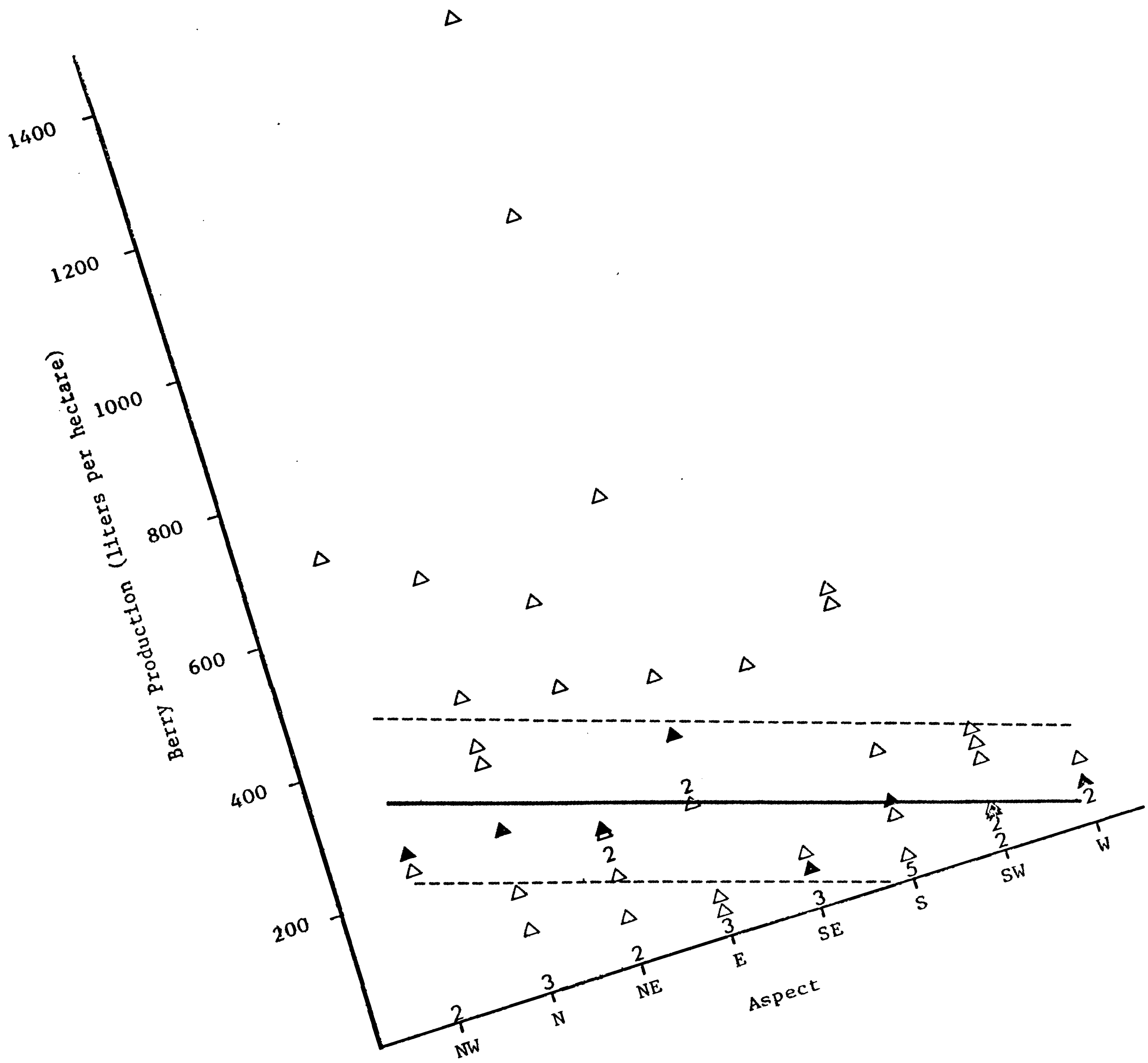
Studies of eastern lowbush blueberries (Subgenus Cyanococcus) deal with constant temperatures over periods of time in controlled environments (Hall and Ludwig 1961; Hall and Aalders 1968). Berry production is higher when temperatures are higher, provided that moisture, nutrient, and light requirements are adequate. Southern and western aspect sites are generally warmer than northern or eastern sites, but available moisture is lower. For example, Schaffer (1971) measured huckleberry production (Subgenus Euvaccinium) on Huckleberry Mountain in Glacier National Park, and found that the least productive site was the most xeric one he measured, and was at a high elevation on a south-facing slope. His most productive plot was on a mesic, subalpine fir/menziesia site, also at a high elevation.

Because the mean productivities of the aspects were so closely related to the mathematical regression, the aspect/volume graph was used to determine which plots were unusually productive or unproductive. I drew parallel lines equidistant above and below the regression line so that all means were within the 2 lines (Fig. 7). Plots above the upper line were considered high producers and were compared with unproductive plots below the lower line. The productive group had a lower percent tree canopy cover, a higher percent globe huckleberry plant cover, and taller huckleberry shrubs with larger berries than the unproductive group (Table 5). The mean elevations and percentages of understory cover were similar for both groups, although beargrass dominated the understory in more of the productive plots.

To control for the aspect variable, the regression line on the volume/aspect graph was extended beyond the West category to the x-axis intercept (the origin). A line was drawn from the origin through each plot productivity to the y-axis. The productivity for each plot was then converted to the value of the y-intercept for that line (Jensen 1973). When the converted volumes were graphed with the other variables, canopy cover again had a negative effect on production, and the total volume of berries increased as the percent cover of globe huckleberry shrubs, the number of berries per plant, and the average berry volume increased.

The post-logging treatment of the site, and time since disturbance, were the most influential variables after aspect was controlled. All plots above the horizontal dashed line in Figure 8 were either disturbed by natural fires 25-60 years ago, or were in

Fig. 7. Parallel lines drawn equidistant from the aspect-volume regression line to determine productive and unproductive plots.



Berry Production (liters per hectare)
1400
1200
1000
800
600
400
200
Aspect
NW
N
NE
E
SE
S
SW
W

Table 5. Comparisons of average characteristics for 17 productive and 11 unproductive plots.

	Productive plots	Unproductive plots
Tree Cover (%)	4	23
Huckleberry Plant Cover (%)	36	22
Height of Huckleberry Plants (cm)	49	31
Average Berry Volume (ml)	0.461	0.071
Elevation (m)	1500	1460
Understory Cover (%)	72	73

Fig. 8. Distribution of plot productivities after the influence of the aspect variables was controlled.

● = Natural burns 25-60 years old

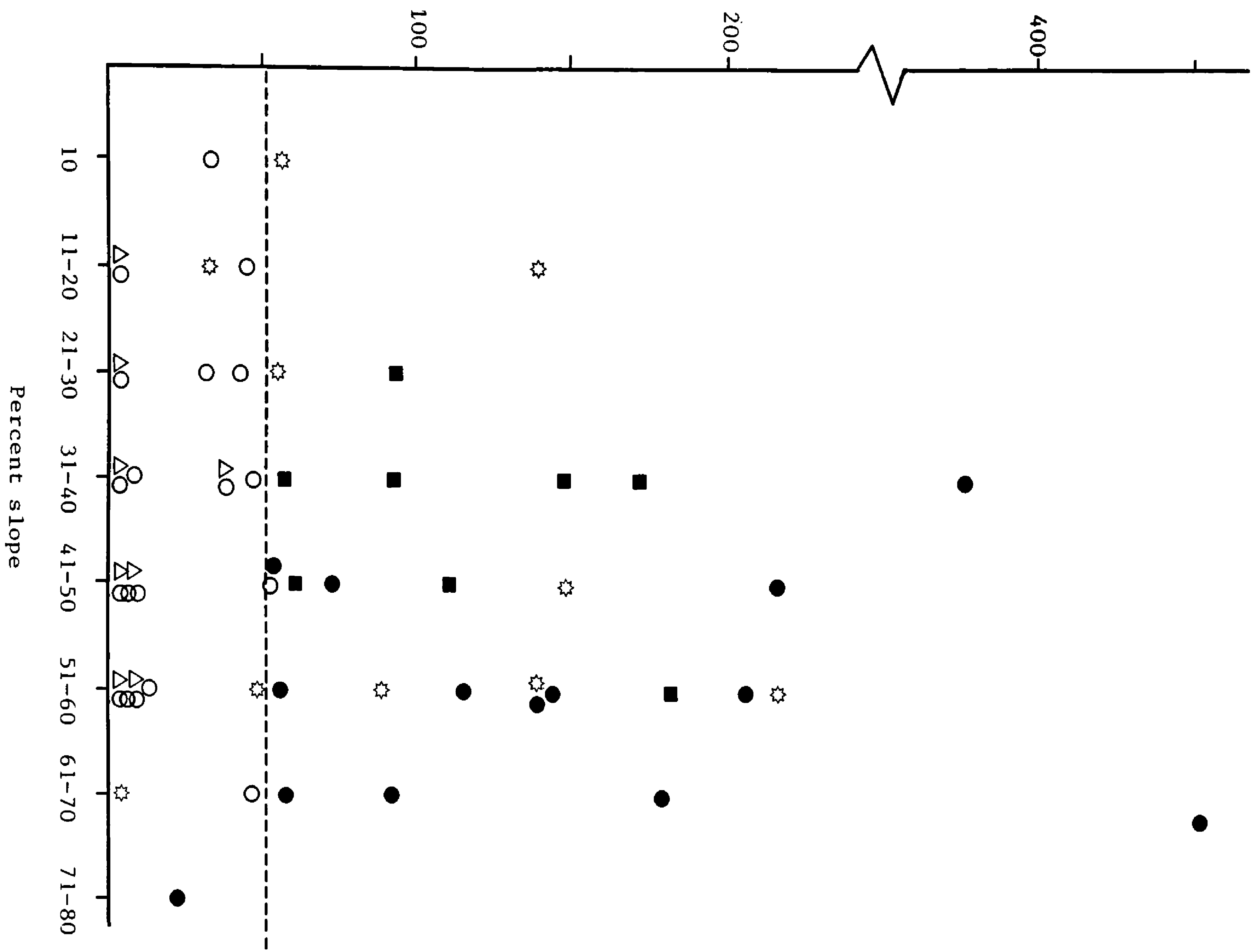
○ = Wildfires 60-100 years old or stands over 100 years old

✡ = Partial cuts-all ages

■ = Broadcast-burned clearcuts on north or east aspects

△ = Scarified clearcuts or broadcast-burned clearcuts on south or east aspects

Aspect-controlled conversions of plot productivities (l/ha)

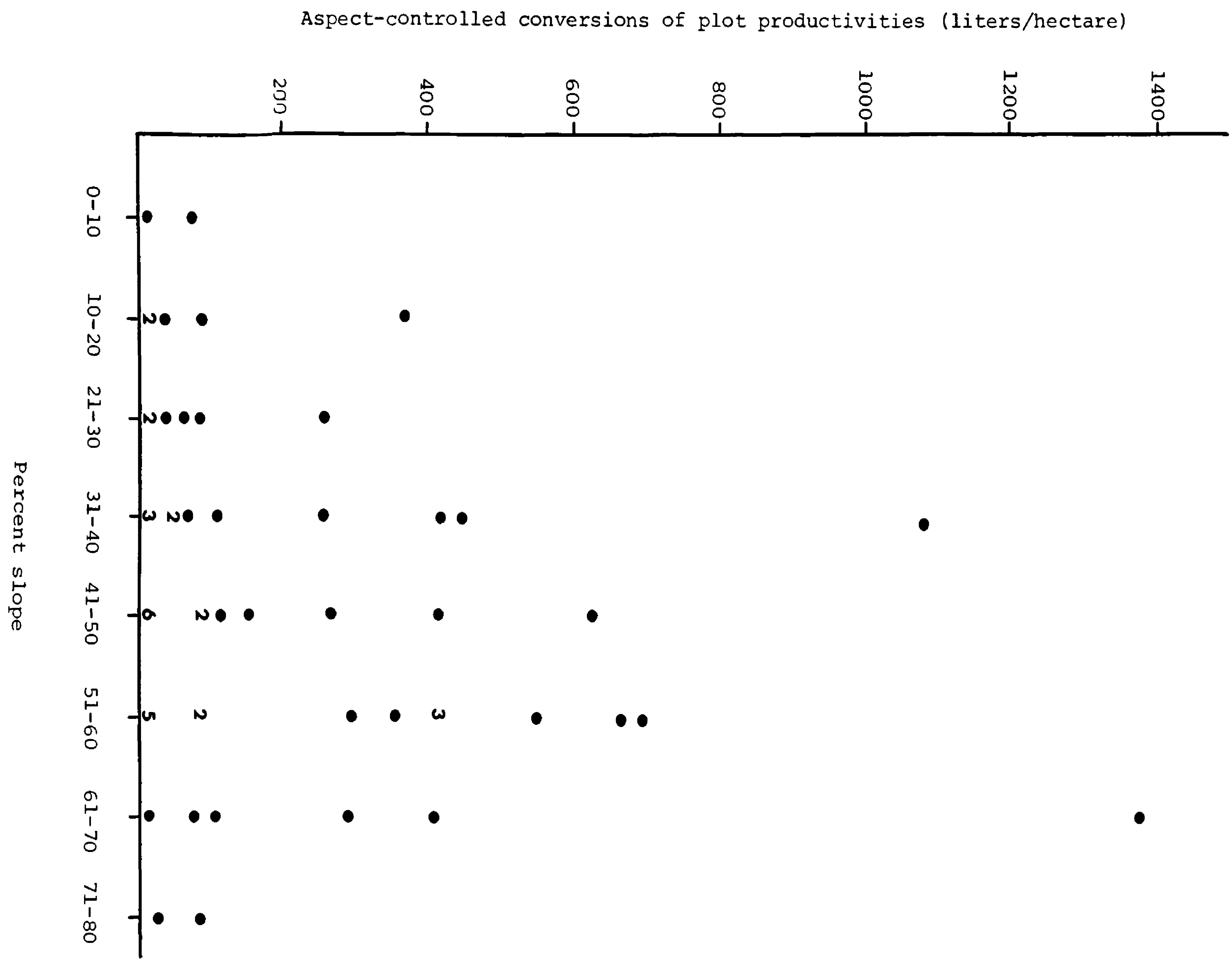


broadcast-burned clearcuts on north or east aspects, except for 8 partial-cut sites. All but 3 plots below the dashed line were in stands that had not been disturbed in the last 100 years, plots in scarified clearcuts, or were in broadcast-burned, clearcut plots on south or west aspects. Two of the 3 exceptions below the line were in partial cut stands, and 1 was in a 50-year-old burn at 2120 m (7000 ft).

Percent slope. In 1977, mean berry production increased irregularly as percent slope increased from 0 to 30 percent and decreased when slopes increased from 30 to 60 percent. The differences were not significant, but 3 categories contained only 1 or 2 samples and no plots had slopes greater than 60 percent. In 1978, the slopes on 2 plots were greater than 70 percent. Their mean production was very low, but one had an elevation of 2120 m (7000 ft), and the other was in a partial cut on a south-facing slope. Mean berry production in 1978 was not related to the percent slope of the site until the aspect variable was controlled. Then the effect of slope on production was bell-shaped with the peak at approximately 45 percent (Fig. 9). In short, productivity was limited on steep slopes (>70 percent) that had thin soils, more radiant energy, and less moisture compared to moderately steep slopes (25-40 percent). Productivity was also low if slopes were more gentle, where competition from other shrubs and herbaceous plants apparently limit production.

Elevation. The elevation of the berry plots ranged from 820 m to 2120 m (2700-7000 ft). Berry production was depressed by

Fig. 9. The bell-shaped effect of percent slope on berry production with the 1978, aspect-controlled variable.


Aspect-controlled conversions of plot productivities (liters/hectare)
200
400
600
800
1000
1200
1400
Percent slope
0-10
10-20
21-30
31-40
41-50
51-60
61-70
71-80
2
2
3
2
6
2
5
2
3

elevation only at low or high extremes. Within a certain elevational range (1300-1850 m), other factors played a more important role in controlling fructification. However, when the 1978 plots with similar total yields were grouped and compared, the 6 most productive plots had a significantly higher mean elevation (1810 m; 6000 ft) than any of the other groups. It seemed that sites at the upper end of the elevational spectrum favorable to berry production were more prolific than those at lower elevations. Shrub and herbaceous coverages on the 6 prolific plots were low, so competition was reduced. Radiant energy is high at high elevations so more flowers formed on high elevation sites, especially if the tree canopy was sparse, than formed at lower elevations with a more dense tree layer.

Topographic position. In 1978, the variation in berry production on 15 upper and 37 middle slope plots was high, and the means of the 2 groups were not significantly different. The 3 ridge plots had different site conditions and vegetative characteristics, but production for all 3 was low. The mean production for 6 plots on lower slopes was also low, but 2 were in old stands (125+ years), one was in a scarified clearcut, one was in a broadcast-burned clearcut on a south-facing slope, and 2 had high coverages of other bushes and herbaceous plants. Only 2 plots were on benches and none was along creeks.

Just as the intermediate elevations and percent slopes were productive, intermediate topographic positions were more favorable for berry production than either ridges or lower slopes. The xeric conditions, shallow and rocky soils, and perhaps winds (on some ridges), are the factors that most likely limit production in such areas. Lower slopes with adequate moisture and deep soils are probably more favorable to other shrubs, herbaceous plants, and grasses, all of which compete with the huckleberry shrubs for space, nutrients, and sunlight.

Comparisons of plots on the same hillsides at different elevations yielded positive gradients in production from lower plots to sites 70-100 m below the ridges, provided that site histories were constant. This is related to the combined effects that elevation, topography, and percent slope have on reducing competition with other plants.

Percent cover on 3 sites with uniform histories increased from lower slopes to upper slopes, and was equal for upper slopes and ridges. Huckleberry shrub height decreased from lower slopes to ridges on uniform sites. In the spring of 1977, after a mild winter with little snow, I observed many huckleberry shrubs with dead stems on the upper portion of the plants. Shallow snow depths on ridges and exposed upper slopes could have similar effects and limit shrub height by exposing plants to winter-kill through lack of protection. Shrub height would be limited to the depth of snow accumulation on those sites. Thus, it seemed that shrub height responded negatively to stress, and that percent cover responded positively to reduced competition. The result was that sites on upper slopes had high coverages of short shrubs which produced substantially more fruit than plots on the same slope at other elevational locations.

It was not possible to determine from the data collected whether the increase in production on relatively steep slopes at high elevations was in response to a decrease in competition, increased moisture, less canopy cover, different sunlight characteristics, or perhaps, an increase in stress. Evidence to support a theory of stress-induced fruit production in shrubs is lacking. Serviceberry (*Amalanchier alnifolia*) stressed from limited moisture or over-browsing, did not produce many berries (Hemmer 1975). Berry production was apparently limited to mature shrubs on favorable sites, and such shrubs did not produce significant current annual growth. Hemmer believed they used their energy to produce fruit, rather than for vegetative growth.

Obviously, severe stress such as very high elevations or excessively steep slopes would limit production, but it is possible that limited stress could improve it. If such is the case, an increase in elevation and steepness of slope, and the subsequent increase in stress and reduction of competition on a mesic aspect, could amplify the positive effects other factors have on production.

Date and location. The date the plot was sampled and the major drainage where the plot was located did not significantly influence the berry productivity of a site.

Site Vegetative Characteristics

Tree canopy, shrub, and herbaceous cover. The percent tree canopy cover influenced berry production more than other vegetative site characteristics. In 1978, the volume of berries produced on each 2.25 m^2 plot was inversely related to the estimated percentages of tree canopy, shrub, and herbaceous cover on that plot, but the r^2 value for each variable was less than 0.04. The estimated canopy cover for the site was inversely correlated with the total berry production for all plots, and for north- and east-slope plots in 1978. Canopy cover was not related to fruit production on south- or west-aspect plots.

