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RHIZOME MORPHOLOGY, SOIL DISTRIBUTION,
AND THE POTENTIAL FIRE SURVIVAL OF EIGHT
WOODY UNDERSTORY SPECIES IN
WESTERN MONTANA.

By

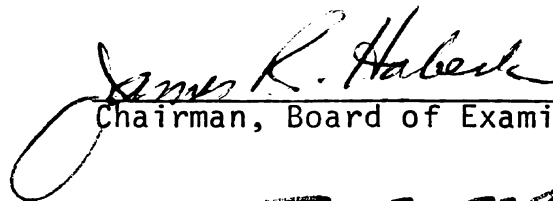
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B.A., The Colorado College, 1977

Presented in partial fulfillment of the degree of

Master of Arts

1984


Chairman, Board of Examiners


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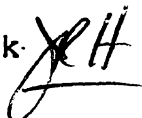
ABSTRACT

Bradley, Anne F., M.A., March, 1984

Botany

Rhizome Morphology, Soil Distribution, and the Potential Fire Survival of Eight Woody Understory Plants in Western Montana

Director: James R. Habeck



Eight woody understory species of western Montana Douglas-fir forests (Pseudotsuga menziesii/Symphoricarpos albus and Pseudotsuga menziesii/Physocarpus malvaceus habitat types) were excavated and examined to assess their post-fire resprouting potential. Rhizome dimensions, soil depth, and percent residence in mineral soil were measured. Of the measures taken, rhizome depth was chosen as the best predictor of potential fire survival. Results were expressed as percent cumulative frequencies to permit an estimate of the percentage of the population's rhizomes lying above or below a given depth.

Species were ranked by their potential for fire survival based on both soil placement and unique morphology. From lowest to highest: 1) Linnaea borealis, 2) Arctostaphylos uva-ursi, 3) Xerophyllum tenax 4) Berberis repens, and Symphoricarpos albus, 5) Amelanchier alnifolia, 6) Spiraea betulifolia and Physocarpus malvaceus. Ranks four and six both include two species. From the data gathered in this study it was not possible to separate the species within these two classes. Individual species morphology, soil texture and length of the fire-free interval may all affect rhizome depth and thus, potential fire survival. The last variable becomes a factor when organic soil horizons build up as a result of infrequent fire. Plants established in these horizons may be eliminated when fire is returned to the site.

ACKNOWLEDGEMENTS

Many people made this study possible through their generous advice and encouragement. Major thanks go to Dr. James Habeck for guiding me through this project. I am also grateful to my other committee members for their helpful suggestions. They are Dr. David Bilderback, Dr. Robert Pfister and Dr. Earl Willard.

For their technical assistance at various phases of my research, thanks to Marti Crane, Bill Fischer, Richard Mackie, Dr. Charles Miller, John Munding, Nonan Noste, Peter Stickney, and Philip Tourangeau.

Lastly, I owe a debt of gratitude to my friends and fellow students, whose companionship and humor made my work so much easier.

This project was made possible by a cooperative agreement (No.INT-80-108-CA) between the University of Montana, USDA-INT Northern Forest Fire Laboratory and the Montana Department of Fish, Wildlife and Parks.

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Chapter 1

Introduction

Fire is a naturally occurring event in the northern Rocky Mountains. It is also frequently used as a land management tool. Scientists and managers are currently seeking ways to predict its impact on forest ecosystems.

An ecosystem's response to fire is dependent on the combined and interacting responses of the individual species within it. Thus, one approach to the problem of prediction is to examine the characteristics of these species.

The fire survival of many perennial plants is influenced by their morphology. Regeneration of these plants from roots or rhizomes is common, but not well described. The present study constituted an attempt to relate morphology and soil placement of perennating organs to potential fire response. Eight common woody species of western Montana were chosen as subjects for this investigation.

The approach taken in the present study was influenced by previous work in the area of plant adaptation. What we understand of plant response to fire results from research in a variety of fields. Many of the studies cited below were not originally designed as investigations of fire

effects. However, taken together, they form a context for the current study of potential fire survival.

Chapter 2

Literature Review

In the last two decades, fire has been recognized as a natural force in the shaping of ecosystems. Komarek (1964) stated: "...there are not many lands, if any, on earth, that at some time or other have not been subjected to recurring ...fires. These have occurred at frequent enough intervals to have lasting effects on plant and animal communities."

In particular, the northern Rocky Mountains has been a fire-prone environment (Habeck and Mutch, 1973; Wellner, 1970). Lyon and Stickney (1976) go so far as to say that in northern forests "... fire should be treated as an internal perturbation of an otherwise stable system"(p 356).

Fire, then, has been and continues to be a recurring and significant event in northern ecosystems. Plants inhabiting regions which burn repeatedly must be adapted to this periodic disturbance.

Adaptation to fire, or any other environmental condition, may be viewed in either an evolutionary or ecological context (Rowe, 1979). However, when analyzing adaptation, it is sometimes difficult to ascribe specific characteristics to the effects of a single selective force.

In other words, "... the influence of fire cannot be sharply set off from that of other perturbations." (Rowe,1979). Because of this, the evolutionary effects of fire may be impossible to determine. Instead, we must content ourselves with observing its ecological consequences.

Classification of Fire Adaptations

The first step in any analysis of adaptations is to find a means to describe them. A classification scheme that would permit the comparison of different species , and allow accurate description within a species, is needed. A variety of approaches to this classification problem have been proposed.

Grime (1979) developed a system of adaptive "strategies" which he defined as

"...groupings of similar or analogous genetic characteristics which recur widely among species or populations and cause them to exhibit similarities in ecology."

He recognized three primary establishment strategies:that of the competitor, the stress-tolerator, and the ruderal,or invasive type. But few species actually display the features of only one strategy. Most plants have a combination of characters which allow their continued existence in a fluctuating environment, so Grime has also

defined secondary establishment strategies which are combinations of the primary strategies.

Van der Valk (1981), in a discussion of wetland succession, noted that not only are the different stages in life cycle important, but also where observations are made. He cites the example of duckweed, Lemna spp., which grows in both temperate and tropical environments. In temperate regions, Lemna is an annual and survives the unfavorable season as seed. In the tropics, the plant acts as a perennial, growing vegetatively the year round.

Another method of analysis which combines both establishment and reproductive strategies has been developed by other researchers.

Noble and Slatyer (1977), and later Rowe (1979), compared certain "critical events" in the life cycle of plants. These events included: 1) replacement of propagules, 2) age of maturity or establishment, 3) age of senescence (the loss of the individual from the community), 4) extinction or the loss of potential propagules from the site.

Knowing the timing and the mechanisms by which these critical events are carried out is requisite to our understanding of these processes. The mechanisms are called "vital attributes" by Noble and Slatyer and are: 1) The

method of arrival or persistence of propagules on a site after a disturbance. 2) The conditions in which the species establishes and grows. 3) The longevity of individuals, and the the time taken to reach critical stages in their life history. 4) The growth rate of a species.

Rowe (1979), has adopted these characters and has described a series of "regeneration niches" based on the vital attributes. He has named the niches in reference to their fire response. These include:

1) Invaders: Highly dispersive, pioneering fugitives with short-lived disseminules.

2) Evaders: Species with relatively long-lived propagules that are stored in the soil or in the canopy.

3) Avoiders: Tolerant species that slowly reinvade burned areas, are late successional, and often have symbiotic requirements.

4) Resisters: Intolerant species whose adult stages can survive low severity fires.

5) Endurers: Resprouting species, which are tolerant or intolerant, with shallow or deep-buried perennating buds.

Life-history models for plant response to fire have been developed for Australian communities (Noble and Slatyer, 1977) and Glacier Park, Montana (Cattelino, et al., 1979).

Although it is possible to compare different "regeneration niches" using the life-history approach, it is difficult to compare species which are in the same niche.

A third approach, that of "life-form" analysis, makes this type of comparison possible. The study of life-forms has a long history in ecology which has been reviewed by Hedberg (1962). Recently one of these classification schemes has received renewed interest in its applicability to fire adaptations.

Raunkiaer (1934) produced a life-form system to describe how plants could maintain themselves through unfavorable conditions. The major life-forms according to Raunkiaer:

1. Phanerophytes-"Plants whose apical-shoots destined to survive the cold period of the year project into the air."

2. Chamaephytes-"Plants whose ...apical-shoots... either lie on the surface of the ground or are situated quite near to it."