The correlation between canopy cover and fructification was low because production was also related to the site history and the aspect of the stand. But, despite the low correlation value, the importance of canopy cover must not be overlooked. The mean canopy cover for the 11 most productive plots was 5 percent, compared to 22 percent for the other 52 plots. Eleven plots that produced a low volume for their aspect were grouped and compared with 11 productive plots (Fig. 7). The mean percent canopy cover for the productive plots was 4 percent; it was 23 percent for the unproductive plots. In other studies, the decrease in light and available moisture that occur as the tree canopy develops, were factors that individually limited commercial, eastern blueberry production (Hall 1958; Trevett 1962). Productivity in this study decreased rapidly when the canopy was more dense than 30 percent, even though the average berry volume increased, indicating that light, and probably the moisture availability at that level, must be too low for flower formation. Because the eastern *Vaccinium* species are more seral than the western species, their flower formation may be inhibited by a tree canopy less dense than 30 percent. The value of the east-west species comparison is limited, but the same factors appear to be influencing flower formation, perhaps at different levels.

Production in old, eastern blueberry shrubs is less than that of younger ones (Hall and Aalders 1975), but huckleberry shrubs in a 300-year-old stand in this study were producing berries in open areas. Western huckleberry shrubs produce fruit as long as development of the tree canopy is delayed (Minore et al. 1978). The eastern blueberries produce fruit within 1 or 2 years after a burn, but western huckleberries are not productive until several years after fire. The actual length of the berry production delay depends on the type and intensity of the burn. Shrubs burned by light, broadcast burns after the trees are clearcut, produce fruit as early as 6 years after treatment (Shearer, pers. comm.), but berries do not become abundant until 8-15 years after the fire. The delay on sites burned by natural fires is even longer because the depth of heat penetration, fire intensity, and subsequent rhizome destruction are greater in hot fires than in cooler, prescribed, broadcast burns.

Tree canopy cover was not inversely related to production on south- and west-slope plots because complete removal of the canopy on dry aspects reduced cover of huckleberry plants. Because plots on south or west aspects with tree canopies of 5-20 percent usually produced fruit, it seemed that the tree layer provided some protection from extreme conditions, such as frost (Arno, pers. comm.) or dessication. Therefore, the percent canopy cover, the related age of the stand, and the site history interacted with aspect to produce a combined effect on berry production.

The percent of ground covered by the understory did not have a predictable effect on total berry production in 1978, but was inversely related to production in 1977. However, mean percent understory cover for the 11 most productive sites in 1978 was significantly lower than the means for plots in 4 other groups based on similar total yields. Again, that suggests that competition with other species of plants limited huckleberry production. Apparently, only the abundance or scarcity of competitors influenced berry production, not which was the competitor. However, because individual species are dependent upon certain site conditions, they are an indirect index to potential huckleberry production.

Indicator species may also predict how globe huckleberry shrubs would respond to different treatments, just as aspect does. If areas with plants adapted predominantly to dry sites are disturbed by logging or wildfire, huckleberry production would probably decline. Conversely, fructification of globe huckleberry shrubs tends to increase on mesic sites dominated by menziesia, if they are disturbed.

Major and minor understory dominants. The major and minor understory dominants for each berry plot were those species (excluding globe huckleberry) that had the highest and second highest percent cover, respectively. The habitat types and major understory dominants, along with the physical characteristics of each plot, are listed in Appendix I. Twelve major understory species and 27 minor species were found. Of those species, beargrass was the major understory dominant on 33 plots and the minor dominant on 13. Beargrass comprised

57 percent of the total herbaceous cover on all the plots. Menziesia was dominant on 11 plots and subdominant on 4; pachistima was dominant on 6 and subdominant on 4.

Characteristics of the Globe Huckleberry Shrubs

Percent cover and mean height of huckleberry shrubs. Berry production was not related to the estimated percent cover of huckleberry shrubs in the 1977 plots, but I believe that was because of estimation errors. It was weakly correlated with the average cover in 1978 ($r^2 = 0.14$). Intuitively, it would seem that the taller a plant is, and the more coverage it has, the more fruit the plant would produce, but such was not the case with the huckleberries of western Montana.

Many sites had moderate to high coverages of huckleberry shrubs but produced no fruit. Some of these sites were in stands with tree canopies of 30 percent or more, but they had not had the canopy long enough to reduce the coverage of huckleberry shrubs, only their productivity. Therefore, there was a lag period between the time productivity declined and the time cover began to decline on the same site. Certain disturbed sites with moderate coverages, but no fruit, could have had shrubs in the late stages of recovering from disturbance that did not yet have the capacity to produce berries. In this case, the recovery of berry production lagged behind recovery of coverage. The volume of berries produced per site was not correlated with the average height of the huckleberry shrubs, presumably because production and growth responded to different environmental influences.

Number of berries per plant and average berry volume. The more berries per plant, and the larger the average volume of each berry, the higher the site's production (Fig. 10, 11). Forty-eight percent of the site-to-site variation in production was associated with these 2 variables in 1978 and they were equally as important in the 1977 samples. The factors that affected the number and average volume of berries are discussed separately, after the berry production section.

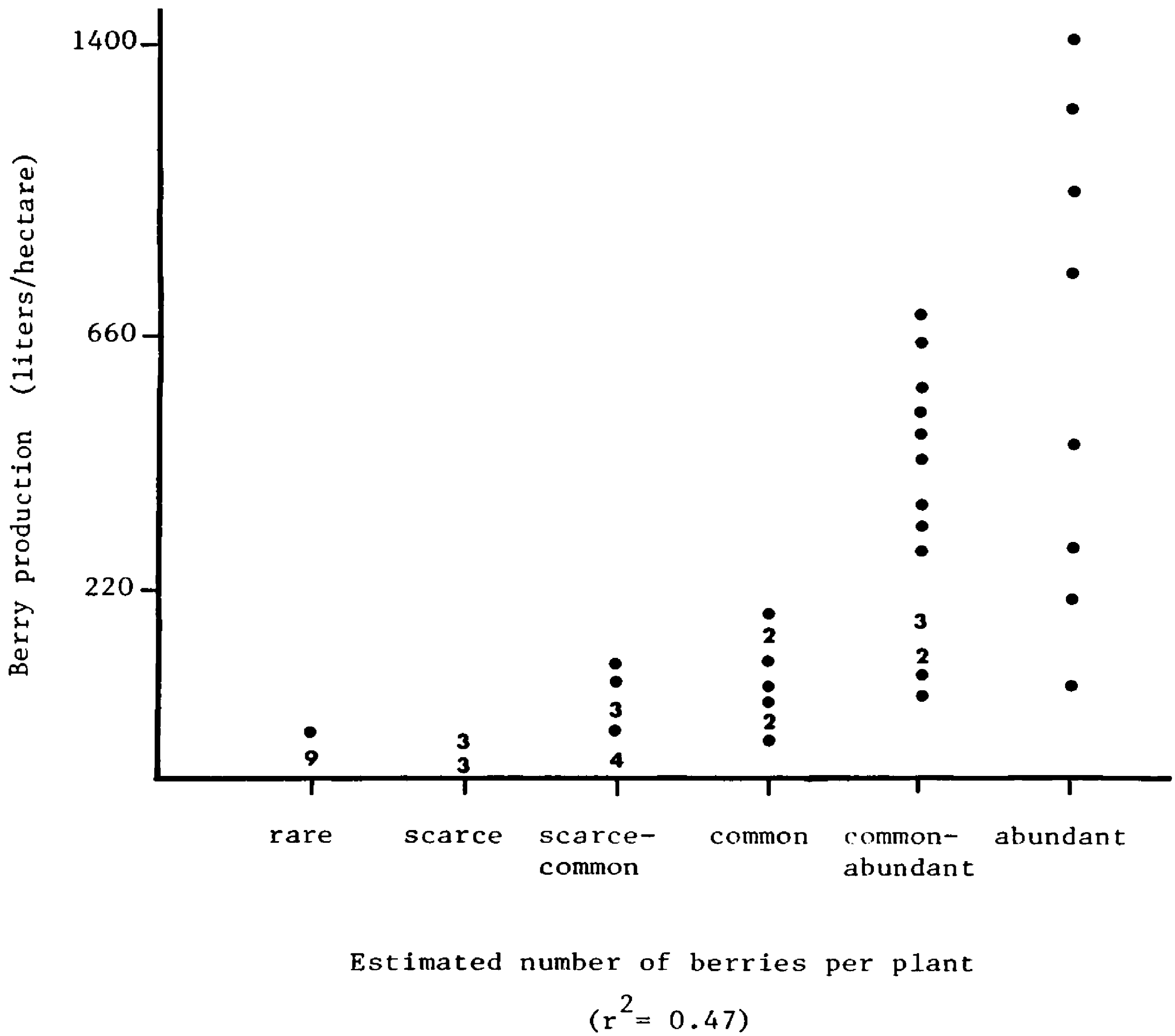
The positive relationship between number of berries and production was consistent, but there were interesting variations in average berry volume compared to production. The most prolific plot had many small berries ($\bar{x}$ = 0.28 ml); several plots had rare, but quite large, berries. However, the positive correlation between the number and average size of berries per plant was strong.

Condition of the huckleberry shrubs. Condition or vigor of the huckleberry shrubs was judged visually by the condition of the plant's leaves at the time the berry plot was sampled. Differences in production were not evident between shrubs in excellent condition and shrubs that were damaged by insects, fungi, or browsing. Shrubs that had small or shrivelled leaves, or were otherwise not in good condition, generally had low productivities. Mean production for the groups of shrubs with red, sunburned leaves (not fall leaves) was significantly higher than that of the shrubs in different conditions.

Site History

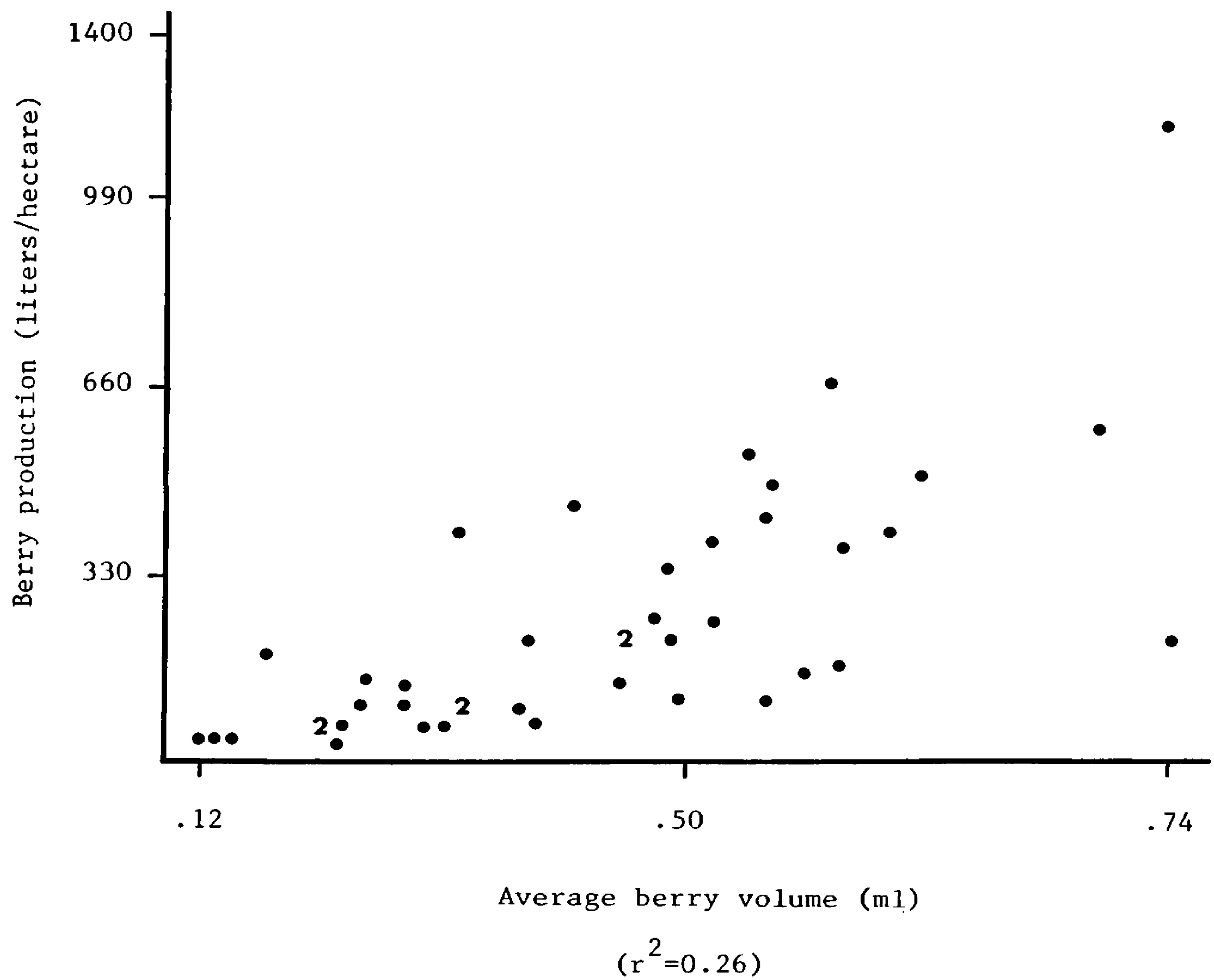
The time since the last disturbance of a stand, and the mode of that disturbance were among the major factors that determined site productivity. The 11 most productive plots were all disturbed in

Fig. 10. Correlation between estimated number of berries per plant and total berry production in 1978.



Berry production (liters/hectare)
1400
660
220
9
3
3
3
4
2
2
3
2
rare
scarce
scarce-common
common
common-abundant
abundant
Estimated number of berries per plant
(r^2= 0.47)

Fig. 11. Correlation between average berry volume and total berry production in 1978.


Berry production (liters/hectare)
1400
990
660
330
2
2
2
.12
.50
.74
Average berry volume (ml)
(r2=0.26)

the last 50 years. Eight of the 11 (72 percent) were burned; 5 in wildfires, and 3 in broadcast-burned clearcuts. Only 16 of the 53 plots with lower productivities (30 percent) had been recently disturbed, and 56 percent of the 35 least productive plots had not been disturbed in the last 75-100 years. Mean characteristics for the plots with the same site history are listed in Table 6.

Mature stands. Eight plots were in stands that had not been noticeably disturbed by either fire or logging in the last 100 or more years. Four of the 8 were in mature, dense stands (canopy cover ≥40 percent), and 4 were in mature, open stands (canopy cover ≤35 percent) (Table 6 and Appendix I). The average elevation and percent slope were higher in the mature, open stands, but the average percent shrub cover, excluding globe huckleberry, was high in both types. The mean percent of globe huckleberry cover was 22 in the dense stands and 23 in the open stands; the mean height of the shrubs was 50 cm and 62 cm, respectively. But, even though the shrubs were tall, berry production was significantly lower than the average of plots with similar huckleberry shrub coverages and/or different site histories, except those in scarified clearcuts.

Productivity ranged from 0 to 13 l/ha (0-1 gal/acre) in mature, open stands and from 0 to 27 l/ha (0-3 gal/acre) in mature, dense stands. One 300+-year old stand (Plot 44) had fruit, but production was limited to areas with open canopies. It is possible that, as the very old stand aged, its canopy was naturally thinned when trees died or fell, and huckleberry production in the understory

Table 6. Mean elevation and percent slope, mean percent coverages of herbs, shrubs, canopy, and huckleberry, and mean volume of berries produced by plots with different site histories.

Site condition	Elevation (m)	Slope (%)	Herb cover (%)	Shrub cover (%)	Canopy cover (%)	Huckle-berry cover (%)	Berry volume (l/ha)
Mature, Dense	1507	38	30	43	51	22	8
Mature, Open	1641	44	33	55	31	23	0
Thinned >15 yrs.	1591	38	27	16	18	34	299
Thinned <15 yrs.	1388	37	28	21	13	33	228
Clearcut, Broadcast-Burned	1546	39	28	33	0	21	229
Clearcut, Scarified	1434	34	28	29	1	9	0
Natural Burn, 25-60 yrs.	1816	57	32	20	5	30	390
Natural Burn, 60-100 yrs.	1623	34	39	22	30	31	27

improved locally. If the fallen trees were continually replaced, the increase in production would be short-lived. If they were not replaced, productivity might continue to increase, especially if the increase in the shrub layer inhibited tree replacement.

Plot 36 (Appendix I) was a stand that was lightly "high-graded" for timber at least 25 years ago. No evidence of other disturbances was found, nor was there much tree regeneration. The site produced 444 l/ha (46 gal/acre). If high-grading imitated the occasional removal of trees in the very old stand's canopy, Plot 36 indicated how berry production would increase in senescing stands. In stands over 70-75 years of age, it was historical and vegetative, rather than physical characteristics of the site, that limited fruit production.

The negative effects of shade on berry production could explain the low productivities in mature stands and in stands burned 60-100 years ago, if the tree canopy is dense. But canopy cover was only 20 percent in 1 mature stand and less than 25 percent on 4 stands in old burns. Old, highly-branched, eastern lowbush blueberry bushes had fewer flower buds than single shoots grown from rhizomes after a burn (Hall and Aalders 1975). If western Vaccinium species respond similarly, it could explain the reason why berry production decreased in the older stands. It would also suggest that production in very old, senescent stands would never be as high as that in stands with similar canopy coverages, but with younger shrubs. But, thin-leaved huckleberry shrubs in old stands in Washington and Oregon continued to produce berries if the tree canopy was not excessively dense. Shrubs that were "released" when the canopy was destroyed but not removed, produced 3 times as much fruit as plants in control stands (Minore et al. 1978), so the old plants were able to produce fruit. Any type of shrub disturbance, such as clearcutting or burning, increased sprouting, but the new shoots did not produce any berries during a 3-year period after treatment (Minore et al. 1978). Therefore, it would seem that, in contrast to eastern Vaccinium species, western Vaccinium species are capable of vegetative growth and berry production in mature stands, and vegetative growth immediately after disturbance, but that berry production is delayed at least 5 years, and usually much longer (20-30 years) in disturbed stands.

Scarified clearcuts. There was no huckleberry fruit on shrubs in any scarified clearcuts, and the mean percent cover of globe huckleberry shrubs was significantly lower than that of sites with other treatment histories ($\bar{x}$ = 9 percent). Globe huckleberry shrubs present in scarified clearcuts were found only around tree stumps or large rocks where tractors or bulldozers could not disturb the soil (Zager, pers. comm.). These remnant plants seem seldom productive (Jonkel, pers. comm.).

Vaccinium species are rhizomatous. Rhizomes are primarily storage organs for carbohydrates, nutrients, and organic fractions, necessary for growth and production (Townsend et al. 1969). Disking, followed by burning, increases the number of new, upright, lowbush blueberry shoots from rhizomes, but produces a high mortality in the living shrubs (Hitz 1949). Some rhizomatous graminoids sprout vigorously after soil disturbances like scarification, but their rhizomes are fibrous. *Vaccinium* rhizomes are woody, so they would tend to break easier than fibrous roots. The internodes are longer and there would be more broken sections without nodes, and thus, fewer sprouts after disturbance (Stickney, pers. comm.). The low coverages of huckleberry shrubs in the scarified clearcuts in this study, and in similar tractor-burn treatments in Oregon (Minore et al. 1978), suggest that coverage of huckleberry plants is significantly reduced in the early years after scarification. Whether or not such shrubs will produce in the future depends on the magnitude of increase in percent huckleberry shrub cover, and how competition from other species increases or decreases as the stand ages.

Eastern species of *Vaccinium* are propagated vegetatively (Hall and Aalders 1975). Northwestern thin-leaved huckleberry hardwood cuttings do not root easily, but seeds from pulped berries sprout vigorously (Minore et al. 1978). Nevertheless, wild seedlings of globe huckleberry in western Montana are extremely rare (Stickney, pers. comm.) or unrecognizable (Lyon, pers. comm.). Undoubtedly, sprouts from rhizomes of existing plants are the most common means of increasing shrub cover, so recovery of globe huckleberry cover to pre-disturbance levels from the low percentages left on scarified clearcuts is apparently very slow, if it occurs at all.

Scarified stands are usually level or gently sloping, and are located in areas where tree growth and competitive, vegetative recovery is rapid. Together with the usual low, post-treatment, huckleberry survival, delayed or inhibited future berry production on these sites is typical. Unfortunately, the exact ages of the scarified clearcut stands was not available from Forest Service records. Long-term monitoring of berry production on such sites is necessary to provide information and formulate definite conclusions about the effects of scarification on fruit production, but for now, I would have to recommend against extensive use of such practices in grizzly bear habitat.

Thinned stands. Four plots were in stands that were thinned less than 15 years ago. This group represented a wide range of elevations and percentages of slope, and had lower means of shrub and herbaceous coverages and a higher mean coverage of globe huckleberry than the mature or scarified, clearcut stands. Unlike the mean volumes for plots with other site histories, the mean volume of fruit produced in thinned stands is not considered representative of the site treatment because it varied considerably between plots, with the highest producing 587 l/ha (61 gal/acre) and the lowest producing only 36 l/ha (4 gal/acre). The least productive plot was on a west-facing slope. I was not positive of the site treatment on one of the intermediate plots and the other was an unusually productive south-facing slope in northeastern Idaho.

Production of 6 plots in stands thinned more than 15 years ago was also erratic. No recognizable differences existed between the productive and the unproductive plots except that canopy cover was only 5 percent for the more prolific plots and 9-25 percent for the less productive ones. The cover of globe huckleberry was 41 percent in the most productive plot and less than 30 percent in the others, but that does not explain the difference in productivities between the second-most productive plot and the least productive ones.

The 2 productive, young, partially cut plots (32 and 47) and the most productive, old partially cut plot (36) had high coverages of tall globe huckleberry shrubs ($\bar{x}_{cover}$ = 40 percent; $\bar{x}_{height}$ = 59 cm). Plot 30A was a partial cut stand that also had tall, dense huckleberry plants. It was productive in 1977 but the berry crop failed there in 1978. Some of the other partial cut plots had high coverages or tall shrubs, but no unproductive plots had both in 1978. Cover was linearly related to berry productivity in the overall analyses; height was not correlated with production. The number and size of the average berry per plant increased as huckleberry shrub cover increased, but only the average berry size increased with plant height.

Minimal soil disturbance and decrease in shade in partial cuts where globe huckleberry shrubs were present before the disturbance should increase huckleberry cover and productivity, although the magnitude of this increase will probably be less than that on broadcast-burned clearcuts because the fire stimulation is absent. However, partial cuts on 5 of 10 sites did not increase productivity, height, or present cover of globe huckleberry shrubs. Of the unproductive plots, one was at a high elevation (Plot 50) and 2 were on west-facing slopes. All the fruit in one unproductive plot (29) was produced in one 0.25 m^2 section; most from Plot 31 came from one section also. The fact that the shrubs on Plot 20 were clumped, and the coverage low, suggested that soil disturbance may have been extensive. The remaining 2 unproductive plots (24 and 28) were sampled in late July in the Swan River Drainage but their low productivities were unexplainable, based on the variables I considered. Mealey et al. (1977) found that the production of total bear foods (forbs, berries, etc.) was much higher on a Rocky Mountain flood plain, partial cut than on an adjacent undisturbed stand.

Broadcast-burned clearcuts. Productivity on 11 plots in broadcast-burned clearcuts ranged from 1 to 783 l/ha (1-82 gal/acre). Four of the plots, 3 of which were on south- or west-facing slopes, did not have any fruit. The fourth unproductive plot was on an east-facing slope, but appeared to have been a hot spot during the burn. Any type of logging disturbance on south and west aspects, followed by scarification or burning, significantly reduced berry production and huckleberry shrub cover. Similarly, mechanical or fire disturbances on harsh sites killed serviceberry shrubs (*Amalanchier alnifolia*), rather than stimulated them, as it did on more favorable sites (Hemmer 1975).

Berry production in 6 broadcast-burned clearcuts on northern and eastern aspects increased as much as 113 times over adjacent, undisturbed stands. Because moisture was adequate, soil disturbance minimal, canopy cover reduced, and rhizome sprouting stimulated by the fire, huckleberry shrub cover increased significantly. Two north-slope plots had low productivities, but the fire temperatures in one appeared to have been high, and I was not sure of the site treatment of the other. One broadcast-burned clearcut was on a ridge. It produced only 62 l/ha (6 gal/acre).

Berry production of the thin-leaved huckleberry in Oregon was limited or non-existent the first 3 years after clearcut, broadcast-burned treatments (Minore et al. 1978), but large quantities of diesel fuel were used to carry the fire and could have had detrimental effects on shrub recovery. It remains to be seen whether production will resume on those sites when they reach the age of the broadcast-burned, clearcut plots in this study.

The mean production for all the sampled plots in broadcast-burned clearcuts was 229 l/ha (24 gal/acre); the mean for the south and west slope plots was 1 l/ha, and the mean for the north and east slope plots, including the 3 unproductive plots, was 360 l/ha (37 gal/acre). If the unproductive north and east slope plots were excluded, the mean for that group was 548 l/ha (57 gal/acre), the highest mean productivity for any category.

How long the broadcast-burned plots have been productive or how long they will continue to produce is a matter of conjecture. They are probably productive earlier than shrubs in wildfires because the fire is less intense and the depth of bud destruction on rhizomes less extensive. The sites should continue to produce berries as long as the tree canopy is light, because the length of time broadcast-burned clearcuts produce browse species (shrubs) depends more on when trees become competitors with the shrubs than on any other factor (Warner 1970).

Wildfires 25-60 years old. The mean total production from 15 plots in wildfires 25-60 years old was significantly higher than that of plots with other site histories. The 2 most productive plots were on east-facing slopes at high elevations, that were burned by wildfires 50 years ago. Both had very low shrub coverages (6 percent) and high coverages of short, globe huckleberry shrubs ($\bar{x}_{huckleberry\ height}$ = 28 and 30 cm). Mean percent shrub cover for all plots in recent wildfires was significantly lower than that in the mature stands and the broadcast-burned clearcuts.

The mean elevation and percent slope for the recent wildfires are also significantly higher than those of the other site histories. The high values are probably related to the characteristics of natural wildfires. Production on recent wildfire sites at high elevations and with steep slopes was probably greater than it would have been on burned sites with less severe physical conditions. So the average production of recent wildfires may have been elevated by the physical site characteristics, as well as by the site treatment. But high-elevation or steep-slope plots with different site treatments were not nearly as prolific as similar plots in recent wildfires.

The mean production of recent wildfires was elevated by the 2 plots that produced over 1111 l/ha (116 gal/acre), but there were also 6 plots that produced less than 125 l/ha (13 gal/acre). One of those 5 plots was on a very steep slope at 2121 m (7000 ft), and 2 were on south-facing hillsides, but the other 2 (Plots 68 and 86) were on north- or east-facing slopes at moderate elevations. The 20 percent tree canopy on Plot 86 was the highest for this site history, and the understory species were menziesia and mosses. The globe huckleberry cover of Plot 68 (14 percent) was significantly lower than that of the other plots in young burns and, although the herbaceous cover was moderately high, it consisted of mostly grasses. Fire intensity was probably high on that plot.

Of the 4 plots which produced 200-235 l/ha (21-25 gal/acre), one was on a southwest-facing hillside and one was on a dry ridge. The other 2 (Plots 63 and 74) were on east-facing slopes at moderate elevations. At first, I suspected that early or late frosts, or a lack of precipitation had limited the east-slope plot productivities, but other plots near them were productive. Undetected pH or soil-type differences may have separated these plots from others in this group, but unfortunately their presence interjected some doubt about the general applicability of the results to all sites. In general, however, berry production in the northern and eastern slope, 25-60-year-old burns was good, and it will probably continue until a tree canopy develops. Conditions that retard or inhibit the development of a canopy, such as high elevations, steep slopes, or shallow soils, should prolong the productive life of those sites.

Wildfires 60-100 years old. Even though the 13 plots in burns 60-100 years old had a moderately high mean percent cover of globe huckleberry, they did not produce much fruit (Table 6). A wide range of elevations was represented in this sample and there were plots on both northern and southern slopes, but none on eastern ones (Appendix I). Canopy cover ranged from 8 to 55 percent; shrub cover was high on 5 plots but low on the others, and herbaceous cover on most plots was high.

The major vegetative difference between young wildfires (25-60 years) and old wildfires (60-100 years) was that the percent tree canopy cover was significantly higher in old burns (Table 4).

Plots with light tree canopies in old burns were the younger ones in that group. Most of the young burns did not have tree canopies, even though they were 50-60 years old. The mean coverages of herbaceous plants, shrubs, and globe huckleberry shrubs were almost equal for the 2 conditions, so apparently the tree canopy on old burns limited fruit production.

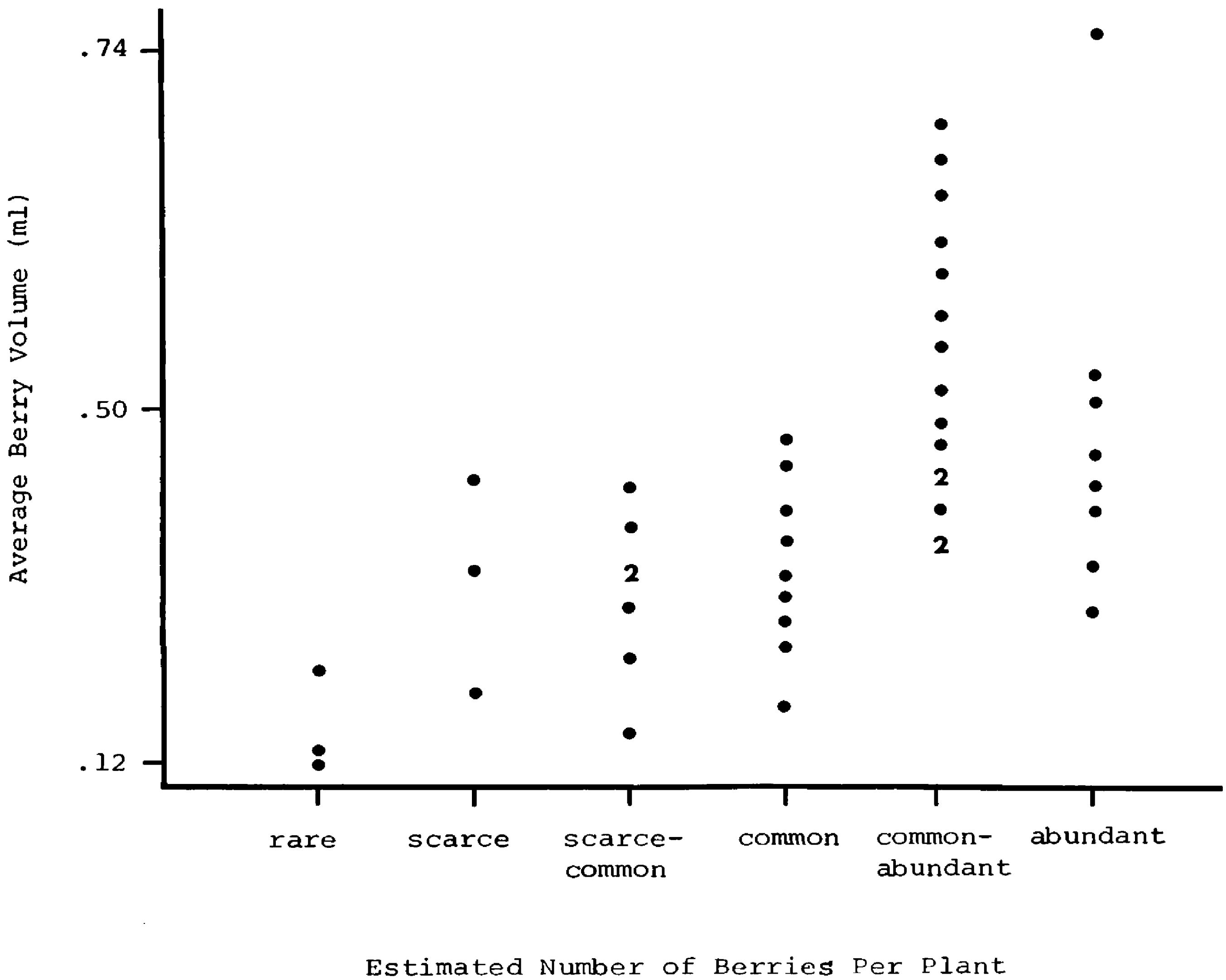
Number of Berries Per Plant and Average Berry Volume

Average berry volume was calculated by dividing the total volume of berries in the sample from each site by the number of berries in that sample. The number of berries per plant was estimated as none, rare, few to common, common, common to abundant, or abundant. The average berry volume for 1977 was 0.34 ml; it was 0.35 in 1978. It correlated best with the estimated number of berries per plant (Fig. 12). The relationship was positive. It was not related to the physical characteristics of a site (Table 3).

Berry volume was negatively correlated with aspect of the site, when aspect was arranged from northwest through east to west ($r^2 = 0.37$). Volume was not related to the site's elevation, percent slope, or topographic position. *Vaccinium* flowers develop in early spring when moisture is provided by snow melt and spring precipitation, thus adequate moisture is available on most aspects. The berries, however, develop in late July or August when moisture differences between aspects are at a maximum.

More flowers form on eastern lowbush blueberry shrubs when temperatures are warm (21°C) than form if temperatures are cool (10°C).

Fig. 12. Correlation between average berry volume and estimated number of berries per plant for the 1978 samples.


.74
.50
.12
Average Berry Volume (ml)
2
2
2
rare
scarce
scarce-
common
common
common-
abundant
abundant
Estimated Number of Berries Per Plant

More flowers probably develop during warm, moist spring seasons than during years with cool or dry springs. Temperature does not influence ultimate berry size or the percent of fruit set of eastern blueberries, but cool temperatures lengthen the berry maturation period. Western huckleberries probably respond similarly to unusually cool, summer or late fall temperatures.

The estimated number of berries per plant was approximately equal for sites with canopy coverages less than 30 percent, but decreased significantly if the canopy was more dense. The volume of an average berry increased as canopy cover increased from 0 to 30 percent, and was considerably less when tree cover was greater than 30 percent. Evidently, the shrubs received enough light under a light tree canopy to produce flowers, but I cannot explain why average berry volume would increase with canopy density up to 30 percent. Perhaps the canopy moderated effects of obscure factors such as moisture regimes at critical periods, or temperature fluctuations.

Conversely, shrubs with sunburned leaves had more numerous and larger berries than shrubs with green leaves. But sunburned leaves were always found on sites with little or no tree canopy, so the relationship in this case was one of mutual response to a single factor (increased light), rather than one of cause and effect. Shrubs that were in good condition had significantly larger berries than shrubs that were in fair condition or had been insect- or fungus-damanged.

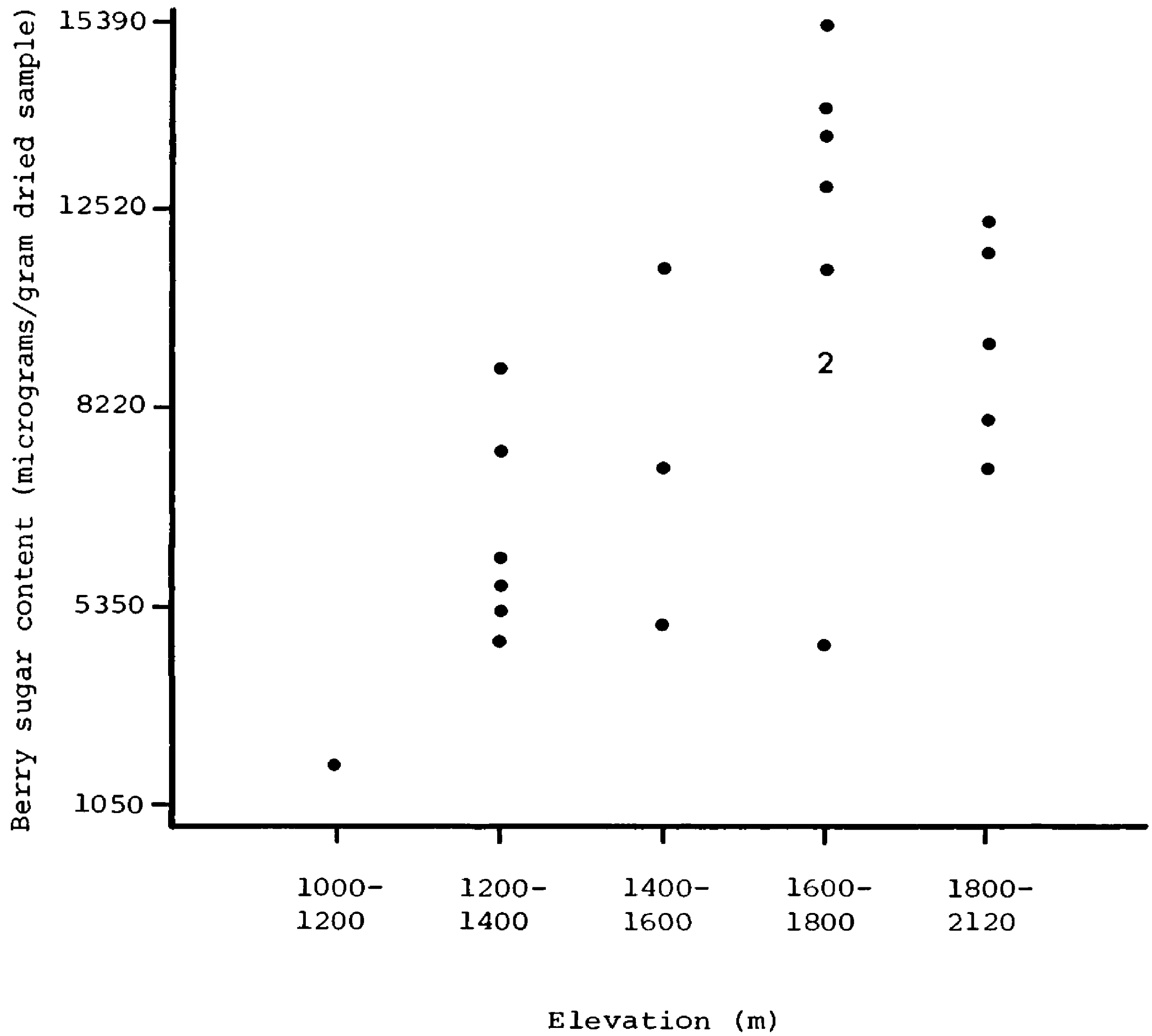
Both the number of berries per plant and average berry volume were positively correlated with the mean percent cover of globe huckleberry shrubs, but only berry volume was correlated with average shrub height. The correlation could be related to age, overstory cover, or clone genetics, but most likely, both height and berry volume are artifacts associated with increases in moisture and with mesic aspects. Either both responded to the influence separately, or the increase in height and the subsequent increase in cover and light interception provided an environment wherein more of the carbohydrates necessary to increase fruit size could be produced.

The percentages of shrub, herbaceous, or total ground cover, and the dominance of beargrass in the understory did not affect the size of the fruit or the number of berries per plant. The important point for bear and timber management was that stand disturbance in the last 50 years, either by logging or fire, induced changes which usually resulted in increases in the number and average size of berries per plant.