3.Hemicryptophytes-"The shoot-apices ...are situated in the soil surface, protected by the surrounding soil."

4.Cryptophytes-"...shoot-apices... are situated under the surface of the ground..."

Raunkiaer developed his scheme to describe mechanisms of perennial plant survival through climatic extremes such as drought or cold winter temperatures. Adams et al. (1983) used the life-form concept to describe plants that survived the volcanic eruption of Washington's Mount St. Helens.

Chapman and Crowe (1981) applied Raunkiaer's life-form system to plant survival after low intensity fire in eastern white pine (Pinus strobus L.) and mixed hardwood/white pine stands in New Hampshire. They reported little change in the array of life-forms after burning, and found that plants in the chamaephyte and hemicryptophyte categories suffered greater damage than did the cryptophytes, indicating that mechanisms for surviving unfavorable climatic conditions also may serve as a means of fire survival.

However, some species do not fit into a single category when both their climate and fire adaptations are considered.

For a fire surviving tree such as aspen (Populus tremuloides Michx. and P. grandidentata Michx.), the location of the overwintering buds put it in the phanerophyte category, while its fire-surviving root buds allow it to function as a cryptophyte.

In Australia, arborescent Eucalyptus species resprout via epicormic buds which are not associated with the ordinarily active nodal buds (Mount, 1969; Gill, 1981). In order to use a fire life-form classification system, some modifications should be made to emphasize unique fire responses.

Gill (1981) has attempted a revision of the life-form system to make it more relevant to fire. This revision is in the form of a key. The portion of the key pertaining to vegetative reproduction appears below:

- (a) subterranean regenerative buds
 - (i) root suckers, horizontal rhizomes.....IV
 - (ii) basal stem sprouts, vertical rhizomes....V
- (b) aerial regenerative buds
 - (i) epicormic buds grow out.....VI
 - (ii) continued growth of active aerial buds...VII

For prediction of future plant frequencies, the dichotomy between horizontal and vertical rhizomes may be an important one.

Keeley (1981) proposed terminology distinguishing between the two vegetative modes. He called reproduction "...any lateral spread with the potential for producing 'new individuals'..." and regeneration "...the production of an individual in situ once it has been largely destroyed." (p.233)

In this way an ecological distinction is made between those species which resprout and replace their original numbers and those which may increase in frequency. This distinction was also recognized by Weaver and Clements (1938) and Purdie (1977) in their discussions of rhizomatous species. Although distinguishing species on this basis is important, assigning a specific meaning to "reproduction" and "regeneration" is not practical given their synonymy in the literature.

The nature of resprouting species was also studied by Naveh (1975). He described resprouters as either "obligate" or "facultative" in their response as did Keeley (1977) in his investigations of chaparral plants of California.

Other terms used to describe post-fire resprouting response were presented by Purdie and Slatyer (1976) and Purdie (1977) (after Vogl (1971)), when she subdivided species into the categories of "increaser " or "decreaser".

Morphology of Resprouting Species

Morphology of plant perennating parts affects their response to fire. To understand the ecology of fire-adapted species, some knowledge of these factors is useful.

Modified stems are common organs for vegetative reproduction. Rhizomes and stolons grow horizontally under or along the surface of the ground, respectively, and produce buds at the nodes or adventitiously (Benson, 1957).

The term "caudex" has been applied to underground stems whose orientation is vertical rather than horizontal (Benson, 1957), although some authors call subterranean stems of any orientation rhizomes (Mueller, 1941).

A common regenerative organ is the lignotuber or burl. Gill (1981) called a lignotuber a "...basal woody swelling with proliferating buds. "and said that its development takes place in the cotyledonary axils of seedlings. Its origin in stem tissue was also confirmed by Bamber and Mullette (1978). According to Kummerow and Mangan (1981) "burls (=lignotubers) are clumps of secondary wood...developed from the transitional zone between hypocotyl and main root of the seedling plant." They went on to say that after several years of development "...bases of major stems and roots become incorporated frequently into the burl producing a very complex structure which cannot be

defined as root or stem."

True root tissues are also involved in the resprouting response of some species (Schier and Campbell 1976, Gardener 1980). Raju, et al. (1966) hypothesized that the presence of many root budding perennial weeds in Saskatchewan farmland was related to the greater depth at which roots are able to initiate buds in comparison to rhizomes. This makes them better able to survive damage by cultivation. The relationship is not clear, however, since several of the species examined were able to resprout from both roots and rhizomes. Any tissue which has preformed buds or primordia produces shoots more rapidly than that which initiates buds after a stimulus is applied (Hayden 1919, Schier and Campbell 1976).

Rhizomes are a common means of regeneration in a variety of habitats, including the alpine (Holch, 1941) and the Nebraska Great Plains (Mueller, 1941). Miller (1976, 1977) and Minore (1975) reported the vigorous post-fire repropouting of Vaccinium globulare and V. membranaceum, respectively. Both these forest species regenerate by rhizomes.

Rundel (1981) noted that while a common feature in Australian resprouting plants, lignotubers are relatively rare in many other fire-adapted ecosystems. Their

occurrence may be evidence of other environmental pressures besides fire. Lignotubers are known to contain both water and inorganic nutrients (Bamber and Mullette 1978), which suits them for survival in arid regions.

Physiological Response

Perennating organs, whatever their origin, respond to environmental cues in their patterns of growth. Raunkiaer (1934) cited studies on stolon growth responses by the Swedish botanist Lidforss. Lidforss found that temperature had a marked effect on shoot growth. At relatively low temperatures, shoots grew horizontally, while at higher temperatures they turned to a vertical orientation. He observed this effect in a number of species including Holosteum umbellatum L., Lamium purpureum L., and Chrysanthemum leucanthemum L. In the first two species this alteration of growth appeared to be due to a change in stem apex sensitivity to gravity.

Raunkiaer also reported studies by the German scientist Haberlandt with Linum perenne L. Haberlandt found that Linum L. shoots grew erect in the higher temperatures of summer, and "irregularly in various directions" in the cooler autumn. Plants exposed to the cooler temperatures were brought into a greenhouse where, upon warming, they resumed vertical growth.

Kender (1967) found significantly longer rhizomes developed in Vaccinium angustifolium Art., the lowbush blueberry, when its clones were exposed to higher temperatures (85° vs. 65° F)

New suckers arise from adventitious buds on lateral roots of aspen (Populus tremuloides and P. grandidentata). Both cutting and burning may stimulate the growth of suckers from established clones (Horton and Hopkins, 1965). Schier and Campbell (1978) studied suckering in P. grandidentata after fire and found in deep seated parent roots significantly more suckers after an intense fire treatment. They believed this was due to the post fire increase in soil temperature. Maini and Horton (1963) also found temperature to be significant in suckering. They exhumed sections of aspen roots and transferred them to sand-filled pots. The pots were then subjected to different temperature regimes. Suckering was greatest on roots maintained at 74° F. Roots incubated at 64° F and 95° F showed considerably less response. In their field observations, Maini and Horton noted prolific suckering in both burned and scarified stands whether or not the canopy was removed. They concluded that temperature, rather than stem removal, was the stimulus for bud initiation.

Light may also play a role in the orientation of perennating organs. In his own experiments, Raunkiaer found that the rhizomes of Polygonatum multiflorum Kunth. could be "tricked" into altering their depth in the soil by changing their light environment. He planted a number of rhizomes in 5 cm of soil and then placed tin cylinders over some of these planted specimens. In essence, he "substitut[ed] for the layer of earth a dark layer of air". At the end of a year's growth, he discovered that rhizomes with the cylinders grew obliquely upward, while the control specimens remained horizontal in their orientation.

The internal factors which govern bud initiation and development are numerous and have a complex interrelationship (Esau, 1977). Leakey and Chancellor (1977,1978) conducted a series of experiments on the rhizomes of quackgrass, Agropyron repens (L.) Beauv. They found that in single-node rhizome fragments taken from the field, regenerative capacity was greater in the winter than in the summer. This response was due to the greater amount of nitrogen stored in the rhizomes during the winter months (1977a). They also applied exogenous nitrogen, as KNO_3 , and discovered a higher number of dormant buds were released with increasing amounts (1977b). Finally, the application of nitrogen delayed the onset of bud dominance. Dominance also was affected by temperature. The rate of establishment

of a dominant bud was maximized between 13 and 20 C (1978).

Komanik and Brown (1967) studied suckering in the sweetgum, Liquidambar styraciflua L. Suckering buds in this species preexist in a repressed state in the lateral roots and they are subsequently released by stimulation. Sweetgum buds may be released when parent stems are removed or when the lateral roots are exposed to light. When the roots were girdled only those buds on the distal end of the girdle were released. Girdling the root prevented the translocation of auxin from the stem to the buds, and auxin is believed to keep lateral buds in a repressed state (Salisbury and Ross, 1978). Miller (1976) also reviewed the effects of auxin on shoot growth in shrubs.

Once shoot growth has been initiated, a complex of other physiological factors governs its continuation. During shoot growth, a measurable change in the stem carbohydrate reserve takes place. Willard (1971) studied sprouting after clipping treatments in Symphoricarpos vaccinoides Rydb. and Chrysothamnus viscidiflorus (Hook.) Nutt. He found that clipping increased the total number of sprouts and that clipped plants had a lower amount of total available carbohydrates. In Chrysothamnus, spring clipping reduced the carbohydrate reserves furthest. The season of clipping appeared to have little effect on the degree of carbohydrate reserve reduction in Symphoricarpos.

Jones and Laude (1960) determined the sprouting potential of the desert shrub Adenostoma fasciculatum by measuring twig moisture and stored starch reserves. An increase in twig moisture and a sharp decrease in starch reserves preceded rapid shoot growth.

Garrison (1971) reported on the findings of several shrub carbohydrate studies. All plants analyzed showed a seasonal fluctuation in their reserves, with spring measurements lowest and fall measurements highest. Garrison also compiled data from studies on clipping effects on rangeland shrubs. From this information he concluded that late spring or early summer clipping was most damaging to shrubs. Fall and winter treatments stressed plants less.

Leege and Hickey (1971) burned Idaho shrub plots to improve browse. Different plots in the same habitat were burned in the spring and in the fall. The results of these treatments showed no statistically significant difference in shrub resprouting response. However, they did note that sprouts produced after fall burns appeared to be longer and fewer in number when compared to resprouts from the spring burned plots. In this study burning was done during two calendar seasons, but in both cases the plants were in a dormant condition. This similar physiological state, or an actual difference in plant response to clipping may explain the lack of concurrence with the studies mentioned above.

Flinn and Pringle (1983) examined the heat tolerances of several rhizomatous forest understory species. They reported that the most important factor in resprouting success was the status of the carbohydrate reserve. Not only the number of sprouts produced, but the actual survival of the rhizome itself depended on an adequate level of carbohydrate. They also determined that species which had shallower rhizomes did not necessarily demonstrate greater heat tolerance.

Rundel (1981), in a summary article, reported that the age of the perennating organ may also affect its ability to resprout. In nonlignotuberous species, resprouting was reduced in older individuals where wood had grown around potential meristematic tissue. In oaks, stump sprouting frequency was found to decrease as stem diameter increased.

Soil Heating and Plant Survival

Hare (1961) reviewed literature on the effects of heat on living tissue. He reiterated Belehradek's (1935) five theories of how heat may actually kill cells. Living cells may be killed by coagulation of protein, by heat destruction of enzymes, by asphyxiation, intoxication, or by lipoid liberation.

Whatever the actual mechanism, cell death does occur within a range of critical temperatures. Meyer, et al. (1973) reported that thermal death of living cells occurred between 50° and 60°C. Flinn (1980), in her studies of soil heating, accepted 55°C as an average measure of lethal temperature. Meyer, et al. also noted that the effects of heat vary with time exposure. A slower warm up period to a given temperature results in greater mortality than an immediate exposure. Thus, duration of heating also influences plant survival.

Fire-surviving plants in a natural setting may use either direct or indirect methods to protect themselves from lethal heating. A direct method is exemplified in the low thermal conductivity of the bark in some arborescent species in fire-prone habitats (Meyer, et al., 1973). An indirect adaptation is exhibited by shrubs which have perennating organs buried in the soil. In this strategy the plants depend on the insulating properties of the soil rather than on inherent anatomical protection. Because soil does provide effective insulation, above and below ground temperatures may differ greatly (Noste, 1982, pers. comm.).

In the study of fire effects, the soil is divided into two major fractions: the organic horizons, and the mineral horizons. The organic layers are further subdivided into litter (O1) and the decomposed fraction (O2). The organic

layers are subject to burning during fire, so it is the mineral portion of the soil which provides the insulation for subterranean plant parts.

Two separate terms have been applied to describe heating above and below ground during fire. Fire intensity describes the heat pulse upward (Noste, 1982, pers. comm.) or the "energy release" (Rowe, 1979). Fire severity refers to the heat pulse downward (Noste, 1982, pers. comm.) and can be measured by "...the degree of organic removal and soil heating." (Rowe, 1979). For plants with subterranean perennating parts, severity is the true measure of fire impact on the individual and the original population.

Measurements of the heat pulse into the soil have been made in a variety of conditions. Heywood (1938) measured heat penetration during ground fires in the long leaf pine region of the southeastern United States. He discovered that a measurable temperature change in the soil could only be recorded on those thermograph bulbs placed less than 1/4 inch in the soil.

Shearer (1975) measured percent root mortality due to heat pulse on Montana larch clearcuts. He found that soil water determined the proportion of roots killed. When soil moisture was high (near field capacity), root mortality ranged from 0 to 30 percent and was restricted to the top

1/2 inch of soil regardless of fire intensity (amount of duff removal). When soil moisture dropped to 15 percent, mortality ranged from 30 to 100 percent and occurred in the top 4 inches of soil in high intensity burns.

Flinn (1980) conducted controlled experiments with samples of wet and dry sand and two natural soil profiles. She used an electric heating element which reached a measured heat flux of 0.27 cal/cm² after a 15 minute period. Sample profiles were placed in a wooden box with thermocouples at 0,1,2,4,6,8,10, and 12 centimeters. In the standard dry sand medium, she found that temperatures of 55° C as deep as 12 cm after 220 minutes. In the wet sand, 55° C was reached after 80 minutes at a depth of 12 centimeters. The two natural soil profiles, from black spruce and hardwood forests, did not conduct heat as effectively as sand and did not reach lethal temperatures below 9 cm and 12 cm, respectively.

Noste (1981) reported the results of thermocouple measurements taken during fall burning at O'Keefe Creek, western Montana. Thermocouples were placed at 1 cm intervals from the soil surface downward to a depth of 6 centimeters. The instruments were placed at the bases of selected Ceanothus velutinus and Physocarpus malvaceus plants. Temperatures up to 200 C were recorded at 4 cm. and remained at this high level for over an hour.

Chapter 3

Study Objectives

Researchers in western Montana are attempting to model understory response to fire based on life-form and the position of perennating organs in relation to mineral soil. To complete this effort, actual depth measurements of the species in question are needed. Studies which consider perennating depth and its relation to potential fire survival are few (McLean 1969, Flinn 1977, Miller, 1976) and specific measurements for Montana plants are even more rare (Miller, 1976, 1977). Therefore, the present study was initiated.

The objectives of this investigation were:

- 1) To explore potential study methods for resprouting species.
- 2) To verify the morphological characteristics of the species examined
- 3) To measure quantitatively the soil position of subterranean perennating organs in these species.

Chapter 4

Study Areas

The Swan Valley

The Swan Valley lies in northwestern Montana, east of Flathead Lake. It is oriented in a north-south direction and is bounded by two parallel mountain ranges. The Mission Mountains form the western boundary, and the Swan Range delimits the valley to the east.

Two river systems drain this intermountain area. The northern two-thirds of the Swan Valley are in the drainage of the north-flowing Swan River. The Swan River is itself a tributary of the Flathead River. The southern portion of the valley is drained by the Clearwater River, a tributary of the Blackfoot River.

Geology

The Swan and Mission mountains are comprised primarily of Precambrian rocks of the Belt Series. The Belt Series is made up of marine sediments which have undergone low-grade metamorphosis to form argillites, limestone and quartzite. These metamorphosed sediments were uplifted during the Rocky Mountain orogeny in the late Cretaceous and early Tertiary periods. The present form of the mountains surrounding the Swan Valley was produced during the late tertiary and early

Quaternary (Antos, 1977, after Benneyfield, et al., 1976).

Extensive glaciation occurred in the Swan Valley during the Pleistocene Epoch. A subsidiary valley glacier to the Flathead Glacier (Alden, 1953) filled the floor of the Swan Valley. Alpine glaciers, which developed in the mountains, were tributary to this valley glacier and also scoured the landscape (Johns, 1964). Glacial activity has left the valley floor with many meters of till (Dutton, 1982, pers. comm.).