Berry Sugar Content

The mean micrograms of sugar per gram of dried berry sample was positively correlated with the elevation of the sampled site (Fig. 13). Although berry size and the number of berries per plant were not correlated with elevation in general, the prolific plots at high elevations often produced many small berries which should have ripened more quickly than larger fruits. Since berry sugar content was positively correlated with elevation, such a theory seems reasonable. The cool temperatures at high elevations would lengthen the fruit maturation time (Hall and Aalders 1968), but increased

Fig. 13. The effect of elevation on sugar content of the 1978 samples.



Berry sugar content (micrograms/gram dried sample)
15390
12520
8220
5350
1050
2
1000-
1200
1200-
1400
1400-
1600
1600-
1800
1800-
2120
Elevation (m)

radiation and less dense tree canopies at high elevations could shorten it. Sugar content was not predictably related to the aspect, percent slope, date the sample was taken, or the topographic position of the plot; nor was it related to the density of the tree canopy. But limited production on plots with tree canopies more dense than 30 percent made collection of berry samples large enough for sugar analysis difficult or impossible in such stands, so the effect of tree canopy on sugar content was not defined in this study.

Large or more numerous berries were not sweeter than small berries. They may have contained more water, but then small berries should have been sweeter than large, and there was no correlation, either inverse or linear, between the characteristics. Evidently, size and number of berries per plant responded to different factors than sugar content did.

The percentage of globe huckleberry shrub cover did not affect berry sugar content. Height of the globe huckleberry shrubs was not correlated with berry sweetness, nor were the number of berries per plant or the average size of a plot's berries. But berries on sites with clumped huckleberry shrubs were sweeter than those from sites with scattered shrubs. Again, clumped shrubs were usually associated with disturbed sites with light tree canopies, so I believe that it was the available sunlight and not the distribution of the shrubs that increased berry sugar content.

Groups of different colored berries can be found in many areas. The variations are probably related to the genetics of the different clones. Samples for sugar analysis were collected from several places (clones) in an area so effects of non-genetic factors on sugar content could best be defined. Samples of different colored berries from the same area might have revealed clonal differences in sugar content. But sugar content of a sample of red berries from Idaho was not significantly different than the sugar content of other berries in the same drainage. Some types of blue fruit pigments (anthocyanin) form in response to sunlight (Dugger 1913), and some are altered by temperature (Denisen 1951). In addition, sugars can accentuate the tendencies of some fruits to form pigments (Leopold and Kreidmann 1964). Therefore, sugar content or stage of fruit ripeness may not be proportional to fruit pigmentation.

Because I tried to sample all plots at approximately the same stage of fruit maturation, there was no correlation between the date the sample was collected and the sugar content of the berries. However, 3 plots on the same site were sampled twice at 2-week intervals. Sugar content dropped from the first samples to the second ones, implying that peak maturation had passed. A hard frost occurred 2 nights before the second samples were collected and many berries, especially from the higher elevation plot, had to be picked from the ground. To adequately determine the trends in sugar content of berries, the same sites should be sampled weekly from 1 August until the fruit falls from the shrubs.

Prediction of Berry Production

Site aspect and history will be used to predict how fruit production of globe huckleberries will respond to a specific treatment or lack of treatment in huckleberry habitat in northwestern Montana. The lines in figure 14 are the regression lines of production and aspect for each site history. Variation within aspects for each site history is high, and some points are based on only 1 sample, so the results should be used in conjunction with the text discussion of aspect and site history. Huckleberry shrubs must be present on the site prior to disturbance for productivity to increase or decrease.

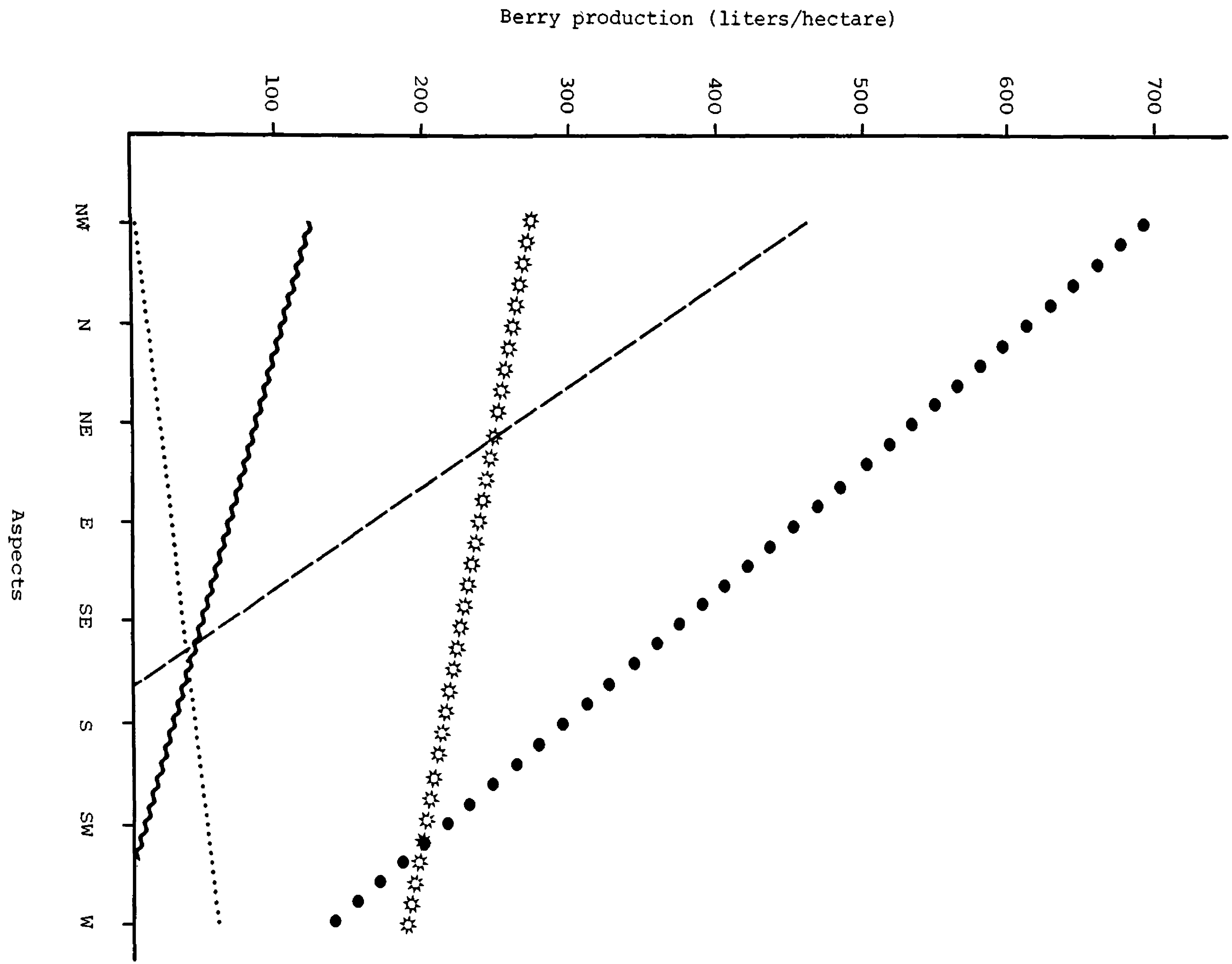
An example of how to use the graph follows:

To predict present berry productivity in a mature stand on an east aspect and future productivity in 8 to 15 years, after the site is clearcut and broadcast burned, first move down the x-axis to East and up to the point of intersection with the mature stand regression line. Then look left, straight across to the y-axis and interpret the value of that point. That value (15 l/ha) is the estimate of current berry productivity. An estimate of production on the same site 8 to 15 years after it is clearcut and broadcast burned can be obtained by moving above the mature stand-east aspect point of intersection, to the clearcut, broadcast-burned-east aspect intersect, then again looking across to the y-axis and interpreting the value (212 l/ha). The system can also be reversed. A 25-year-old burn on a north aspect can be expected to produce 625 l/ha of huckleberries. When that stand is over 100 years old, productivity will have dropped to about 7 l/ha.

The regression line for partial cuts should not be used for treatment response predictions because the slope of the line is not

Fig. 14. Regression lines for predicting globe huckleberry fruit production response to different types of disturbances.

● ● ● ● ●	25-60-year-old wildfires (r^2=0.07)
....	60-100-year-old wildfires (r^2=0.13)
— — — — —	8-15-year-old, broadcast-burned clearcuts (r^2=0.52)
☼☼☼☼☼☼☼	partial cuts (r^2=0.04)
~~	mature stands greater than 100 years old (r^2=0.17)


Berry production (liters/hectare)
100
200
300
400
500
600
700
Aspects
NW
N
NE
E
SE
S
SW
W

significant and production in partial cuts is erratic. It is included because it implies that less drastic treatments than wildfires or clearcuts are preferable for berry production on xeric southern and western aspects.

The magnitude of the y-axis did not permit enough resolution to include the insignificant regression line for scarified clearcuts. The y-intercept was -3; the line intersected the West aspect category at 1.3. Fruit productivity in scarified clearcuts was low on all aspects.

Again, the major difference between sites burned by wildfires 25-60 years ago and those burned 60-100 years ago, was the presence of a tree canopy layer in the old burns. Sites where the development of a canopy is delayed after a wildfire will probably be productive longer than 60 years. There is overlap in productivities between the categories of young and old burns.

Percent Globe Huckleberry Cover

The percent cover of globe huckleberry plants was estimated with coverage classes in 1977 (Pfister et al. 1977). As such, it correlated only with the percent of understory cover and the height of the huckleberry shrubs. The correlations were positive. In 1978, percent cover of huckleberry shrubs was estimated to the nearest 5 percent and was negatively and significantly correlated with the percent coverages of both other shrubs and herbaceous plants in the 576 plots 2.25 m^2, but was not related to the overall percent cover of the understory for each site (Table 3). The positive correlation with understory cover in 1977 was probably a reflection of general site characteristics. Conditions that were favorable for good understory growth were favorable for globe huckleberry growth. The negative correlations with shrubs and herbaceous plants in 1978 again suggested that interspecific competition limited cover and, ultimately, productivity of the globe huckleberries.

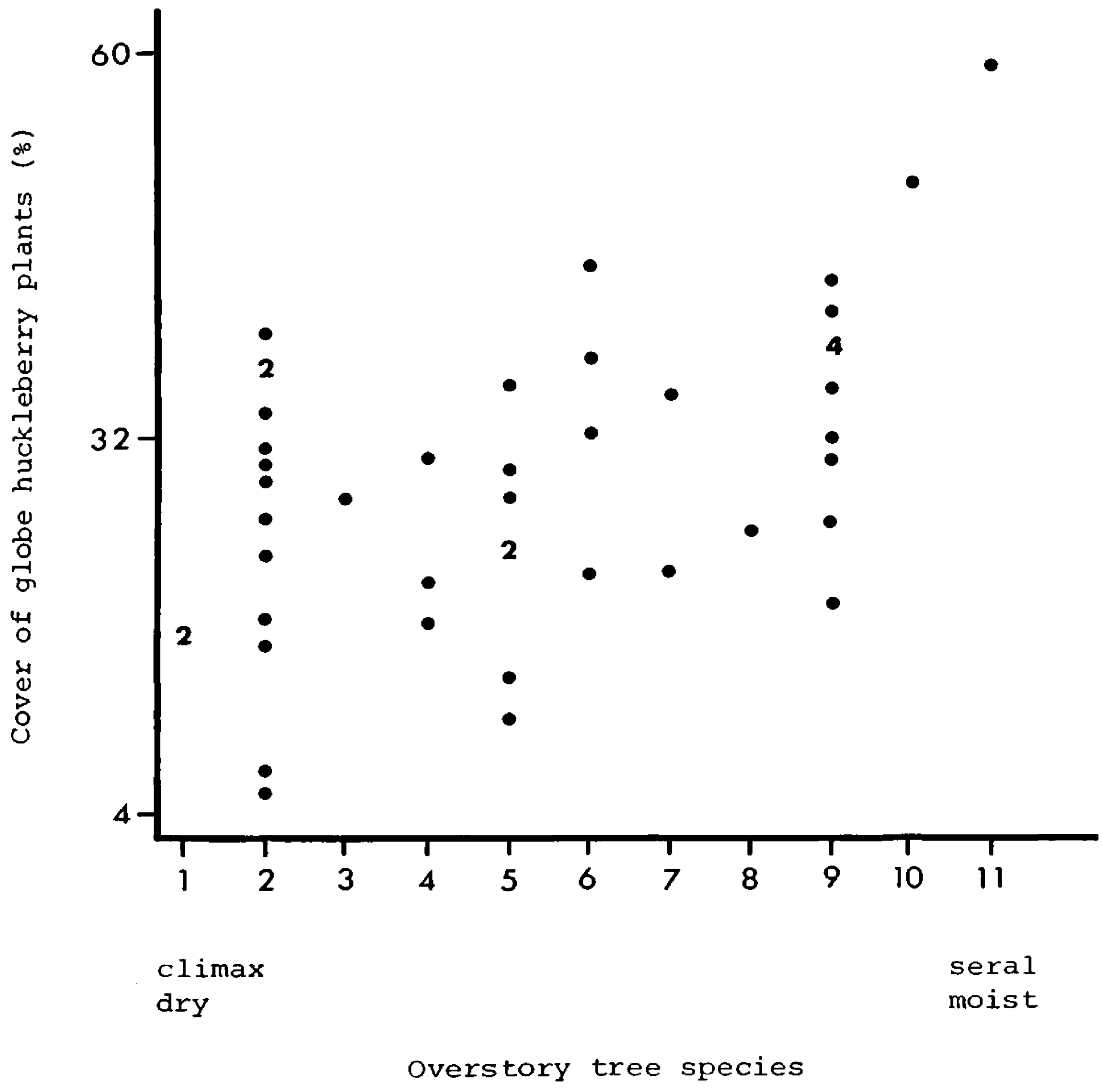
Percent cover increased significantly when the canopy cover increased from 1 to 30 percent, and decreased significantly as the canopy increased from 31 to 80 percent, much the same as berry production did. It is important to note that, even though percent cover decreases as the forest matures, the huckleberry shrubs are not entirely eliminated, even in very old stands. The rhizome network maintained under mature canopies allows the shrub cover to increase when conditions again become favorable, and is most important to consider when site alteration is planned.

On plots with at least some canopy cover, if the tree species were arranged from climax to seral and/or dry- to wet-site species, there was a positive correlation between the different tree species in the overstory and the percent cover of huckleberry shrubs (Fig. 15). In other words, the more seral the stand, the higher the percent cover of globe huckleberries was. That does not necessarily imply that the globe huckleberry is seral, because it was found in the old-aged stands, but it was less important there than in earlier seral phases.

In general, mean percent cover of huckleberry shrubs was not related to a site's aspect unless there was no tree layer. Then cover decreased when the aspects were arranged from northwest through

Fig. 15. Relationship between percent cover of globe huckleberry shrubs and overstory tree species.

1= Pseudotsuga menziesii
2= Abies lasiocarpa
3= Abies lasiocarpa-Pinus albicaulis
4= Pseudotsuga menziesii-Larix occidentalis
5= Abies lasiocarpa-Pseudotsuga menziesii
6= Abies lasiocarpa-Pinus contorta
7= Abies lasiocarpa-Larix occidentalis
8= Thuja plicata-Larix occidentalis
9= Pinus contorta
10= Pinus contorta-Larix occidentalis
11= Larix occidentalis



Cover of globe huckleberry plants (%)
60
32
4
2
2
2
4
1
2
3
4
5
6
7
8
9
10
11
climax
dry
seral
moist
Overstory tree species

east to west ($r^2 = 0.25$). Also, mean percent huckleberry cover of combined northern and eastern aspect plots was significantly higher than that for combined southern and western aspect sites.

The percent cover of huckleberry shrubs on drier habitat types, such as subalpine fir/beargrass-globe huckleberry or Douglas-fir/globe huckleberry-beargrass, in west-central Montana decrease for a 10 to 20-year period after disturbance on predominantly southern or western aspects. In those habitat types, globe huckleberry shrubs seem to persist on disturbed sites around downed logs, tree skirts, or protected areas until the tree canopy is re-established (Arno, pers. comm.). Percent cover can increase when the tree canopy is removed, but on dry sites, the shrubs are more susceptible to moisture stress, frost, etc., when the tree layer is absent.

Mean huckleberry shrub cover was not predictably affected by the percent slope, the elevation below 2120 m (7000 ft), or the major drainage of a site. It was high on upper slopes (33 percent), intermediate on middle slopes (25 percent), and low on lower slopes (19 percent). Mean cover was highest on benches (40 percent), but there were only 2 such samples; ridges averaged 31 percent huckleberry plant cover. Unlike globe huckleberry shrub height, the coverages of huckleberry shrubs were equal on ridges and on upper slopes. If other requirements were met, shrubs continued to propagate and spread vegetatively on ridges where moisture, thin soils, and winds limited vigorous height growth. Above 2120 m, temperatures were evidently too cold and seasons too short for growth phases to occur in one season. Below 2120 m, requirements for growth were adequate and other factors, such as site history, were more influential than elevation.

As noted previously, the mean percent huckleberry cover was significantly lower in scarified clearcuts than in areas with different site histories (Table 6). The mean coverages did not vary significantly between the other 7 site histories.

Height of Globe Huckleberry Shrubs

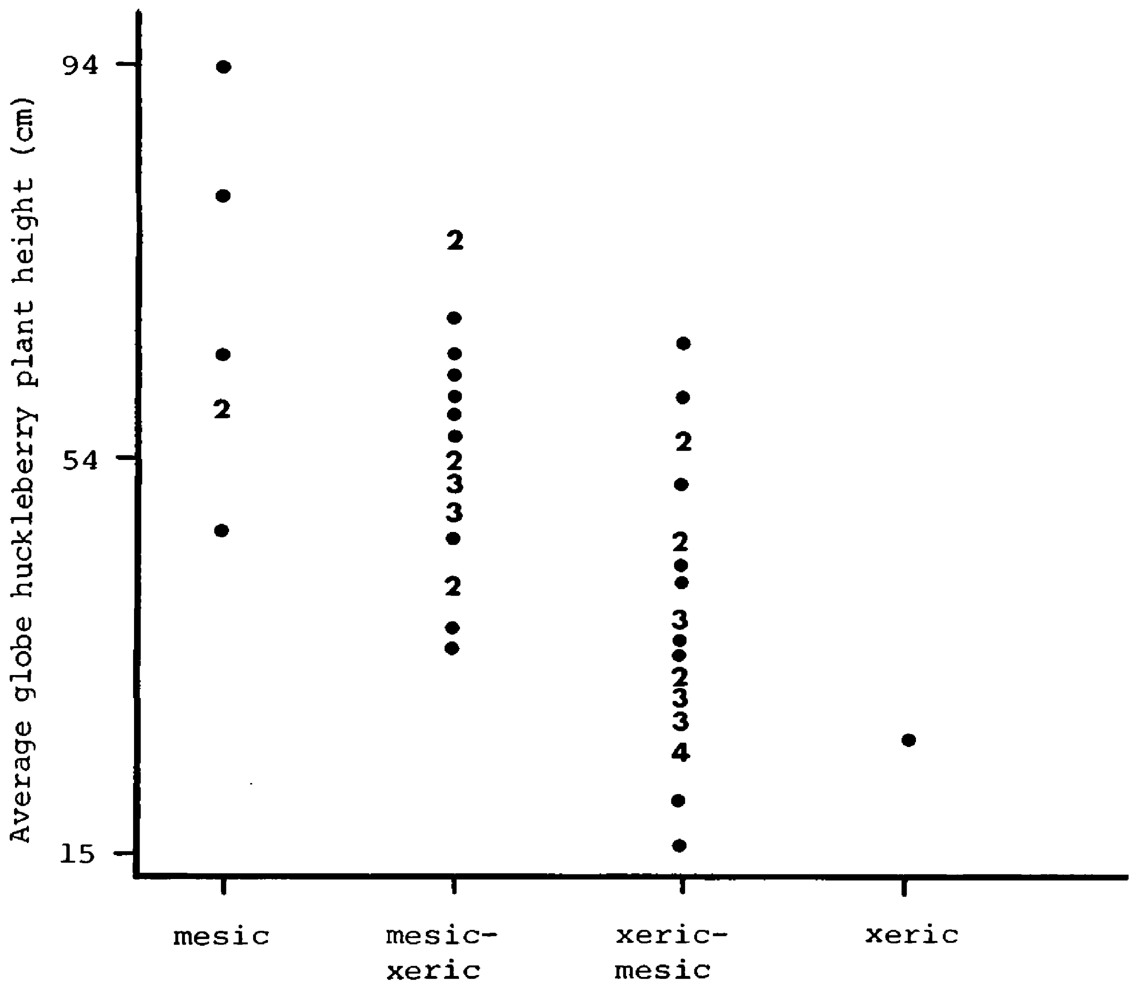
Hitchcock and Cronquist (1973) list the height range of globe huckleberry as 40-200 cm with plants rarely less than 50 cm. Height of globe huckleberry shrubs in this study, measured as the vertical distance from the point where the stem entered the soil to the highest leaf on the plant, ranged from 10 to 116 cm; the longest stem was 210 cm. Average huckleberry shrub height was 48 cm in 1977 and 49 cm in 1978.