Soils

Soils in the Swan Valley are variable, due to the mixture of potential parent material and extremes of slope and aspect. The Foothills Trail which abutts the study site, runs along the interface of two different soil groups. Above the Foothills Trail, parent materials are derived from the Piegan Group and consist of limestone and calcareous argillites. The slopes here are steep and the soils very rocky. In some places the soils are quite thin, with bedrock within 50-100 cm. of the surface. All but the southern aspects have a surface horizon 12 to 26 cm. deep of volcanic ash-influenced loess dating from the Mount Mazama eruption of 6600 years before present. The moisture and nutrient holding capacity of this andic layer are better than that of subsoil horizons and plant roots tend to

concentrate in this surface layer.

Below the Foothills Trail, parent materials are mostly glacial till with the andic horizon overlying them. These till soils have a compacted layer which occurs at depths ranging from 35 cm. to a little over 3 meters. This compaction was caused by the weight of the valley glaciers on the land surface during the Pleistocene (Barry Dutton, 1982, pers. comm.).

Vegetation

In the Swan Valley, eleven different forest habitat types (Pfister, et al., 1977) have been mapped by the Montana Dept. of Natural Resources and Conservation (1978): PSME/CARU, PSME/SYAL, PSME/VAGL, PSME/LIBO, PSME ARUV, PICEA/CLUN, ABGR/CLUN, THPL/CLUN, ABLA/CLUN, ABLA/MEFE, and ABLA/XETE. Logged areas account for approximately 30 percent of the valley, with clearcuts ranging in size from 2 to 65 hectares (Mundinger, 1980).

On moist sites up to 1500 meters, grand fir (Abies grandis) is the indicated climax species. Above 1500 meters, or in cold pockets at lower elevations, subalpine fir (Abies lasiocarpa) is the potential climax dominant. In the southern end of the Swan Valley, or on drier exposures, Douglas-fir (Pseudotsuga menziesii) habitat types dominate. Isolated very moist sites may have western red cedar (Thuja

plicata) as the indicated climax species (Antos and Shearer, 1980).

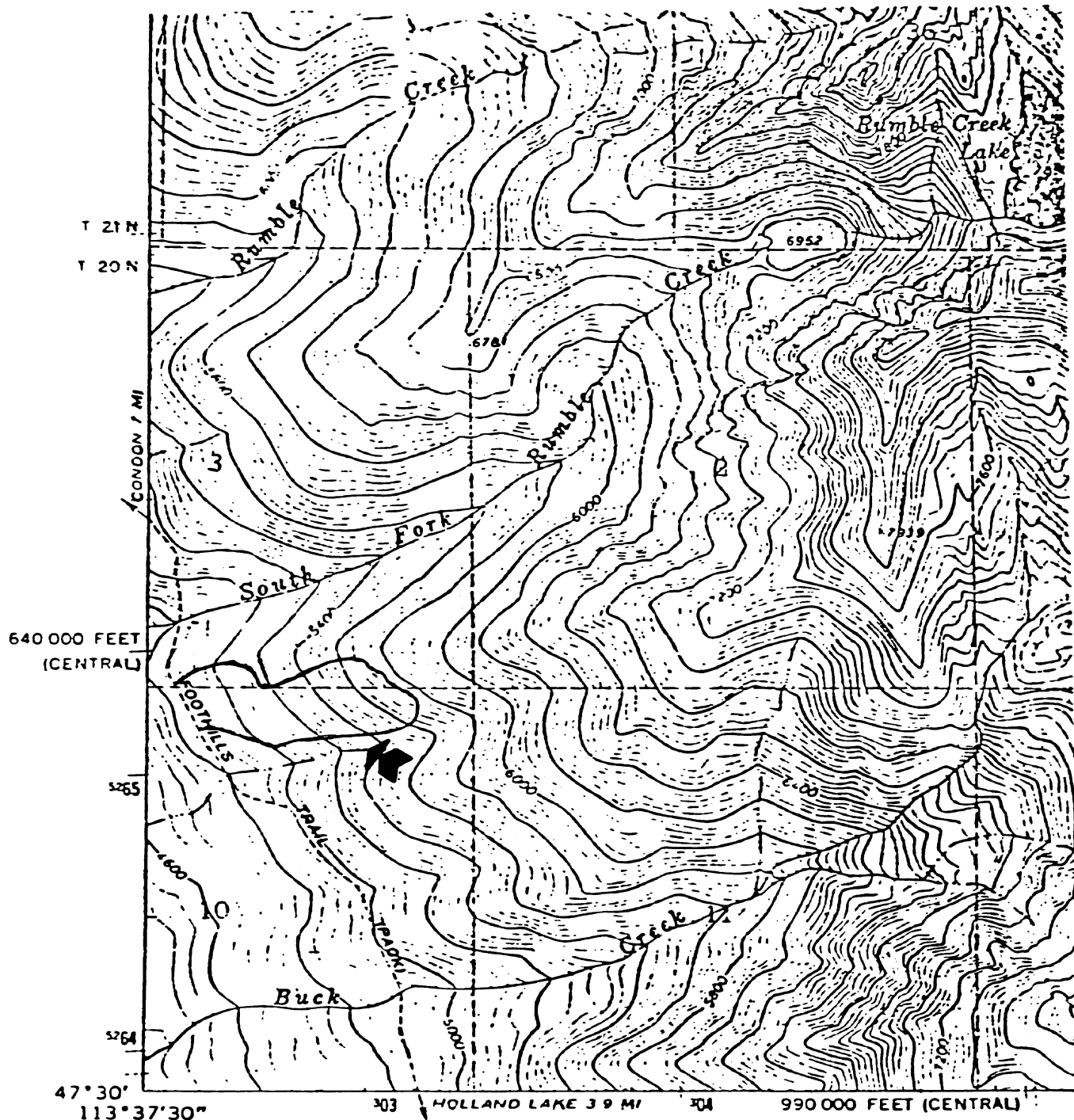
Climate

The climate of the Swan Valley is dominated by Pacific air masses that bring moisture from the west. There is a moisture gradient present in the valley, with the northern end considerably more moist than the southern end. Antos (1977) reported a yearly mean precipitation of 756 mm at Swan Lake (960M) and a yearly mean of 566 cm at Seeley Lake (1250 M). Year around readings are not available for Condon, which is the population center closest to the actual study site. The change in moisture from north to south is the result of a rainshadow cast by the higher peaks at the southern end of the Mission Mountains that effectively block much of the Pacific moisture.

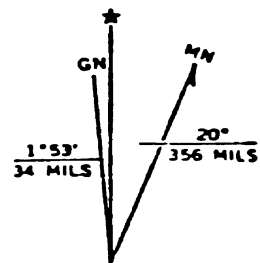
Study Area

The chosen study area resulted from a 1977 wildfire and is known as the Rumble Creek Burn. The burn lies on a west-facing flank of the Swan foothills between Buck Creek and the south fork of Rumble Creek. At its lowest point, it is adjacent to the Foothills Trail (figure 1).

Figure 1. The Rumble Creek Burn, located on the east side of the Swan Valley, near Condon, Montana.



Mapped, edited, and published by the Geological Survey



UTM GRID AND 1965 MAGNETIC NORTH DECLINATION AT CENTER OF SHEET

Wildfire burned approximately 16.2 hectares leaving a burn elliptical in shape lying between 1488 and 1768 meters in elevation with an average slope of 20.8 degrees.

The fire which burned at Rumble Creek was both intense and severe. All standing trees were killed and mineral soil was exposed throughout the area affected by fire. Some soil organic matter remains around the perimeter of the burn. the current vegetation is dominated by Epilobium angustifolium, with other herbs and shrubs present in much lesser quantities.

A control stand was chosen adjacent to the burn. This stand has an overstory of dense, small diameter Douglas-fir and a sparse understory of shrubs and herbs. The burned stand also evidences a prior overstory of dense Douglas-fir. The control stand, and presumably the burned stand, are in the Pseudotsuga menziesii/ Symphoricarpos albus habitat type, possibly Calamagrostis rubescens phase.

Pattee Canyon

Pattee Canyon is a drainage located in the northern end of the Sapphire Range of north-central Montana, just south of the city of Missoula.