In 1978, height of the huckleberry shrubs was related to the percentages of canopy, understory, and huckleberry shrub cover (Table 3). In 1977, it was correlated only with the percent cover of huckleberry shrubs ($r^2 = 0.19$). Mean percent cover and height were correlated in both years, even though they did not always respond similarly to environmental factors. In general, as the shrub heights increased, the branches spread, more leaves were produced, and the crown of the plant increased.

Huckleberry shrub height responded differently than either percent shrub cover or berry production to changes in aspect, unless there was no tree layer. Then height, cover, and production were all significantly higher on northern and eastern slopes compared with southern or western aspects. Apparently, the negative effects of decreased moisture and increased temperature were moderated by the canopy. In my study, the correlation between height and all canopy coverages was positive; the correlations between percent huckleberry shrub cover and production, with tree canopy, were negative. Even though percent huckleberry shrub cover was reduced under a canopy, the shrubs that remained continue to grow, so that the shaded environment was not detrimental to huckleberry shrub growth. Such continued growth habits in old stands were suggestive of climax or late-seral stage species. Serviceberry, a seral species, also survived in mature stands, but only as short, suppressed plants with little coverage (Hemmer 1975; Warner 1970).

Shrub heights in 1978 were best correlated with the estimated moisture conditions of the site (Fig. 16). When the shrubs were divided into 3 groups based on heights, the effects of moisture, canopy, and percent understory cover on height were even more pronounced (Table 7). As the heights increased, the percentages of shrubs from sites with the relatively dry subalpine fir/beargrass-globe huckleberry habitat type decreased and the percentages from the moist subalpine fir/queencup beadlilly-menziesia type increased. Similarly, the percentage of sites dominated by beargrass decreased as height increased, and menziesia was more prevalent in plots with taller shrubs. This positive relationship between height and moisture is understandable, and is reinforced by the smaller heights of shrubs on drier aspects, if no canopy is present. At some point, moisture is a limiting factor for huckleberry shrub growth, percent cover, and berry production.

Fig. 16. The effect of estimated site moisture conditions on average height of globe huckleberry shrubs.



Estimated site moisture conditions
(r^2=0.38)

Table 7. Habitat types, major understory dominants, and estimated moisture conditions of plots with short, medium-height, or tall globe huckleberry shrubs.

	Shrubs <33 cm (%)	Shrubs 34-53 cm (%)	Shrubs >53 cm (%)
Subalpine fir/ beargrass-globe huckleberry	59	49	18
Understory beargrass dominated	85	45	29
Understory menziesia dominated	0	14	41
Xeric-mesic site*	82	55	24
Mesic-xeric site	0	41	41
Mean understory cover	58	74	75
Mean canopy cover	10	20	23

*See text for explanation of estimated moisture conditions.

Huckleberry shrubs on ridges or lower slopes were shorter than those on upper or middle slopes. In general, other physical site characteristics did not influence shrub height unless the elevation was above 2120 m (7000 ft). Then the shrubs were short (15 cm). However, within sites with uniform site histories, shrub height decreased as elevation increased.

In contrast with percent cover or production, the height of the huckleberry shrubs was correlated with the understory species. If beargrass was the major understory species, the shrubs were significantly shorter than if another species was dominant. Plots dominated by menziesia had significantly taller shrubs than other plots. Huckleberry shrub height was significantly related to the moisture conditions of a site, and menziesia was found on mesic sites; beargrass in more xeric areas. The globe huckleberry shrubs were probably responding more to the different moisture conditions than to the presence of beargrass or menziesia. If these species influenced the huckleberry shrubs at all, it was probably as competitors. No mention of menziesia as a huckleberry competitor was found in the literature, but beargrass was reported as one of the thin-leaved huckleberry's "most serious competitors" (Minore 1972).

Intrasite Distribution of Globe Huckleberry Shrubs

Globe huckleberry shrubs in this study were either clumped together or individually scattered. In 1977, the sites with clumped shrubs produced significantly more fruit than sites with scattered shrubs. However, when the variance of the cover of huckleberry shrubs was graphed with the volume of berries produced, there was no correlation (clumped shrubs would have a higher variance than scattered ones). Productivity was not related to shrub distribution in 1978.

The huckleberry shrubs were usually scattered on sites with high canopy covers and clumped if the canopy cover was low or nonexistent. If the dominant tree species was seral, rather than climax, the shrubs were also clumped. The density of the understory or the dominance of beargrass in the understory did not affect the intrasite distribution of the huckleberry shrubs, nor did any of a site's physical characteristics.

The mean percent coverages of huckleberry shrubs for each site were grouped as less than 17 percent, 17-31 percent, and greater than 31 percent. The percentage of plots with clumped distributions decreased as percent cover of huckleberry shrubs increased. More plots that were burned or disturbed within 50 years had clumped distributions than plots that were not burned or not recently disturbed. Clumped or scattered huckleberry shrub distributions were manifestations of other site characteristics and site history. When a site was disturbed, cover was reduced; plants survived in small microhabitats. As the conditions for growth improved, more rhizomes and shoots formed. Eventually, some clumps grew together and distribution became more even. The weak relation between clumped shrubs and production in 1977 was probably related to the fact that young stands were more productive than old stands. The clumped shrubs were more productive, and sugar content of their berries was higher because tree canopy cover was less.

Year-to-Year Plot Comparisons

Eleven of 21 plots sampled in 1977 were not sampled in 1978. One was clearcut before I could resample it. I could not relocate 4 of the 1977 plots and 4 were either past the peak of production, or were picked before I returned in 1978. The trails to one plot on Huckleberry Mountain and one at Quartz Lake in Glacier National Park were closed in 1978 because of bear activities in the areas. Comparisons of repeated plots are listed in Table 8.

The total volumes produced, the average percent cover of globe huckleberry shrubs, and the average height of the shrubs were not consistent from 1977 to 1978. The 1977 starting point for most of the plots was marked with surveyor flagging. Some flags were removed and some were missing in 1978, so the exact starting point might not have been the same for both years. In addition, none of the locations of the other 8 plots 2.25 m^2 were marked in 1977. It is possible that they, too, were not in the same locations in both years. However, if the plots were representative of the sites, variation between years due to sampling errors should have been minimal.

Of the 10 plots that were resampled in 1978, 3 had crop failures. Plot A was sampled in 1977 because it had a history of consistent, high productivity (Jonkel, pers. comm.). The reasons for year-to-year variability or failure were not evident. There were many shrubs with small, aborted, dry, white fruits, so the flowers formed, but were not pollinated or did not mature. There was a late snowstorm in the area on 24 May that may have affected the flowers or the pollinators.

Table 8. Comparisons of plots sampled in both 1977 and 1978.

Plot	Date sampled	Total volume of sample (l/ha)	Mean huckleberry shrub cover (%)	Mean huckleberry shrub height (cm)
A:1977	7 July	146	66	47
1978	1 August	57 (114.4)	56	57
B:1977	12 August	186	19	36
1978	18 August	89 (133)*	39	40
C:1977	12 August	556	21	50
1978	18 August	431 (791)	34	75
D:1977	13 August	236	21	33
1978	2 September	124 (177)	21	35
E:1977	13 August	155	12	45
1978	17 August	93 (155)	29	56
F:1977	26 August	253	8	39
1978	27 August	36	27	57
G:1977	27 August	351	16	34
1978	27 August	218	24	47
H:1977	28 August	226	14	55
1978	18 August	111 (204)	23	39

Table 8. Comparisons of plots sampled in both 1977 and 1978 (Continued).

Plot	Date sampled	Total volume of sample (l/ha)	Mean huckleberry shrub cover (%)	Mean huckleberry shrub height (cm)
I:1977	31 August	204	21	41
1978	29 August	0	7	36
J:1977	1 September	111	24	29
1978	28 August	386	24	29

*Number in parentheses represents green-fruit-to-ripe-fruit conversion (See: Materials and Methods)

A second crop failure occurred near Granite Park Chalet in Glacier National Park at 1939 m (6400 ft). It snowed about 6 inches on 7 July 1978 at the Chalet just at the time the green fruit was starting to mature (Granite Park Chalet Ranger, pers. comm.). The small green fruits were still on the bushes 29 August 1978, but had not matured noticeably beyond the stage they were at when it snowed in July. The difference in appearance of the fruits on the 2 sites with crop failures implies that development was impaired at different stages. There are, no doubt, physiological or other explanations for both, but at present I can merely document their occurrence.

The plot with the third crop failure was moderately productive in 1977, but contained little fruit in 1978. Plots nearby at higher elevations, or on different aspects, were not any less productive than expected. Limited pollination, limited nutrients, or "premature abscission of flowers and newly set fruits" can limit fruit set (Leopold and Kriedemann 1964). Without specific weather data for the site, it is impossible to determine which factors were responsible for the crop failures in the area.

Two resampled plots were not in exactly the same locations in subsequent years (Plots C and G), but they were on the same sites and conditions were very similar. Percentages of huckleberry shrub cover and average heights did not vary more between years in these pairs than in other plots repeated in the same areas in both years. Because variations within each plot were high, the different mean coverages and heights for the different years are not significantly different.

Plot D was sampled on 13 August 1977 and most of the berries were ripe. Not even half were ripe on 17 August 1978, so the plot was repeated 2 September 1978. Even then, the fruits were only 70 percent ripe. Plot G was done 10 days earlier in 1978 than in 1977, but was only 55 percent ripe. Time did not permit returning to the plot at a later date.

By the time Plot J in Glacier National Park was sampled in 1977, several grizzlies had been seen feeding in the area. The plot was located where little evidence of bear use was obvious, but the production measure still could have been artifically low. No bear sightings were reported from that site in 1978 before the plot was sampled, but one black bear scat was found and people had picked berries in the area. In general, the production measures of this plot are probably not representative of the site's physical, vegetative, or historical characteristics.

Only 2 plots (B and E) were sampled in the same area, were not conspicuously influenced by weather, berry pickers, or animals, and were repeated in 1978 within 6 days of the date they were sampled in 1977. Plot H was also comparable in both years, even though sampling dates and percentages of ripe fruits varied.

As noted previously, the accuracy of the 1977 percent globe huckleberry cover estimates is questionable. The mean heights for Plot B are not significantly different, nor are those for Plot E, even though they appear to be, because of high variations within each sample. Total production for Plot E was equal in both years. It was lower in 1978 than in 1977 for Plot B; I could not explain the reason.

The yearly variation in productivity within a site emphasizes the importance of weather in determining berry production. In one area, frost was localized so production failed in only one portion of the drainage. Two late snowstorms in different areas had more widespread effects, but production in nearby drainages or at different elevations was normal. Minore et al. (1978) noted that weather, more than any site characteristic, influenced annual berry crops, and suggested that no conclusions about site production should be based on samples from 1 to 2 years. However, information was obtained from the samples in this study because the plots were widespread, and therefore, not all subject to one meterological event.

Bears and Berries

Berries as a Source of Bear Food

Huckleberries are a major component of both black and grizzly bear diets from late July to September in western Montana (Schaffer 1971; Jonkel 1966; Tisch 1961). Whether the bears are dependent on the berries for late summer nutrition, or just strongly prefer it, has not been investigated. Rogers (1977) noted marked declines in black bear cub production after 3 consecutive years of berry crop failure. Jonkel and Cowan (1971) found a positive correlation between abundant berry crops and black bear reproductive success, but said it may have been coincidental. On the other hand, when an early July snowstorm stopped fruit maturation around Granite Park Chalet in Glacier National Park in 1978, at least some grizzlies did not leave the area in August, even though there were no ripe fruits (Granite

Park Ranger, pers. comm.). Like many quality bear habitats, the Border Grizzly area contains many high elevation bogs, flood plains, ridge top, seeps, etc., which produce alternative foods for the bears. For example, several large, fresh digging sites were evident near the Chalet.

Black bears and grizzlies change elevational distributions in mid- to late-July when huckleberries start to ripen (Amstrup and Beecham 1976; Schaffer 1971; Jonkel 1966; Martinka, pers. comm.). Black bears, too, shift their patterns of use from year-to-year in relation to huckleberry crop failures at different elevations on different sites (Jonkel 1966). It seems that, with such percentages of use and correlations with phenology, the bears are at least partially, if not substantially, dependent on the berries for some aspect of nutritional or reproductive success, if not for long-term survival.

Bear Utilization of Huckleberry Habitats

The primary goal of this research was to find out more about an important grizzly food. Both grizzly and black bears in northwestern Montana used low elevations during the spring and early summer. From mid-July to September, use shifted to middle elevations for black bears and middle to high elevations for grizzlies (Schaffer 1971, Jonkel 1966, Tisch 1961). Grizzlies generally exclude black bears from high elevation, open areas (Schaffer 1971), but black bears sometimes moved to higher elevations in late summer for berries (Jonkel 1966). Within the low and middle elevations, Jonkel and Cowan

(1971) reported that black bears do not use clearcuts in the spruce-fir/pachistima association until about 10 or more years after disturbance.

Black bears on Long Island in Washington selected areas logged within 8 years and avoided sites not logged since 41 years ago, but they used areas cut 17-24 years ago more than those cut 9-13 years ago (Lindzey and Meslow 1977). Increased use of clearcuts was related to an increase in the abundance of bushes and berries compared to older conifer or alder stands. Higher coverages of shrubs and regenerated trees made the older cuts more attractive than recent cuts even though berries were less abundant.

No radio-collared grizzlies in northwestern Montana were located in clearcuts in 1977, but that may have been because tracking was only done during daylight hours (Kiser et al. 1978). Five clearcuts with evidence of grizzly bear activity were found. Three of those were in subalpine fir/queencup beadlilly-menziesia habitat types which produce abundant shrubs with fruits used by grizzlies if they are logged (Pfister et al. 1977). The other 2 sites were in the subalpine fir/menziesia habitat type which was the least important of 8 types classified by importance values computed from presence of bear foods (Kiser et al. 1979). Tisch (1961) reported that the spruce-fir/menziesia type offers little food for black bears and is used only occasionally in the fall. On the other hand, Schaffer (1971) said more than one habitat was used by bears in any season, but that grizzlies use high elevation, open spruce-fir/huckleberry, and white bark pine habitats frequently in the fall. In addition, percent cover of globe huckleberry increases in burns in subalpine fir/queencup beadlilly-menziesia sites in natural burns (Zager 1978) and in broadcast-burn clearcuts on north and east slopes.

Little evidence of grizzly use was found in broadcast-burned clearcuts in subalpine fir/queencup beadlilly-menziesia or subalpine fir/menziesia habitats, but the cuts were all 8-15 years old and shrub cover less than 1.5 m tall with little or no tree regeneration. When cover reaches 2-3 m, bear use, especially grizzly use, will probably increase on these sites.

The subalpine fir/beargrass-globe huckleberry habitat type was listed as the second-most important type for bears, based on importance values computed from presence of bear foods (Kiser et al. 1978). Grizzlies use the high elevation, open areas in middle-aged burns in this type in the fall. Since not many other bear foods occur in this type (Haroldsen, pers. comm.), the huckleberries are probably the main attractants for bears. In fact, the subalpine fir/smooth woodrush-grouse whortleberry type was the most important type in the North Fork of the Flathead River in Montana in 1977 (Kiser et al. 1978). Only 2 of my plots were in this type, and both were less productive than broadcast-burned clearcuts or natural burns in the habitat types discussed previously. The huckleberry shrubs had berries, but coverage was moderate and the shrubs were short, presumably stunted by the high elevation and short growing season. Because the environment in this habitat type is harsh, any man-caused disturbances would probably cause long-term reductions in productivity and coverage of the huckleberry shrubs, and make the area less attractive for bears.

Taxonomy

All leaf figures are photo reproductions of collected, pressed leaves. Stem pieces were placed on a copy machine with labels, and reproduced. Scientific names are used for brevity in this section.

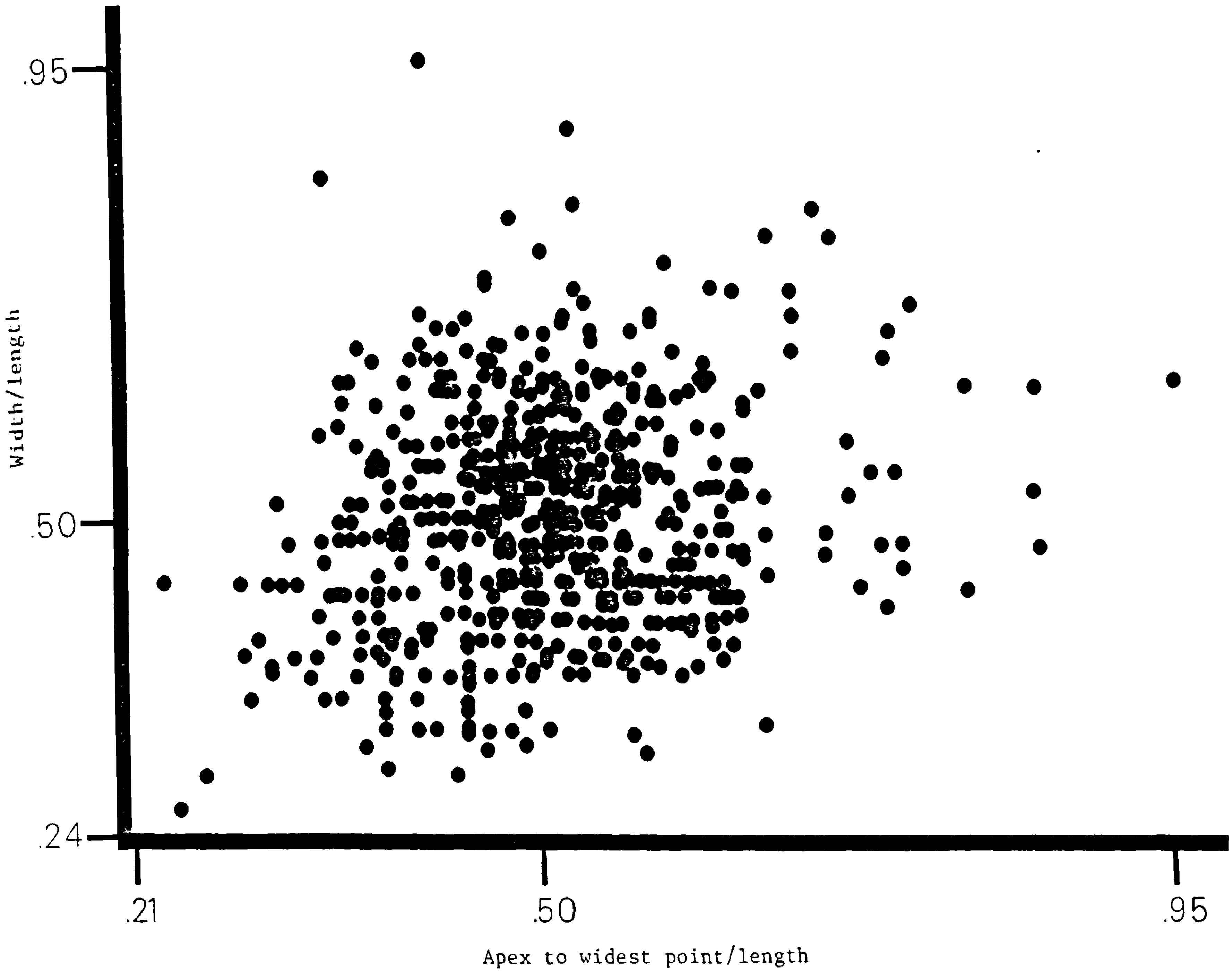
The shape of most of the fresh V. globulare, V. membranaceum flowers collected in western Montana, northern Idaho, northern Oregon, and eastern Washington are broader than long. A few were equally as long as they were broad, but none was longer than broad. Hitchcock and Cronquist (1973) pictured the corollas of V. globulare flowers as broader than long, or round, and those of V. membranaceum as longer than broad. I intended to use corolla shape to differentiate between the 2 species because leaf shape is influenced by environmental conditions. But I have no flower collections from the type locality of V. globulare in the Madison Range of Montana, or from the central distribution of V. membranaceum in the Cascade Range in Washington. Collections and measurements of fresh flowers from the Cascades are necessary before any concrete conclusions about the strength of the corolla character can be made. However, even flowers I collected near the type locality of V. membranaceum north of Mount Hood in Oregon were broader than long, but Camp (1942) mentioned that the nomenclatural localities for the 2 species are probably not representative of the biological types.