Geology

The Sapphire Range, like the Swan Range and the Mission Mountains, is composed of Belt Series argillites and quartzites. After the Tertiary uplift, subsequent erosion produced a deep colluvium of clays and gravels of the Missoula Valley and the Sapphire Range foothills. The present study site is in these foothills.

Pattee Canyon was not glaciated during the Pleistocene. However, glacial activity did affect the area. A lobe of the Cordilleran ice masses dammed the Clark Fork River near the Montana-Idaho border. Water impounded behind this dam formed Glacial Lake Missoula which, at its peak, covered an estimated 3300 square miles (Johns, 1970). Lake Missoula extended into Pattee Canyon with its highest shoreline reaching approximately 1326 meters (Keller, 1980).

Soils

The study area lies above this highest shoreline. Soils in this vicinity have parent materials of colluvial gravels. The soils of this area are in the Tevis Series. Soils in this series are found between 920 and 1680 meters and on slopes between 8 and 60 percent (Dutton, 1982, pers. comm.).

Vegetation

In Pattee Canyon, Douglas-fir is ,on most sites, the indicated climax species. On the study site itself, the potential vegetation is the Physocarpus malvaceus phase of the Pseudotsuga menziesii/Physocarpus malvaceus habitat type (Pfister, et al. 1977, Schuler, 1968, Keller, 1980)

Climate

Weather patterns are similar to those of the Swan Valley with moist Pacific air masses bringing most precipitation. Occassional winter storms from east of the continental divide contribute some snow and very cold weather.

The mean annual precipitation in the city of Missoula is between 304 and 381 millimeters. The precipitation received in Pattee Canyon is somewhat higher. Dr. R. Erickson maintained an weather station in the lower reaches of Pattee Canyon from 1975 through 1979. Comparative data were presented by Keller (1980) and are reiterated here (figure 2).

Figure 2. Pattee Canyon precipitation data, collected by R. Erickson.
(from Keller, 1980)

Precipitation data from the weather station at the Missoula Airport (M.A.) and Dr. Erickson's weather station in Pattee Canyon (P.C.).

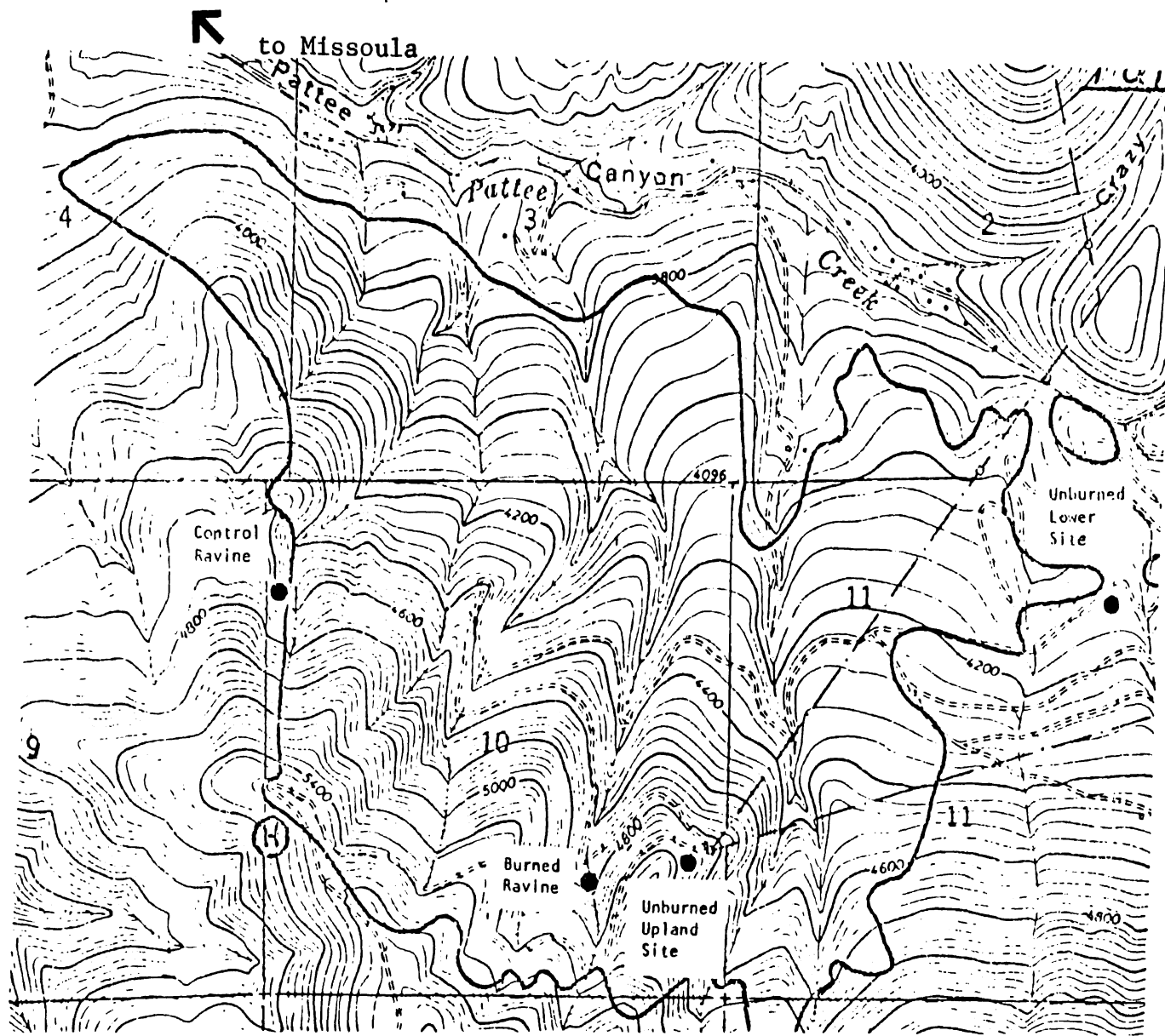
Precipitation in millimeters

Year	1975		1976		1977		1978		1979
Station	M.A.	M.A.	P.C.	M.A.	P.C.	M.A.	P.C.	M.A.	
January	51.6	22.9	26.2	16.8	20.3	29.2	37.1	31.8	
February	45.0	26.4	37.3	4.6	1.5	16.8	37.8	26.4	
March	18.8	10.2	16.5	24.9	38.1	17.0	29.5	31.0	
April	25.7	23.9	51.3	2.0	3.6	27.4		26.4	
May	34.3	20.1	34.5	54.1	86.9	50.3		18.8	
June	51.3	38.6	81.0	16.8	27.4	19.6		17.0	
July	38.4	30.5	38.1	18.3	23.9	14.5		19.6	
August	51.6	22.4	36.8	32.5	33.8	28.2		33.3	
September	13.0	14.7	21.6	42.4	48.8	45.2		1.3	
October	89.2	8.4	12.4	18.3	25.7	.3		24.6	
November	29.2	5.6	16.0	25.9	40.1	25.4		12.7	
December	21.6	6.4	8.4	73.2	105.7	25.1		20.6	
TOTAL	469.4	229.9	380.2	329.7	455.7	298.7		263.4	

Study Area

The Pattee Canyon study area is a 486 hectare burn which resulted from a 1977 wildfire (figure 3). It is located on a north-facing slope below Mount Dean Stone. The elevation of the burn ranges from approximately 1098 to 1707 meters. The slope of the study area ranges from essentially level ground to ravines with side slopes nearing 100%. Much of the area is dominated by Douglas-fir, with larch an important component on east-facing slopes. In the higher reaches, lodgepole pine is prevalent on slopes with a westerly exposure. The Pattee Canyon burn was both intense and severe, killing most trees and removing the soil organic mantle over much of the area. Patches of lesser affected forest also exist in the burn, mostly in ravines. For a more detailed description of the fire and its effects, see Keller (1980) and Crane[Keller] and others (1983).

Figure 3. Pattee Canyon Burn and Study Areas, east of Missoula, Montana.



Chapter 5

Methods

Comments on Site Selection and Methodology

In this exploratory study, it was necessary to choose study sites carefully. After consultation with my committee, the initial goal set for site selection was to find burned and unburned paired stands in a variety of forest habitat types in the Swan Valley of western Montana. Once field reconnaissance was begun, and with further consultation, a new set of criteria were devised.

It was thought that selection of burns less than five years old would provide the opportunity to observe the relative amounts of sexual and vegetative regeneration on a site. I also added a size limitation—that the burns be greater than class "A" (1/4 acre), because finding burns smaller than this on the landscape is very difficult. Finally, I decided to restrict study sites to those burns which had not been salvage logged and had not experienced any major post-burn disturbance. My goal was to compare the perennating organs of plants on burned and unburned sites. Any existing differences between these sites would be confounded by the added variable of soil disturbance.

Finding sites in the Swan Valley which fit the revised criteria was difficult. The valley has a patchwork of ownership patterns, with U.S. Forest Service, Swan State Forest, Burlington Northern Railway, and other private holdings, adjacent to each other. Timber, recreation and private development are land-use priorities, so wild or human-caused fires are seldom permitted to spread. The large network of roads and the generally gentle terrain facilitate fire suppression. Burns which result from wild or prescription fires are often salvage logged. The subsequent yarding and burning of slash is a serious disturbance to the site. One wildfire examined in the Swan Valley fit my criteria - the Rumble Creek Burn near Condon, Montana.

My search for other study sites expanded to the Lubrecht Experimental Forest, where I examined several forest utilization plots. These were rejected because of post-fire disturbance or inadequate fire treatment.

For my second study area I then selected the burn created by a 1977 wildfire in Pattee Canyon near Missoula, Montana.

The methods initially chosen also underwent some modification during the course of the study. Few studies of fire and its impact on perennating organs have been reported

in the literature to serve as models. My original sampling scheme followed that of Flinn and Wein (1977), where transects were established with shrub sampling stations at regular intervals. There was a rather low shrub frequency on my study sites, so a more rapid way to chose random samples was devised. It is decribed below.

Study Species and Sampling Methods

A suite of eight common shrubs was chosen for this study:

Arctostaphylos uva-ursi (L.) Spreng.

Amelanchier alnifolia Nutt.

Berberis repens Lindl.

Linnaea borealis L.

Physocarpus malvaceus (Greene) Kuntze

Spiraea betulifolia Pall.

Symphoricarpos albus (L.) Blake

Xerophyllum tenax (Pursh) Nutt.

The study sites consisted of two sets of burned and control stands. At Rumble Creek, one pair of stands was located on a toe slope of the Swan Range. At Pattee Canyon, a pair of ravine stands was chosen. In addition, two unburned sites were chosen around the fire-affected area to allow further collection of Arctostaphylos and Linnaea (figure 3).

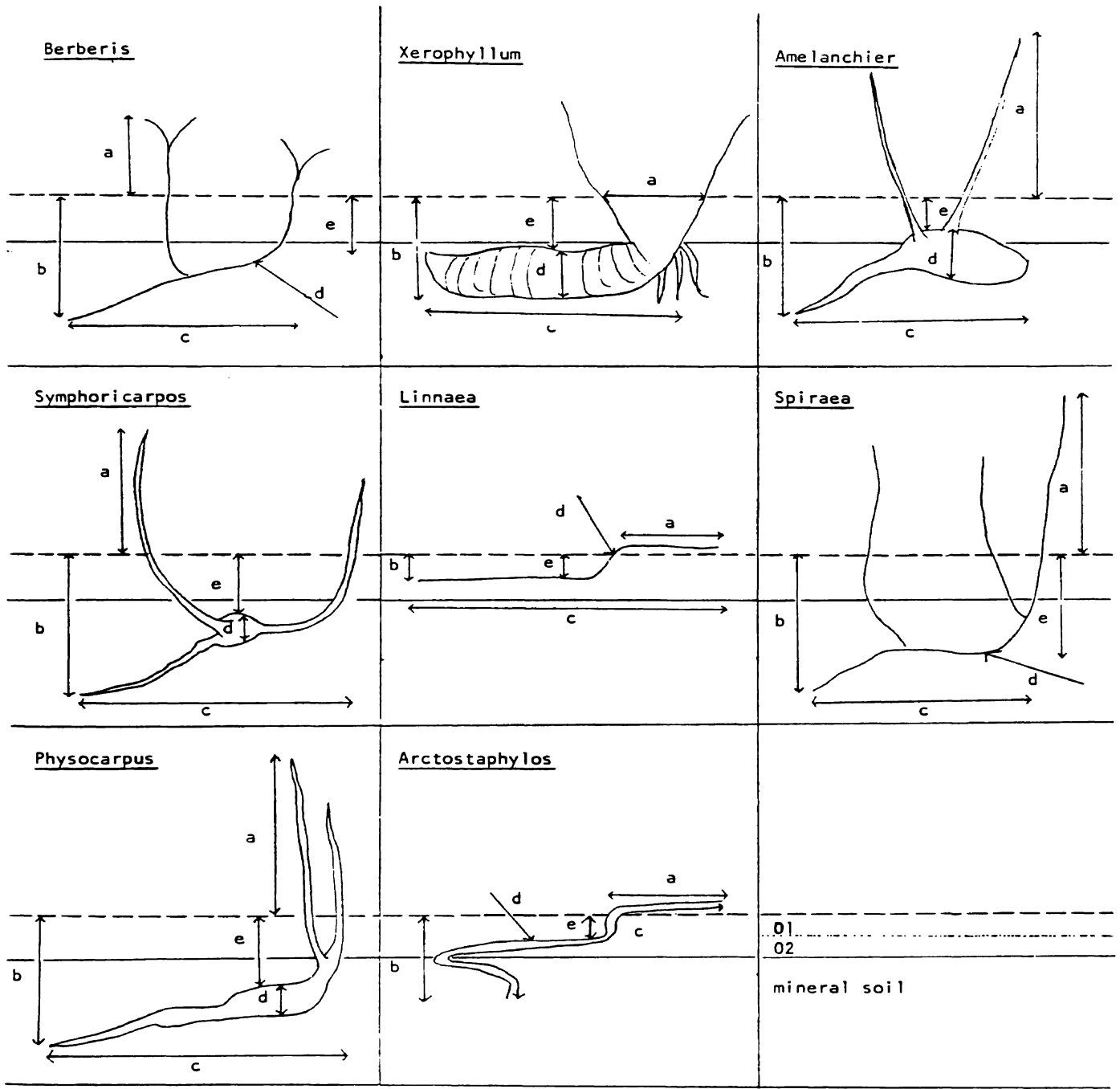
Once a stand was established, individual shrubs were selected in a stratified random fashion. A surveying pin was tossed into the site to serve as a starting point. I walked a random compass line from this point until I encountered a shrub. Subsequent samples were chosen in the same way, with the first plant sampled serving as the starting point.

The rhizome measurements made on excavated shrubs include: maximum depth, maximum horizontal extent, maximum diameter, and "main rhizome depth"-or the soil depth where the perennating organ turned from a vertical to a horizontal orientation. Above ground, the number of stems and the height of the tallest stem were recorded. How these measurements corresponded to the individual morphologies of the sample species is illustrated in figure 4.

The soil around the rhizome was considered as three fractions for measurement purposes- O1 (litter), O2 (humus and fermentation layers, together known as duff), and mineral soil. The depth of the O1 and O2 were measured in a circular plot with a radius of 30 cm from the stem base of smaller shrubs and a 1 meter radius from the major stem bases of the two larger shrubs sampled, Amelanchier and Physocarpus. The percent of the perennating organ residing in mineral soil was estimated for each plant. In addition, rough sketches were done of each specimen illustrating the

Figure 4. Study Species Measurements.

- a. tallest stem, or longest above ground stem
- b. maximum depth
- c. maximum length
- d. maximum diameter
- e. main rhizome depth



orientation of the rhizome to each of these soil fractions and to above ground parts. For a number of individuals, scaled drawings were made which convey the same information in a more detailed manner.

Site characters recorded include slope and aspect of the terrain surrounding each sample, and plant species associated with the shrubs. "Associated" plants were those which fell into the same circular plot defined for soil measurements.

Plant coverage values were obtained for burned and unburned sites through use of one meter square quadrats. A minimum of 10 and a maximum of 30 quadrats were randomly placed and read at each excavation site.

Chapter 6

Results and Analyses

Statistical Analysis

Results and analyses of this study are presented here in a species by species narrative. An attempt was made to compare burned and unburned sites to test the null hypothesis that no differences exist between the measured features of the selected plant populations on these paired sites. In order to test this hypothesis, Student's T-test was employed. In the T-test, log-transformed and untransformed data for all measured features were analyzed. Logarithmic transformations were performed on the data because graphed semi-log cumulative frequency distributions of the linear data from some maximum depth samples indicated possible skewing to the right. A log transformation will often make such data more symmetrical (Sokal and Rohlf, 1981). Plotting the logarithmic data provided some line-straightening, but a larger sample size is needed to determine whether maximum depth is truly log-normally distributed. distributions.