To see if the species could be differentiated by leaf shape, I graphed the leaf ratios of 555 collected and herbaria specimens. The scatter diagram of the third-leaf measurements is pictured in Figure 17. The diagrams for the terminal- and second-leaf ratios were very similar to the third-leaf ratio diagram. The points were clustered around 0.45-0.55, with a few outlying points on all the graphs. Therefore, most of the leaves were elliptic (widest at the midpoint) and about half as wide as long, regardless of the geographic locations or the physical or vegetative characteristics of the collection sites.

However, the leaves of some plants collected in different areas with similar site conditions had different shaped apices (Figs. 22 and 23). The leaf shape represented in Figure 18 is from a plant collected in northeastern Washington. The one in Figure 19 was from the northern Blue Mountains in Oregon. Both specimens were from benches with 90 percent canopy cover and similar estimated moisture conditions in old growth (100+ years) stands. The plant in Figure 18 had tear drop-shaped leaves which tapered gradually from the widest portion of the leaf to the apex. The leaf in Figure 19 was elliptic with an abruptly acute tip.

Camp (1942), after an extensive review of herbaria collections, described the leaves of V. membranaceum as ovate, often with conspicuously acuminate apices and sharply serrated margins. He used these characteristics to distinguish V. membranaceum from V. globulare, which he said seldom had acuminate apices, and had finely serrated margins. Schultz (1944) described the 2 species similarly. Hitchcock

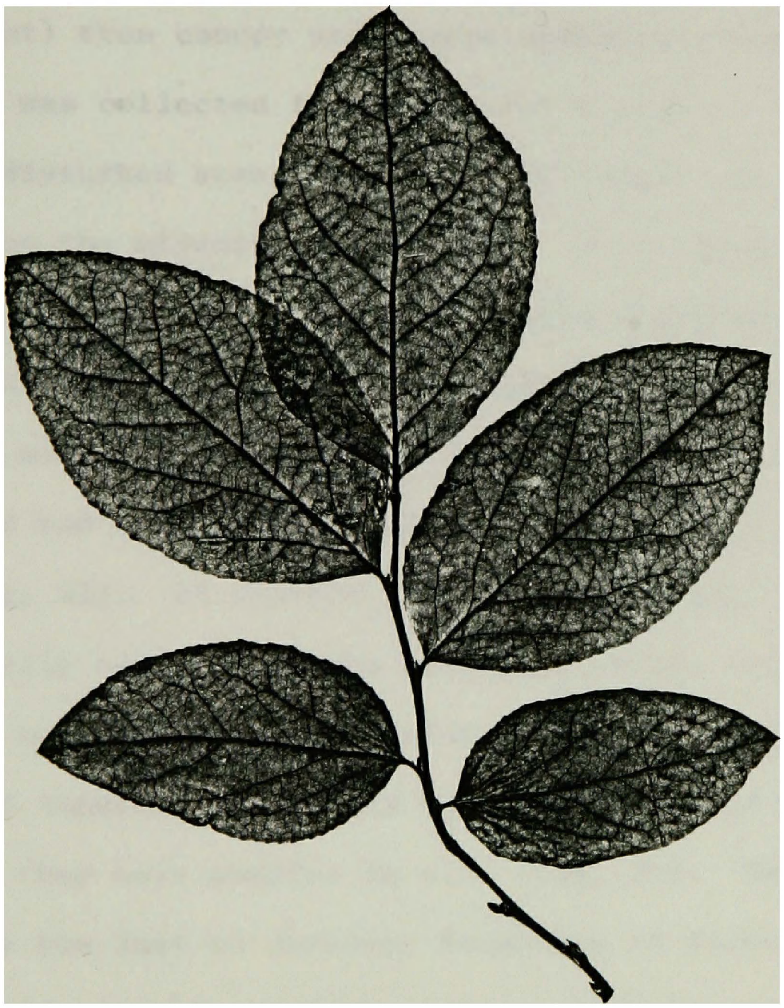
Fig. 17. Scatter diagram of leaf ratios from the third leaves of collected specimens and herbaria specimens from western Montana, northern Idaho, eastern Washington, and northern Oregon.



.95
.50
.24
Width/length
.21
.50
.95
Apex to widest point/length

Fig. 18. Tapered leaf apices of V. membranaceum specimen from eastern Washington.

Fig. 19. Rounded leaf apices of *V. globulare* specimen from the northern Blue Mountains in Oregon.



and Cronquist (1973) described the leaves of both species as sharply serrulate.

In my study, plants collected from the same site under different conditions exhibited both extremes in leaf apex shape. Figure 20 was from a relatively undisturbed stand with a dense (90 percent) tree canopy and sparse understory cover. The plant in Figure 21 was collected in an adjacent clearcut. Huckleberry leaves in the undisturbed stand were not only larger and thinner, but tapered slowly from the midpoint to the apex. Those from the plant in the clearcut were smaller, thicker, and more abruptly acute.

Variability in leaf shape and size occurred even on one plant. Leaves on stems formed as resprouts after damage to the main stem were larger and had more variable shape than the other leaves on the same plant (Fig. 22). On current annual growth stems, variation in leaf shape usually occurred in the terminal, third, and/or fourth leaves. There was no pattern to the variation in the terminal leaves. Often, their tips tapered more slowly than the apices of other leaves, or sometimes they were smaller in size (Fig. 23). Because the terminal leaves are the last to develop, formation of flowers in the axils of the third, fourth, or fifth leaves could have inhibited their maturation or affected their ultimate shape (Stickney, pers. comm.). The third and/or fourth leaves of a stem with flowers in the axils were often smaller and rounder than the second and terminal leaves (Fig. 24). The flowers probably affected their shape, too.

Camp (1942) described a "master population" of _V_. _globulare_ plants derived from _V_. _ovalifolium_ x _V_. _caespitosum_ and _V_. _ovalifolium_ x

Fig. 20. Specimen of *V. globulare* from an undisturbed stand with a dense tree canopy and sparse undergrowth.

Fig. 21. Specimen of _V. globulare_ from a clearcut adjacent to the undisturbed stand referenced in Figure 20.

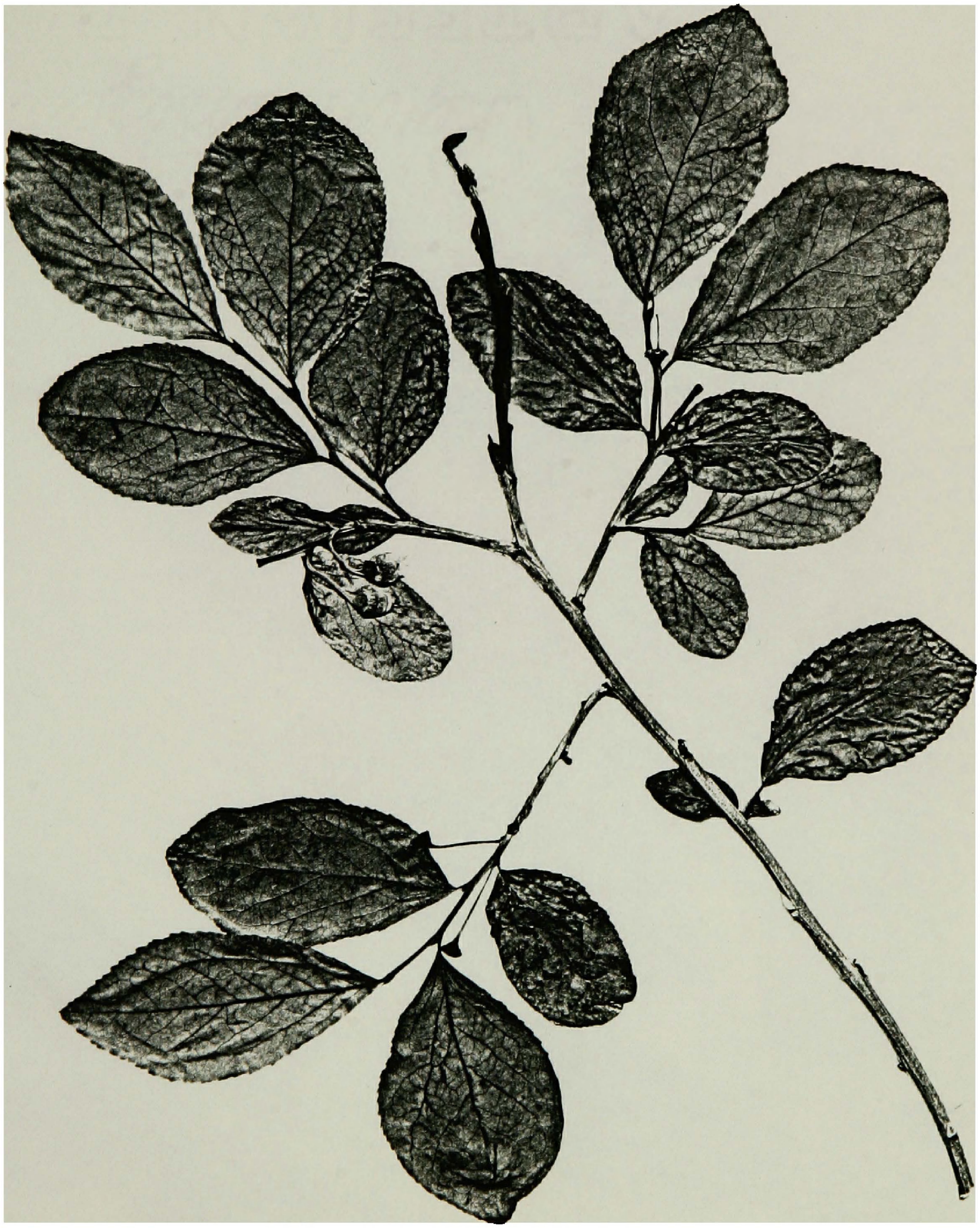


Fig. 22. Variation in shape and size of resprout leaves compared to leaves on current annual growth twigs.

Fig. 23. Variation in terminal leaf shapes on current annual growth twigs.

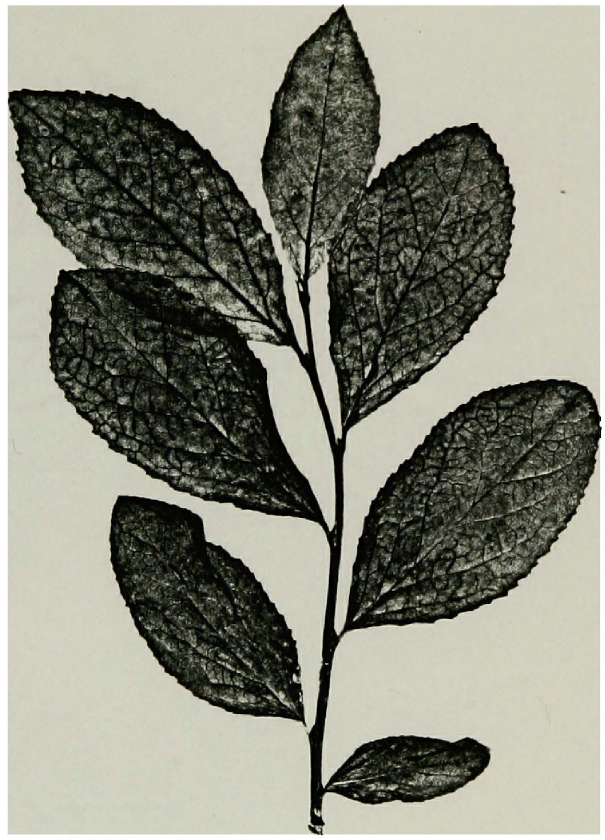
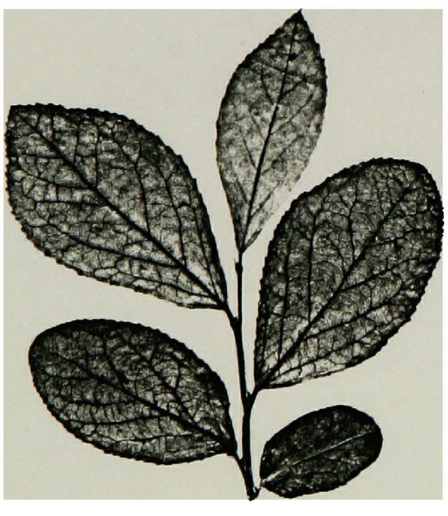
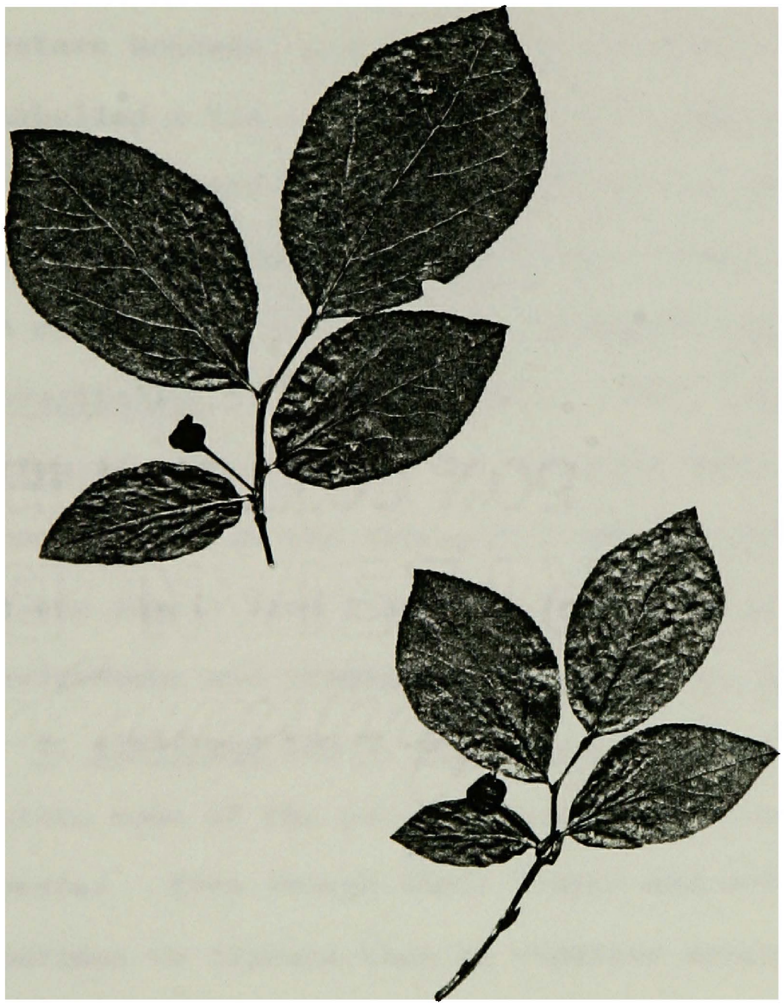



Fig. 24. Effect of flower formation in the leaf axil on the size and shape of the leaf.



V. scoparium crosses, that had variable leaf shapes dominated by the common ancestral form of V. ovalifolium leaves (See Table 9 for gametic chromosome numbers). He said the population's distribution was "remarkably consistent" in the Blue Mountains of Oregon, Washington, and Idaho, and that this was the common bilberry in Idaho, western Montana, and Wyoming as far south as the Grand Tetons. He also labelled a few specimens from the eastern foothills of the Cascades in Washington as V. globulare, but noted that V. membranaceum was by far the more common species in that area.

A cytological study of the Washington Vaccinium species revealed that V. ovalifolium is a tetraploid (n = 24), but V. caespitosum and V. scoparium are diploids (n = 12) (Schultz 1944). Hybridizations or backcrosses between the tetraploid and the diploids are possible, but would not likely form a new species unless it was highly adapted to the environment and propagated vegetatively, as triploids are often sterile. V. globulare and V. membranaceum are tetraploids, which could explain some of the population and individual variation inherent in the species. Even though their status and origins are questionable, I will continue to discuss them as separate species, as do most taxonomic authors.

Schultz (1944) said V. globulare ranged from eastern Washington north into British Columbia, east into Montana, and south to Utah. He found 3 V. globulare plants in eastern Washington, intermixed with V. membranaceum plants and believed that area was the western-most extension of V. globulare's Rocky Mountain distribution. Both Schultz and Camp described V. membranaceum as a more widely

Table 9. Gametic chromosome number of some Pacific Northwest Vaccinium species (from Schultz 1944).

Species	Gametic chromosome number (n=12)
V. caespitosum	n
V. myrtillus	n
V. scoparium	n
V. globulare	2n
V. membranaceum	2n
V. ovalifolium	2n

distributed species occurring as far east as Lake Superior, and south along the coast, into California. In contrast to Camp, Schultz said V. membranaceum was also common in the Blue Mountains.

Geologic descriptions of how the V. globulare, V. membranaceum complex plants obtained their present distributions vary. Daubenmire (1975) described 3 groups of plants that developed during the Rocky Mountain Uplift of the Miocene. One group persisted east of the mountains, one west, and one occurred on both sides. V. membranaceum (the name he applied) was in the group that persisted west of the mountains and later returned to the Rocky Mountains. Habeck (1967) did not discuss V. membranaceum specifically, but included it in a diagram of plants that originated in the Rocky Mountains and whose ranges expanded west toward the coast. If Daubenmire's description is applied to the present distributions and the type localities of north Oregon and south-central Montana, V. membranaceum and V. globulare could have been separated during the uplift. The area of variable plants in northern Idaho and western Montana could be where the 2 species hybridized when their ranges again expanded into that area. That does not, however, explain the presence of good V. globulare plants in the Blue Mountains of Oregon. Habeck's generalized description for western Montana does not provide an insight into the present distributions in the other western states.

Camp considered V. membranaceum leaves less variable than those of V. globulare. Schultz did not discuss intrapopulation variability in V. globulare, but said field studies of V. membranaceum proved that identification was less complex than herbaria studies tended to imply. He atrributed the variability to environmental responses, and did not believe V. membranaceum should be separated into subspecies. He also discovered that both species were tetraploids which tend to be more variable than their diploid ancestors.