Results of the T-test using separate variance estimates showed no significant differences between most means at the 95% confidence level. Where exceptions existed, they are

noted in the text.

Cumulative frequency distribution was calculated only for the maximum depth measurements of species sampled. I believe that this measurement is the one that is most useful for prediction of a plant's potential fire survival, as did Flinn (1980) and Flinn and Wein (1977) .

Percent cumulative frequencies are reported tabularly and graphically, for both adjusted and unadjusted values. In order to compare the proportion of plant rhizome in mineral soil on burned and unburned sites, I subtracted the organic fraction from the maximum depth measurement.

The depths of the O1 and O2 layers were measured to the nearest millimeter in a circular plot already described. A mean value for each organic fraction on a site was calculated from the sum of the separate O1 and O2 measurements for all species sampled on that site. The mean values were then subtracted from the maximum depth measurements and the cumulative frequencies recalculated. These recalculations constitute the before mentioned adjusted values. The means and their 95% confidence intervals are reported in the appendix.




The amount of organic material across any forest landscape is highly variable. A measurement made at the stem does not necessarily correspond to the depth of this material over the deepest seated portion of the rhizome. It was not possible to predict the length or direction of growth of a rhizome before its excavation. When an excavation was completed, soil above the specimen was either completely removed or was highly disturbed, making accurate depth measurements difficult. Hence, the mean value was used as an estimate of the proportion of organic material on a site.

The organic fraction subtracted from the Rumble Creek burn measurements totaled less than one centimeter. In the percent cumulative frequency graphs which follow, the adjusted values from Rumble Creek have not been plotted to reduce confusion in interpreting the lines.

Ranges of sample values, means and standard deviations are reported for each species in tables in the appendix. Histograms of comparative range values for adjusted and unadjusted depth measurements are presented in figures 5 and 6.

Figure 5.