At any rate, depending on how many leaves were present on the current annual growth, the shapes of the second, and sometimes the third and fourth leaves from areas with moderate sunlight, were least altered by physiological developments from position on the stem or flower formation. Those leaves should be used for species differentiation. The shape of the apices of the second and/or third leaves on the current annual growth from personally collected specimens and herbaria specimens varied from one location to another even if environmental conditions were similar. But in general, leaves from plants north of Mount Hood and south of the Columbia River in Oregon had apices that tapered gradually to the tip, but their flowers were globular shaped. Farther east, in the southern and northern Blue Mountains, the second and third leaves of huckleberry plants were abruptly acute, and the flowers, round. Collections from Idaho around Lightning Creek and Deer Creek north of Clark Fork, and from the Priest Lake area were mixed. Some were gradually acuminate with sharply serrated edges, others were abruptly acute, and some were mixed or intermediate. No pattern of distribution for any type was obvious. Plants with good V. membranaceum leaves that tapered gradually to the apices were less common in western Montana than plants with abruptly acute leaves. No leaves with sharp serrations were found there and apex shapes were quite variable. Camp (1942) described a variable population of Vaccinium he thought was derived from hybridization between V. myrtillus and V. globulare whose range formed an arc north and east of the Blue Mountain population of V. globulare. Such an arc would include northern Idaho and western Montana. But because V. myrtillus is a diploid, a cross between it and V. globulare might introduce new genes into the tetraploid population that would make it different from the original, but would not likely form a new species.

From personal observations and collections from the areas he mentioned, it seems that Camp's description of the distributions of the different types in the V. globulare, V. membranaceum complex are accurate. Questions about the origins and interrelationships, and consequent separation or lumping of the types still exist, even though Schultz (1944) determined the chromosome number and structure of all the species that are probably involved. Further comparisons of chromosomal differences and hybrid affinities between plants collected from the Cascades of Washington and Oregon, the Mount Hood region, the Blue Mountains, northern Idaho, western Montana, the Madison Range of Montana, and northwestern Wyoming, together with consideration of the geologic histories of plant migration patterns, should reveal the relationships between the tetraploid V. globulare V. membranaceum-type plants.

Two other variations of the V. globulare, V. membranaceum plants were found. One form had distinctly rounded, small leaves

(Fig. 25). This type was found in the Kah Mountain area in the South Fork of the Flathead River in Montana, and near Granite Pass in northeastern Washington. Plants with *V. globulare*-type leaves were associated with the round-leaf plants at both locations, but rhizome excavations revealed that the two types were separate plants.

The round-leaf plants could have been mutations, but the possibility that 2 similar forms would develop in 2 remote areas seems small. The leaves do not resemble those described for any *Vaccinium* species in the Pacific Northwest (Hitchcock and Cronquist 1973). Again, cytological studies would be the best way to determine the genetic consitution of those plants.

The other variation was found in only one location in eastern Washington on the Idaho border. The margins of the leaves were much more serrated than those of the other *V. membranaceum* plants, but the apices were gradually tapered (Fig. 26). Camp (1942) and Schultz (1944) both said *V. membranaceum* was more serrated than *V. globulare*, so the serrated-margin plant fits the general descriptions of *V. membranaceum*.

Even though the very mesic northwest corner of Montana north of the Yaak River was searched extensively, *V. ovalifolium* was not found. It is possible that the species exists in some habitats not examined in this study, but if it does occur in western Montana, *V. ovalifolium* is rare. The Cabinet Gorge of the Clark Fork River on the Montana-Idaho border serves as an inland extension for some coastal plants, like the Columbia River Drainage does (Stickney, pers. comm.). Some unusual *V. globulare*-type plants about 70 cm tall collected near

Fig. 25. Round-leaf form of V. globulare found on 2 locations in the study area.

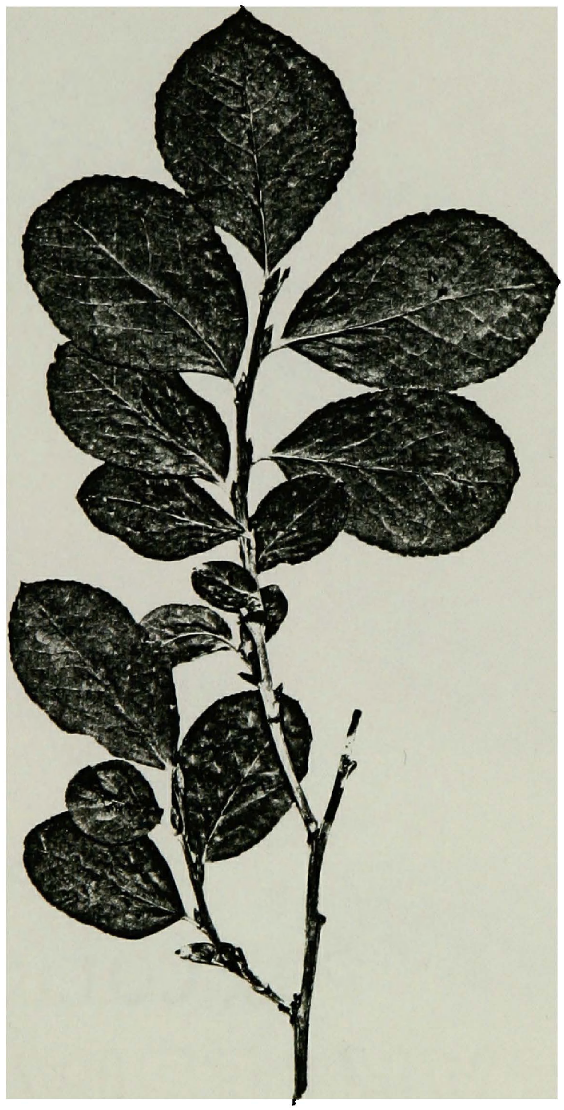
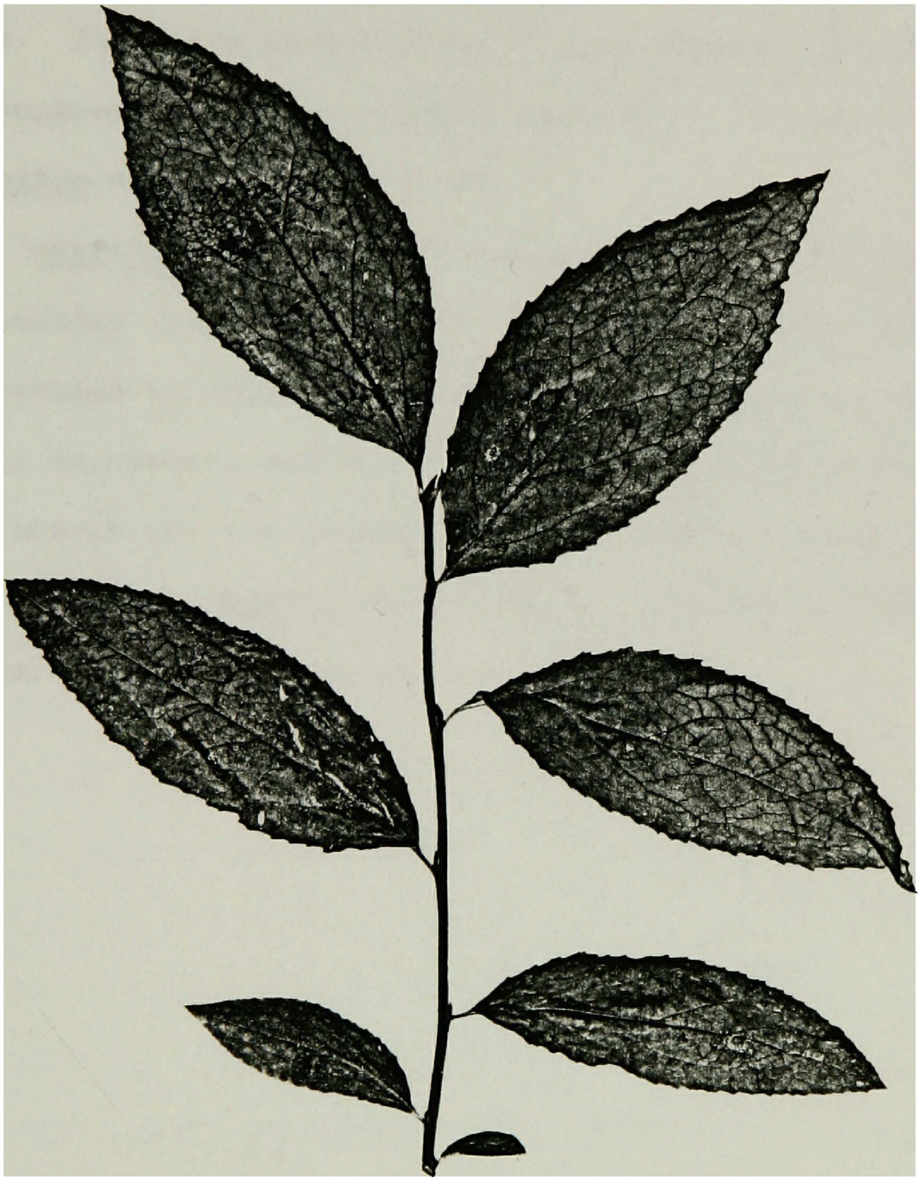


Fig. 26. *V. membranaceum* specimen from eastern Washington with very serrated leaf margins.



Noxon, Montana, in the Cabinet Gorge by Jonkel (pers. comm.) had a few green stems on the upper portions of the plants. The plants were collected in late fall, so no leaves were present to determine leaf shape. These are probably not V. ovalifolium plants, but their presence suggests that some unusual forms exist in the area and V. ovalifolium might be found there.

V. myrtilloides was not located anywhere in northwestern Montana, besides the west entrance of Glacier National Park. It is not described by Hitchcock and Cronquist (1973) as a species of the Pacific Northwest, but it is widespread in Alberta (Moss 1959). I did not search the area south of that Province for the species, so it is possible V. myrtilloides occurs at locations in Glacier National Park, other than at the west entrance.

Management Implications

The management recommendations given are only for the improvement and maintenance of one facet of grizzly bear habitat in northwestern Montana, recognizing that the bears require many kinds of habitats for year-round subsistence.

The most productive plots (1399 l/ha; 146 gal/acre) sampled in this study were in areas burned by wildfire 25-60 years ago. Mesic, 8 to 15-year-old, broadcast-burned clearcuts were also productive (783 l/ha; 82 gal/acre), but apparently not used frequently by either grizzly or black bears until significant tree or shrub cover developed. The implications of this study were that management of grizzly bear habitat for fruit production of globe huckleberry plants should be on a long-term rotation basis, and that benefits from manipulations would not be attained for at least several years after treatment.

Huckleberry picking provides many hours of recreation for people in the Flathead National Forest where this study was centered but confrontations between bears and people are not likely. If necessary, fields for recreational use could be developed in places unattractive to grizzlies.

Implications for specific treatments are listed by habitat type in the following paragraphs. Scarification is considered a detrimental post-logging treatment on all sites because of the almost total destruction of plants. When the information is available, the 50-year site indices and elevational ranges from Pfister et al. (1977), potential berry crop size, the expected lag time between treatment and fruit production, and the anticipated productive life span of berry production for the treated sites from this study, and potential grizzly use from Kiser et al. (1979) are given. Unless otherwise noted, the physical and vegetative characteristics of the habitat types are from Pfister et al. (1977).

A. Subalpine fir/beargrass-globe huckleberry

1. Site indices: lodgepole pine-45; Douglas fir-40

2. Elevation range: 1510-1910 m (5000-6000 ft)

3. Aspect: relatively dry exposures

4. Treatments:

a. Wildfire

(1) Potential berry production: very high

(2) Lag period after treatment: 15-25 years

(3) Productive life span: 30+ years; depends on tree canopy regeneration

(4) Potential grizzly use: high

(5) Tree regeneration potential: low; depends on size of burned area and intensity of fire

(6) Suggestions and clarifications:

Wildfires in the mesic aspect (north- and east-facing slopes) range of this habitat type offer maximum potential for fruit production. The lag period is long, but so is the productive life span, especially where tree regeneration is inhibited by high elevations or lack of a seed source. In such cases, production should continue as long as the tree canopy does not develop. If productivity declines, 75 or more years after the original fire, even when tree canopy does not develop, a spring broadcast burn should reduce interspecific competition and improve fructification. This treatment would be best applied to maintain productivity in certain areas that were inadvertently burned by wildfires, where the maintenance of grizzly habitat is deemed important.

b. Clearcut, broadcast burn

(1) Potential berry production: low for first 15-25 years

(2) Lag period after treatment: more than 15 years

(3) Productive life span: ?

(4) Potential grizzly use: low (so far as is known)

(5) Potential tree regeneration: moderate

(6) Suggestions and clarifications:

No samples of broadcast-burned clearcuts in this habitat type were older than 15 years, so the productive life span cannot be predicted. Berry production and percent cover was very low in all samples 8 to 15 years old, but tree regeneration was also limited. Berry production could increase if the percent cover of huckleberry plants increases before trees are reestablished, but the recovery rate for both trees and huckleberries will be slow.

This treatment is not recommended for the improvement of grizzly habitat in the subalpine fir/beargrass-globe huckleberry type because recovery of berry production and natural tree regeneration are both unlikely. It could be a useful treatment to eliminate shrub competition, if the trees are artificially reestablished.

B. Subalpine fir/queencup beadlily-menziesia

1. Site indices: Douglas fir-66
spruce-66
lodgepole pine-60
western larch-63

2. Elevation range: 1360-1730 m (4500-5700 ft)

3. Aspects: all but driest south slopes

a. Wildfire-no samples

The percent cover of globe huckleberry was higher in burns less than 35 years old than in old-growth stands of this type (Zager 1978). I have no samples from these areas, but production probably increased 15-25 years after the burn. The life span will be shorter than that of burned areas in the subalpine fir/beargrass-globe huckleberry type because the potential for tree canopy recovery is higher.

b. Clearcut, broadcast burn

(1) Potential for berry production:	high
(2) Lag period after treatment:	8-10 years
(3) Productive life span:	20-30 years (?)
(4) Potential grizzly use:	moderate to high
(5) Potential tree regeneration:	moderate to high

(6) Suggestions and clarifications:

Broadcast-burns in clearcuts of the subalpine fir/queencup beadlily-menziesia type increase berry production significantly if huckleberry plants are present in the undisturbed stand. The increase occurs much sooner than after wildfires in other habitat types, presumably because the fire is less intense, but the productive life span is shorter, again because of the high potential for tree canopy recovery.

Three of 5 grizzly activity sites found in clearcuts by personnel of the Border Grizzly Project were in this habitat type, but along the overgrown skid roads with few globe huckleberry shrubs, and not in the cut where the berries would have been.

Menziesia-globe huckleberry shrub fields that would inhibit conifer regeneration could develop in burned cuts in this phase of the habitat type. If the original tree canopy was dense and the understory light, the problem would be slight, but increases in huckleberry production would probably be less because there would not be a rhizome network in the soil to produce new shoots.

Menziesia is more of a competitor to tree regeneration in shrub fields than the globe huckleberry (Shearer, pers. comm.), so if it could be controlled without harming the huckleberry plants, the cuts could be managed to produce fruit during the early years of a rotation and trees in the later years. Globe huckleberry is a rhizomatous shrub. If menziesia has a different root structure, some treatments might favor huckleberries and reduce menziesia cover.

C. Subalpine fir/queencup beadlily-beargrass

1. Site indices: (same as menziesia phase-site indices are averages for all phases)

2. Elevation range: 1270-1690 m (4200-5700 ft)

3. Aspects: dry, cold; south or west slopes

4. Treatment:

a. Wildfire-no samples

Because most of the sites within the subalpine fir/queencup beadlily-beargrass habitat type are on dry, cool, south- or west-facing slopes, wildfires on those sites are likely to reduce the percent cover of globe huckleberry and lengthen the recovery period, more so than they would in the menziesia phase of the habitat type. However, this habitat phase is more mesic than the subalpine fir/beargrass-globe huckleberry type, which is very productive after wildfires on eastern aspects. Some mesic sites within the subalpine fir/queencup beadlily-menziesia habitat type could produce abundant berry crops if burned by wildfire, but cover and fruit production of globe huckleberry plants on sites with dry aspects will probably decrease. More samples are needed to reinforce these speculations.

b. Clearcut, broadcast burn

(1) Potential berry production: low to moderate

(2) Lag period after treatment: 10-15 years

(3) Productive life span: ?

(4) Potential grizzly use: low (so far as is known)

(5) Tree regeneration potential: fair, with site preparation

(6) Suggestions and clarifications:

Berry productivity in broadcast-burned clearcuts in the subalpine fir/queencup beadlily-beargrass habitat type was low (0 to 200 l/ha; 1 to 20 gal/acre), even on east aspects. The most plausible explanation for the lack of globe huckleberry recovery in the beargrass phase of the habitat type was the dry moisture conditions. After 9 years, percent cover of globe huckleberry did not recover to even half the pre-treatment levels in broadcast-burned clearcuts in the subalpine fir/queencup beadlily-beargrass habitat type (Stickney, pers. comm.). On similarly treated plots in the more mesic menziesia phase of the habitat type, coverage of globe huckleberry was almost equal to pre-treatment coverages after 9 years (Stickney, pers. comm.).

Only 6.5 percent of total grizzly use in August was in the subalpine fir/queencup beadlily-beargrass habitat type. No use of the phase was recorded in June, July, or September through November (Kiser et al. 1977). Because globe huckleberries in this phase do not respond positively to logging, it offers little potential for improvement of grizzly habitat through manipulation. However, if the radio locations and activity sites are representative of grizzly use of habitat types, the subalpine fir/queencup beadlily-beargrass type is not used frequently by bears, so reducing globe huckleberry plant cover might not significantly affect the grizzlies.

D. Subalpine fir/menziesia

1. Site indices: western larch-67
spruce-60
subalpine fir-57
lodgepole pine-56
Douglas-fir-60

2. Elevation ranges: 1610-2000 m (5300-6500 ft)

3. Aspects: cool exposures

4. Treatments:

a. Wildfire-no samples

Average cover of globe huckleberry on paired plots decreased in wildfire burns 25 and 47 years old in the subalpine fir/menziesia habitat type, but cover was only 12 percent in old-aged stands and 3 percent in burned stands (Zager 1978). Apparently, wildfires decrease the percent cover, and thus, the already limited, potential berry productivity in the subalpine fir/menziesia habitat type.

This habitat type was the least important of 10 habitat types ranked by presence and cover of bear foods, but it was used the same amount by grizzlies as the highest-ranked type (Kiser et al. 1978). The authors did not specify what the site histories of the used stands were, but thought they were resting and loafing areas. Jonkel (pers. comm.) said certain basins and upper ends of avalanche chutes in this habitat type produced large amounts of huckleberry fruit. They also offered seclusion and a late-autumn food source. Berry samples from areas with this habitat type that were burned by wildfires are needed, since it appears to be an important part of grizzly habitat.

b. Clearcut, broadcast burn

(1) Potential berry production: high

(2) Lag period after treatment: 5-10 years

(3) Productive life span: ? (no samples older than 15 years)

(4) Potential grizzly use: ?

(5) Potential tree regeneration: variable

(6) Suggestions and clarifications:

Sites in the subalpine fir/menziesia habitat type react much the same as those in the subalpine fir/queencup beadlily-menziesia type to broadcast burning of clearcuts, though creating shrub fields with prescribed burns could be more of a problem in the subalpine fir/menziesia type, because the average percent cover of menziesia in old-aged stands is higher (45 percent vs. 29 percent in this study); the percent cover of globe huckleberry is lower (13 percent) than in the subalpine fir/queencup beadlily menziesia type (22 percent). Broadcast burning is about the only feasible method of site preparation on the steep slopes in much of this type (Pfister et al. 1977). Because of the moist conditions and cool temperatures, burning can only be done at certain times (Pfister et al. 1977), and burns will probably not be hot enough to destroy the globe huckleberry rhizomes. Therefore, shrubfields that inhibit tree regeneration might develop.

Even if fruit production increases in the shrub fields, grizzly use will probably decline in the absence of cover, unless the bears use the cuts at night. But there is a potential for improving bear habitat in the old-aged, subalpine fir/menziesia habitat type if cover from a tree layer develops after disturbance. The bears could use old-aged stands for loafing and resting, and adjacent, old clearcuts for feeding on fruit. The period over which the cuts would be useful to bears is probably related to cut size, and would be limited to the relatively short span (±50 years) between development of tree cover and the time decreased light interferes with flower formation on the huckleberry plants (when the tree canopy density is about 30 percent). Manipulations for habitat improvement in this type, as in others, would have to be planned 15 to 25 years in advance. This is an extensive habitat type and food is widely available at many elevations during the time fruit production occurs in this type, so perhaps specific treatments for bears are not widely necessary here.

E. Scarification

Scarification after clearcuts significantly reduced the percent cover and production of globe huckleberry plants in the 3 habitat types sampled. Because scarification extensively damages rhizomes, it would probably reduce the percent cover and production in most situations. It would be an effective way to control shrub competition from globe huckleberries and menziesia with tree regeneration on sites where it is applicable. Forbs and graminoids are often the dominant species in clearcuts after scarification. However, scarification would not improve habitat for grizzlies, since the bears seldom use the cuts in the early summer when they are feeding on the graminoids and forbs (Zager 1978).

F. Partial cuts

In general, berry production in partially thinned stands is erratic and not related to the parameters considered in this study. But intuitively, it seems that thinning on dry aspects or in xeric habitat types would cause less damage to existing globe huckleberry plants than clearcuts in the same situations. At the same time, thinning would reduce the tree canopy, increase the light, and more flowers would form, so more fruit would develop. Huckleberries in one, old "high-graded" stand, responded better to that treatment than those in an adjacent, broadcast-burned clearcut in the subalpine fir/queencup beadlily-beargrass habitat type, but there was no tree regeneration in the old stand. However, a longer period of time had elapsed between treatments, so a direct comparison may not be valid (Arno, pers. comm.).

Huckleberry shrubs in shelterwood cuts on the Coram Experimental Forest in Montana were very productive (Shearer, pers. comm.), but I did not obtain information about the physical characteristics of those sites. My tentative recommendations would be to use thinning or shelterwood cuts on xeric aspects or in xeric habitat types in uneven-aged stands with globe huckleberry shrubs, but more data is needed about what influences fructification in thinned units before reliable productivity predictions can be made. If fructification improves after treatment, cover for grizzlies would be available in thinned stands sooner than in clearcuts, so the bears could probably take advantage of the berry crop earlier in the rotation.

With partial-cut systems, it might be feasible on some sites to maintain both berry crops and timber production throughout the rotation. On a Rocky Mountain flood plain, partial cutting increased many bear foods including huckleberry fruit production (Mealey et al. 1977). Partial cuts on such sites for bear food production may be justified, with or without the globe huckleberry considerations (Jonkel, pers. comm.).

CHAPTER VI

CONCLUSIONS

1. A lack of moisture limits height, percent cover, and fructification of globe huckleberry shrubs.
2. Overstory shading, old-aged huckleberry shrubs, and competition from other plant species limited berry production in stands not disturbed in the last 100 years, or stands burned by wildfires 60-100 years ago.
3. Berry production increased in 15-25 years if mesic northern or eastern aspects with globe huckleberry shrubs were burned by wildfire. It increased in 5-10 years if mesic sites were clearcut and broadcast-burned. Wildfires or prescribed, broadcast burns reduced competition from other species such as menziesia, and increased fructification by increasing the number of productive huckleberry stems per acre.
4. Fruit production and coverage of globe huckleberry plants declined if xeric aspects were disturbed by wildfire or logging followed by any site preparation treatment.
5. Fructification in selectively-thinned stands was unpredictable. It was not related to the percent of tree canopy that remained or the aspect of the site, but high productivities were associated with plots that had dense coverages of tall huckleberry shrubs after treatment.
6. Berry production increased with elevation presumably because competition from other species decreased. It was evidently

limited by shallow soils and low moisture levels on ridges.

7. The critical tree canopy density beyond which flower formation and fruit development was inhibited was 30 percent.
8. Fructification was not correlated with the percent cover of huckleberry shrubs because globe huckleberries are a late seral or climax species that can persist under dense tree canopies, but their fruit production is meso-seral and inhibited by an absence of sunlight.
9. Height of globe huckleberry shrubs was not correlated with berry production because the shrubs continued to grow as the stand aged, but fructification declined with stand age.
10. Berry sugar content was not related to the date of sample collection because all were picked at approximately the same stage of fruit maturation. Berries from high elevations were sweeter than those from lower sites.
11. Weather significantly influences annual berry crops. Late or early frosts or snowstorms check fructification in drainages, on microsites, or at certain elevations, but seldom cause crop failures widespread enough to prevent bears from obtaining berries.
12. Other studies suggest that grizzly bear use of mesic, broadcast-burned clearcuts with substantial berry crops will probably increase as the tree and shrub covers increase, though there is evidence that they use the cuts at night, even when cover is limited.

13. Grizzly bears do use middle-aged burns with high-elevation, open areas in the subalpine fir/beargrass-globe huckleberry habitat type if berry production is good (Kiser at al. 197).

14. No useful, morphological characteristics that could be used to differentiate _V. globulare_ from _V. membranaceum_ were found during this study. Cytotaxonomic studies will be required before identification problems within the complex will be solved.

15. If _V. ovalifolium_ occurs in western Montana, it is rare.

16. _V. myrtilloides_ could occur in western Montana in areas other than the single known location in Glacier National Park that were not searched during the course of this study.

CHAPTER VII

SUMMARY

Berry production of globe huckleberry shrubs in northwestern Montana was determined by interactions between a site's physical and vegetative characteristics, and the stand history. Site disturbance by clearcutting and broadcast burning 8-15 years ago, or by natural fires 25-60 years ago on mesic north- or east-facing slopes induced changes which resulted in increased fructification, an increase in percent cover of globe huckleberry shrubs, more berries per plant, and larger average berry volume. Production decreased if sites with southern or western aspects were clearcut and/or burned, or if clearcuts on any aspect were scarified.

The effects of elevation and topography on berry production were visible only within areas where the site history was uniform. Then production and percent cover of huckleberry shrubs increased with upward changes in topography and increases in elevation from 2050 to 2120 m (6750-7000 ft). Above that elevation, or on ridges, fructification and cover were limited. Huckleberry shrub height decreased in plots from lower slopes to ridges on the same site. The coverage and berry production presumably responded positively to the decreases in competition that accompanied increases in elevation. Height responded negatively to the elevation-related increase in stress.

Shrub height increased as the thickness of the tree canopy increased, but coverage, berry production, the number of berries per

plant, and the average berry size were limited if the tree canopy exceeded 30 percent cover. Huckleberry shrub cover in stands over 100 years old was limited by competition, production by available light. Thus, when the tree layer was removed by a natural fire or a clearcut, and competition from other shrubs reduced by fire that did not destroy the huckleberry rhizomes, fructification increased if moisture was adequate.

Dense undergrowth cover of most species limited productivity and cover of huckleberry shrubs. Dominance of one species or another did not depress or increase production or cover, but huckleberry shrubs were short if beargrass was dominant and tall if menziesia was. Apparently, huckleberry shrubs responded positively to increases in moisture and perhaps shade, and huckleberry cover and production, again, to competition.

Fructification was not related to the percent cover or height of the huckleberry shrubs. In stands where globe huckleberry was present in the seral stages, it is not entirely eliminated when the stand matures. If the mature stand is disturbed, the plants persist, but it is several years before berries are produced. Therefore, the globe huckleberry is a late-seral or climax species capable of continued existence on a disturbed site. But, the fruit is produced only during the intermediate stages of succession.

The more berries there were per plant and the larger the volume of the average berry, the more productive a site was. The average berry volume was less on xeric aspects than on mesic sites, but the number of berries per plant was not influenced by aspect.

The flowers formed in the spring when moisture was adequate on most aspects. The berries increased in size in mid-to late-summer when moisture could have been limited on southern or western aspects. Berry volume was also correlated with huckleberry plant height which responded positively to increases in moisture.

Berries for sugar analyses were collected when the berry plots were sampled. Because I tried to sample all plots at approximately the same stage of fruit maturation, there was no correlation between the collection date and berry sugar content. The small, numerous berries produced on high-elevation plots were sweeter than large berries from lower elevations. Questions about the effects of clonal variation on sugar content were not answered in this study.

Fructification in thinned stands was erratic. Productive, thinned stands had high coverages of tall huckleberry shrubs and unproductive plots either had high coverages or tall shrubs, but not a combination of both characteristics. Otherwise, variation in productivity between selective cut sites with similar characteristics was unexplainable.

Year-to-year variation in production emphasized the impact weather has in annual berry crops. Three productive plots from 1977 produced very little fruit in 1978 because of late frosts or snow-storms. However, the effects were localized by drainage or elevation and berries were produced in nearby areas.

Diurnal black and grizzly bear use of berry-producing clearcuts in subalpine fir/queencup beadlily-menziesia habitat types is apparently limited. Evidence of nocturnal use of clearcuts by grizzlies exists, but use by either species is probably limited until some shrub or tree cover develops (Lindzey and Meslow 1977). Conversely, in mid- to late-summer, grizzlies frequently use open, subalpine fir/beargrass-globe huckleberry types that were burned 25-50 years. Any type of logging and post-logging treatment in this habitat type reduced globe huckleberry shrub cover and fructification, so most use of the type by bears is probably in middle-aged (25-60-year-old) wildfires. Inadequate sample size precludes a discussion of concrete results of different treatments in other habitat types identified as important for grizzlies by personnel of the Border Grizzly Project.

Hitchcock and Cronquist (1973) pictured the corolla of *V. membranaceum* as longer than broad, and those of *V. globulare* as broader than long. All the corollas of the flowers collected from *V. globulare-membranaceum* type plants in western Montana, northern Idaho, eastern Washington, and northern Oregon were broader than long, or as broad as long. But no flowers were collected from the type locality of *V. globulare* in the Madison Range, Montana, or of *V. membranaceum* in the Washington Cascade Mountains. Conclusions about the strength of the corolla character cannot be made until fresh flowers from western Washington are collected.

The leaves of most collected specimens were elliptic and half as broad as long, regardless of the geographic location of the collection, but the tips of the leaves from the mid-point to the apex varied from site to site. Plants from Mount Hood, Oregon, and northeastern Washington had gradually tapered leaf apices like those described for V. membranaceum. Plants from the Blue Mountains of Oregon had abruptly acute, V. globulare-shaped leaves (Hitchcock and Cronquist 1973).

Leaf shape also varied within sites or within plants. Leaves from plants collected in clearcuts were thicker and more abruptly acute than leaves from plants in adjacent, undisturbed stands. Within plants, leaves on resprout stems were larger and differed in shape from leaves on current annual growth stems. Terminal leaves, or third and fourth leaves with flowers in their axils, were smaller and had more irregular shapes than second or third leaves with no flowers in the axils on the same stem.

Two uncommon leaf shapes were discovered. A round-leaf form of V. globulare was found in isolated areas in western Montana and northern Idaho. Both cases were associated with V. globulare plants, but had separate rhizome systems. A V. membranaceum plant with exceptionally serrated leaf margins was found in one location in eastern Washington.

V. globulare-membranaceum-type plants in northern Idaho were more variable than those of Oregon. Some areas had leaves with gradually tapered apices, others were abruptly acute or intermediate in shape. Shapes of western Montana leaves were also diversified, though none had the consistent, gradually tapered apices of V. membranaceum.

Two other species of *Vaccinium* were reviewed in this study. *V. ovalifolium* is found in northern Idaho and in British Columbia about 50 km (30 miles) north of the Canada-Montana border. Even after intensive searches, I did not find it in northwestern Montana. Other than a population of *V. myrtilloides* previously known to exist near the west entrance of Glacier National Park, no other locations of that species were found in western Montana.

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APPENDIX I

Summary of the physical and vegetative characteristics for each sampled berry plot grouped by site history *

Plot #	Aspect	Elev. (m)	Slope (%)	Herb-aceous cover	Shrub cover	Tree cover	Globe huckle-berry cover (%)	Pro-duction (l/ha)	Height of globe huckle-berry plants (cm)	Habitat type	Major undergrowth species
Mature stands with tree canopies >40 percent											
44	W	1390	25	49	53	60	15	27	46	Abla/Clun-Mefe	Mefe
62	S	1580	30	20	36	60	27	4	49	Abla/Clun-Mefe	Mefe
66	E	1545	50	17	69	40	8	0	50	Abla/Clun-Clun	Tabr
80	SE	1510	49	33	13	45	37	0	55	Abla/Clun-Xete	Rupa
x̄		1506	38	30	43	51	22	8	50		
Mature stands with tree canopies <40 percent											
49	N	1720	40	29	68	35	15	0	61	Abla/Clun-Mefe	Mefe
56	NW	1650	52	23	58	20	25	13	68	Abla/Mefe	Mefe
60	NW	1710	43	54	66	35	19	13	58	Abla/Mefe	Mefe
79	S	1545	40	25	28	35	34	4	60	Abla/Clun-Mefe	Mefe
x̄		1656	44	33	55	31	23	8	62		
Stands thinned <20 years ago											
29	W	909	73	12	34	10	15	36	41	Abla/Clun-Xete	Xete
32	S	1333	53	50	14	26	36	440	55	?	?
47	Bench	1727	0	28	5	15	44	587	54	Abla/Xete-Vagl	Xete
50	NE	1909	25	17	12	38	39	133	40	?	Caru
x̄		1590	38	27	16	18	34	299	48		
Stands thinned >20 years ago											
36	NE	1360	45	36	33	5	41	444	68	Abla/Clun-Mefe	Sorbus
33	SE	1480	52	22	10	5	28	338	33	Tshe/Clun-Clun	Xete
24	E	1480	48	24	14	9	28	204	31	Abla/Xete-Vagl	Xete
28	NE	1690	55	36	25	10	28	138	46	Abla/Xete-Vagl	Xete
31	W	1390	15	33	19	25	27	129	42	Abla/Clun-Xete	Xete
30A	NE	909	3	14	25	22	45	116	59	Thpl/Clun-Clun	Libo
x̄		1386	37	28	21	13	33	228	46		
Stands clearcut, broadcast-burned; 8-15 years of age											
55	NW	1640	52	13	54	0	34	791	75	Abla/Mefe	Mefe
39	NE	1390	38	37	10	0	31	520	46	Abla/Xete-Vagl	Xete
46	N	1710	40	10	60	0	42	502	94	Abla/Clun-Mefe	Mefe
23	N	1500	25	11	31	0	20	378	45	Abla/Xete-Vagl	Pamy
35	NE	1360	45	42	20	0	30	200	56	Abla/Clun-Xete	Xete
38	Bench	1390	0	37	13	0	18	62	42	Abla/Xete-Vagl	Xete
37	NE	1370	40	32	36	0	13	67	30	Abla/Clun-Xete	Alsi
61	S	1530	55	36	26	0	10	0	19	Abla/Clun-Xete	Xete
59	E	1710	42	32	42	0	16	0	41	Abla/Xete-Vagl	Mefe
78	SW	1550	40	36	42	0	6	0	42	Abla/Clun-Xete	Epan
82	SE	1910	48	22	28	0	16	0	32	Abla/Xete-Vagl	Xete
x̄		1551	39	28	33	0	21	229	47		
Stands clearcut, scarified											
41	N	1330	30	33	23	0	4	0	31	Abla/Clun-Xete	Grass
53	E	1390	20	27	32	0	15	0	28	Abla/Libo-Xete	Pico
81	SE	1580	52	25	60	0	7	0	36	Abla/Clun-Clun	Rupa
x̄		1433	34	28	29	1	9	0	33		

Plot #	Aspect	Elev. (m)	Slope (%)	Herb-aceous cover	Shrub cover	Tree cover	Globe huckle-berry cover (%)	Pro-duction (l/ha)	Height of globe huckle-berry plants (cm)	Habitat type	Major undergrowth species
Stands burned between 25-60 years ago											
70	E	2000	62	33	6	0	41	1399	30	Abla/Xete-Vagl	Xete
64	E	1880	40	22	6	10	38	1111	28	Abla/Xete-Vagl	Xete
69	E	1730	52	47	23	0	24	644	42	Abla/Xete-Vagl	Xete
87	N	1880	62	36	23	1	38	622	53	Abla/Luhi-Mefe	Mefe
73	E	1770	61	37	28	4	47	467	29	Abla/Xete-Vagl	Xete
75	E	1430	58	35	28	0	33	387	40	Abla/Xete-Vagl	Xete
74	E	1770	61	37	28	5	24	218	47	Abla/Clun-Xete	Pamy
63	E	1820	55	38	13	15	24	236	27	Abla/Xete-Vagl	Xete
84	SW	1800	56	18	34	0	28	200	38	Abla/Xete-Vagl	Pamy
85	S	1940	52	28	1	15	34	209	28	Abla/Xete-Vagl	Pamy
86	N	1610	62	47	29	20	42	124	65	Abla/Clun-Mefe	Mefe
68	E	1670	65	32	28	0	14	98	35	Abla/Xete-Vagl	Pamy
72	S	1940	54	21	10	2	41	80	26	Abla/Xete-Vagl	Xete
71	SW	1910	45	27	34	5	27	36	57	Abla/Xete-Vagl	Mefe
65	E	2120	71	22	13	4	30	18	15	Abla/Xete-Vasc	Xete
$\bar{x}$		1818	57	32	20	5	30	390	39		
Stands burned between 60-100 years ago											
30B	SE	1240	15	20	29	20	40	84	42	Abla/Libo-Xete	Libo
77	SW	1670	39	43	39	20	21	124	36	Abla/Xete-Vagl	Xete
40	N	1330	30	30	34	35	20	0	31	Abla/Clun-Xete	Xete
54	N	1788	40	18	2	30	40	58	50	Psme/Vagl-Xete	Xete
22	SW	1580	35	53	58	25	55	44	43	Psme/Vagl-Xete	Pamy
45	S	1730	45	42	15	15	41	36	31	Abla/Xete-Vagl	Xete
48	Bench	1390	0	48	12	35	35	0	38	Abla/Xete-Vagl	Xete
51	SW	1970	5	53	13	40	40	31	40	Psme/Vagl-Xete	Xete
76	SW	1940	12	70	9	8	7	0	36	Abla/Luhi-Vasc	Xete
83	S	1880	55	47	13	55	23	0	44	Abla/Xete-Vagl	Xete
25	S	1650	42	28	15	30	36	0	40	Abla/Xete-Vagl	Xete
26	NE	1420	70	26	19	35	15	0	30	Abla/Xete-Vagl	Xete
27	NE	1510	55	25	34	40	25	0	51	Abla/Xete-Vagl	Pamy
$\bar{x}$		5357	34	39	22	30	31	27	40		

*Four-letter abbreviations for the habitat types are formed from the first 2 letters of the plant's genus and the first 2 letters of the species (Pfister et al. 1977). The following species were included in the appendix.

Abla	Abies lasiocarpa
Alsi	Alnus sinuata
Caru	Calamagrostis rubescens
Clun	Clintonia uniflora
Epan	Epilobium angustifolium
Libo	Linnea borealis
Luhi	Luzula hitchcockii
Mefe	Menziesia ferruginea
Pamy	Pachistima myrsinites
Pico	Pinus contorta
Psme	Pseudotsuga menziesii
Rupa	Rubus parviflorus
Tabr	Taxus brevifolia
Thpl	Thuja plicata
Tshe	Tsuga heterophylla
Vagl	Vaccinium globulare
Vasc	Vaccinium scoparium
Xete	Xerophyllum tenax