Maximum Depth Means and Ranges
for Rumble Creek Species

-  = Control
-  = Adjusted Control Value
-  = Burn

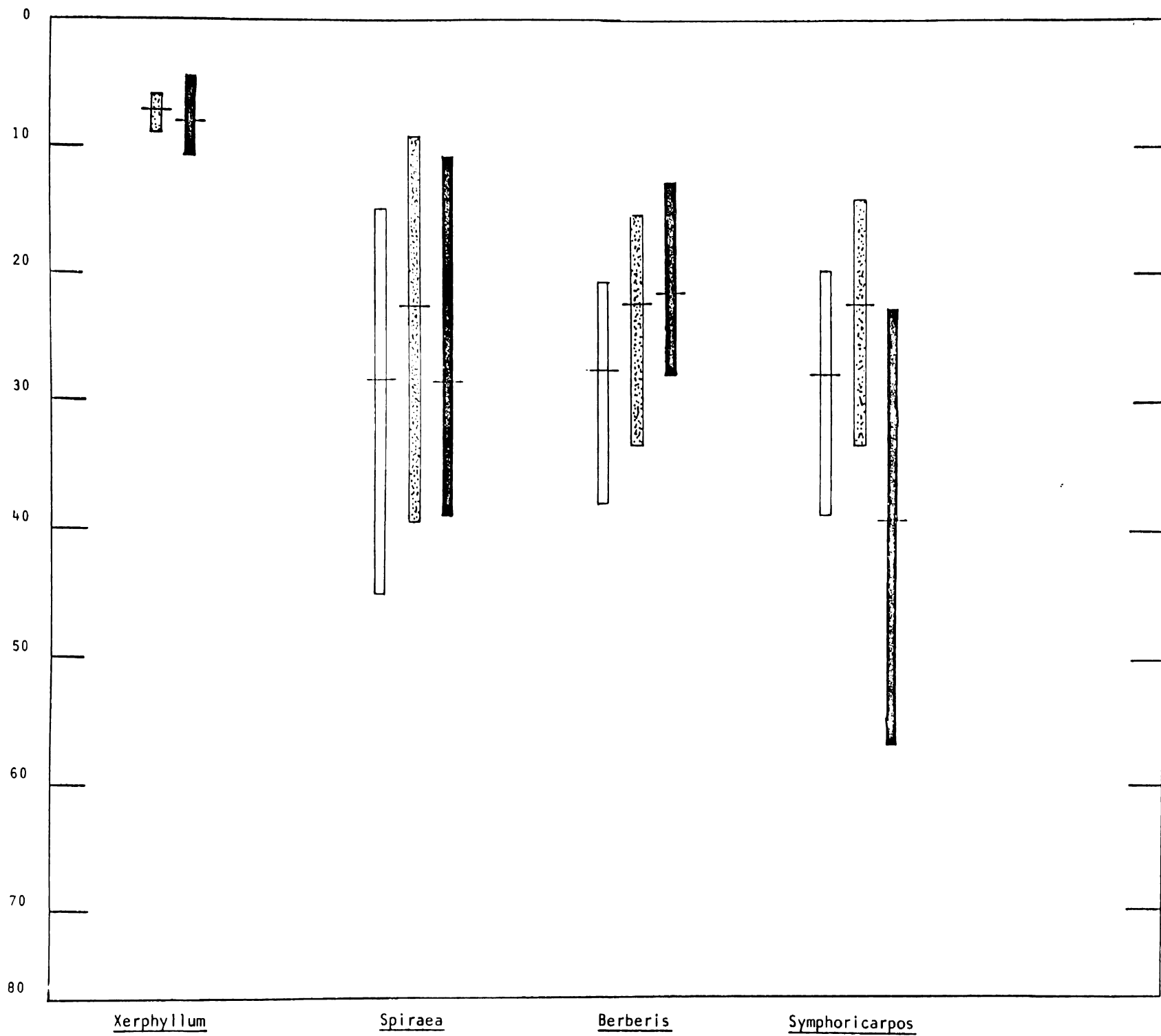



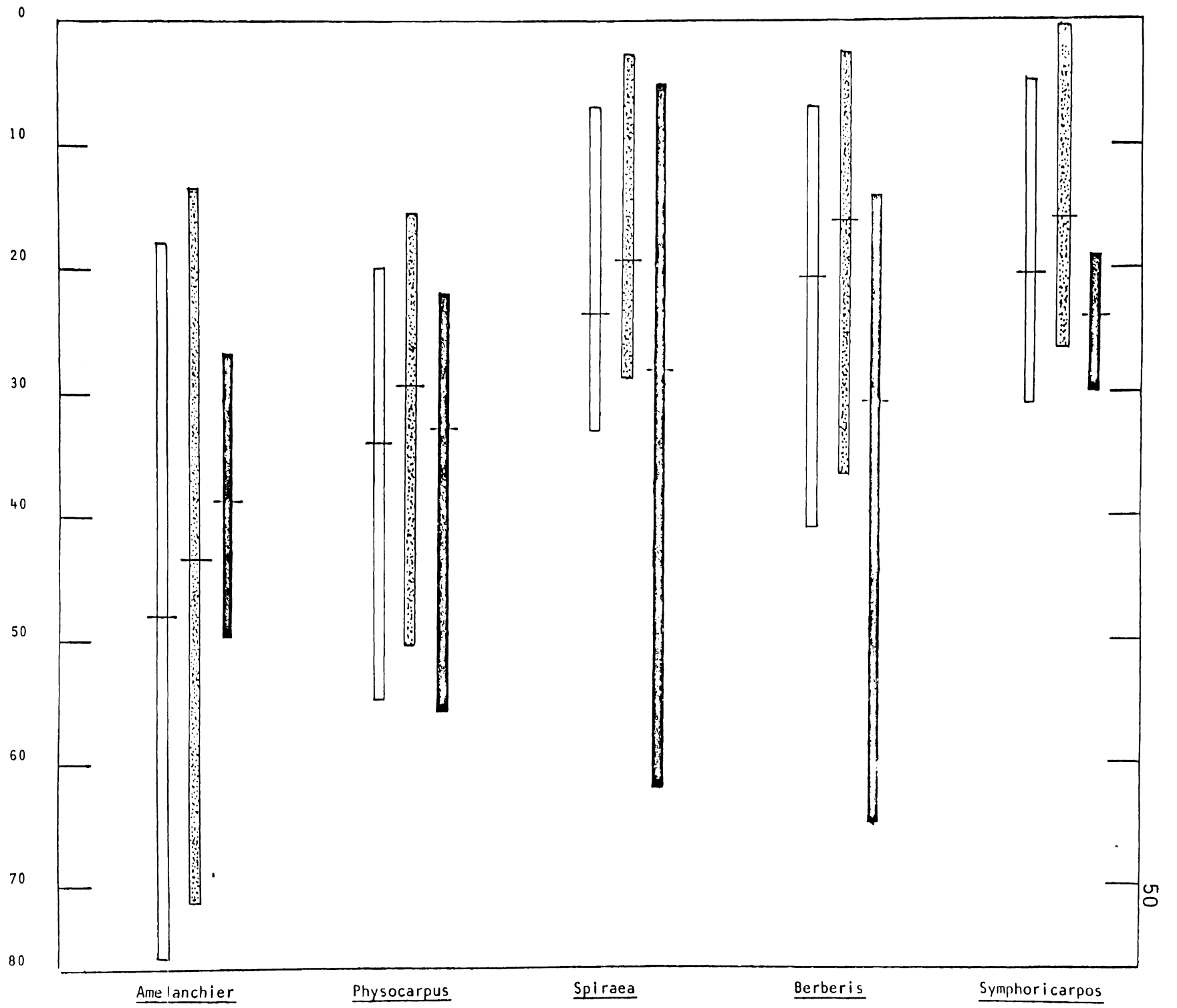


Figure 6.
Maximum Depth Means and Ranges
for Pattee Canyon Species

-  = Control
-  = Adjusted Control Value
-  = Burn



Species Descriptions

The eight species excavated may be subdivided on the basis of the position of their post-fire perennating organs:

I Species with Deep Rhizomes

A. horizontal or vertical orientation

1. Amelanchier

B. generally horizontal orientation

1. Physocarpus

2. Spiraea

3. Symphoricarpos

4. Berberis

II Species with Shallow Rhizomes or Stolons

A. shallow rhizome

1. Xerophyllum

B. surficial rhizomes or stolons

1. Arctostaphylos

2. Linnaea

Deep and shallow rhizomes reside mostly in mineral soil. The largest proportion of surficial rhizomes or stolons is restricted to the organic soil horizons.

All eight shrubs did not occur on both study areas. Berberis, Spiraea, Symphoricarpos, and Xerophyllum were sampled at Rumble Creek. At Pattee Canyon, the species sampled were Arctostaphylos, Amelanchier, Berberis, Linnaea,

Physocarpus, Spiraea, and Symphoricarpos.

Amelanchier alnifolia

Amelanchier alnifolia is a tall shrub whose subterranean organs may be in either a horizontal or vertical orientation. Hitchcock and Cronquist (1964) describe individuals of this species as follows:

"Low and spreading to erect shrubs or sometimes small trees, mostly 1-5 (0.5-10)m. tall [growing in] ..open woods, canyons, and hillsides, from near sea level to subalpine, s. Alas. southward to Calif., e. to Alta., the Dakotas, Neb., Colo., N.M., and Ariz."

Extensive sampling of this shrub was done by Lonner (1972) and Hemmer (1975) in Montana. Lonner reported on a project designed to age serviceberry populations in western Montana. He noted two major growth forms. A dwarf (low-growing) form was composed of plants less than 1.5 m. tall. These plants were made up of individual sprouts produced from rhizomes. The second form consisted of plants which were taller and whose stems grew in distinct clumps. He found a geographical separation between these forms, with 65% of the dwarf form occurring on sampling transects in the northwestern portion of Montana and 64% of the tall variety occurring in west-central Montana.

Plants sampled by Lonner ranged in age from 2 to 85 years in age. "Roots" of serviceberry were sampled in six of the specimens and their ages ranged from 10 to 36 years older than the above ground stems. Dwarf-form plants were shorter lived than those of the clumped form, and serviceberry in general had a shorter life span than other important browse species sampled (e.g. Rhus trilobata, Artemisia tridentata).

Hemmer (1975) recognized five general growth forms and three basic subterranean systems: "either ...deep vertical taproots, lateral roots ,or combinations of the two"(p.17). He also noted that "...root growth form appeared to be related primarily to substrate." (p.17). In his study, those plants with a strictly "taproot" system were restricted to talus slopes.

In the present study, Amelanchier was excavated from burned and unburned ravines of Pattee Canyon. These sites were very rocky, with much of the burned sampling area on or adjacent to a talus slope. Examples of some observed Amelanchier growth forms are presented in figure 7.

Three of the burn-surviving plants on this site had masses of more or less horizontally oriented woody tissue from which individual stems or clumps of stems arose (figure 8). Major roots descended from these masses, often at

Figure 7. Amelanchier growth forms - six representative specimens.

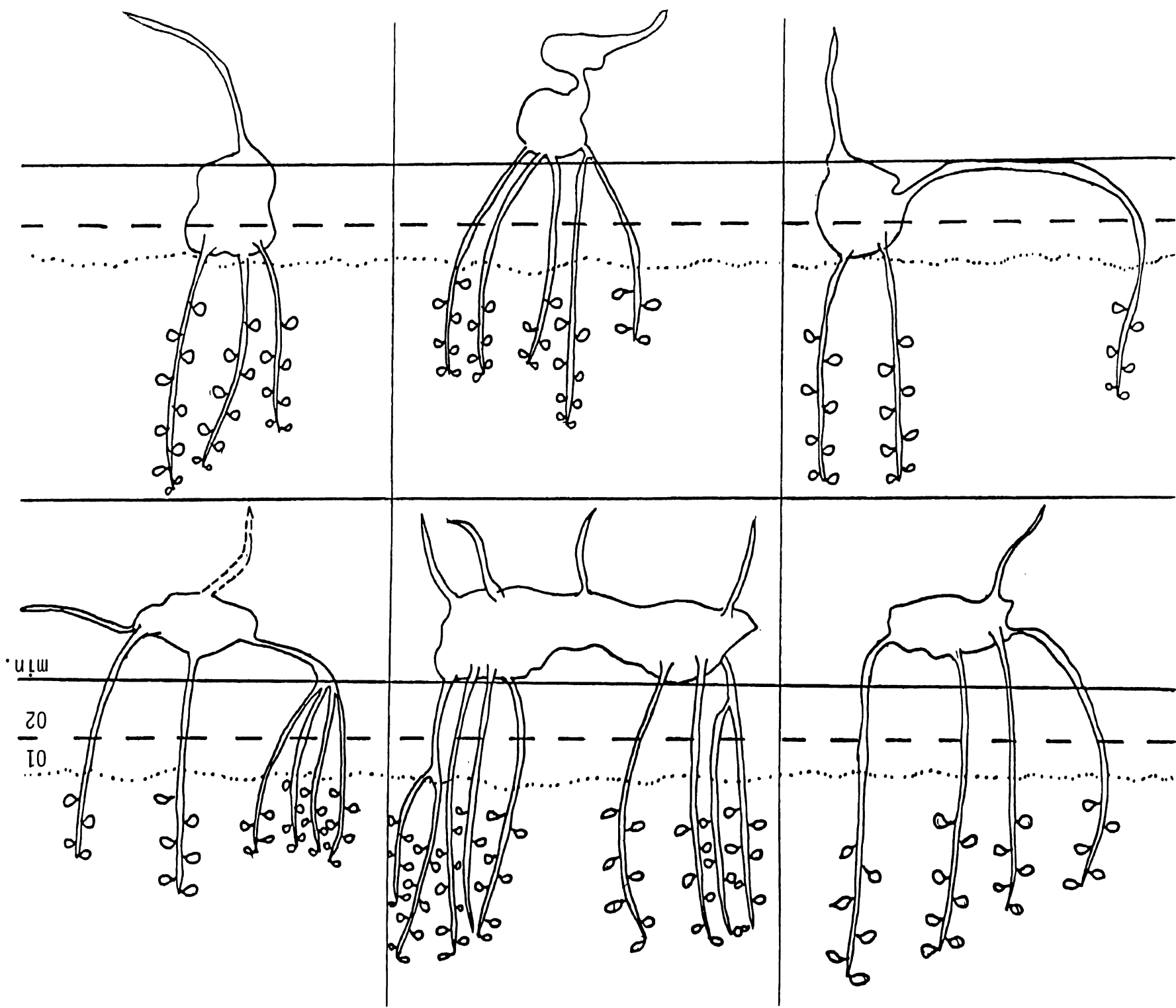
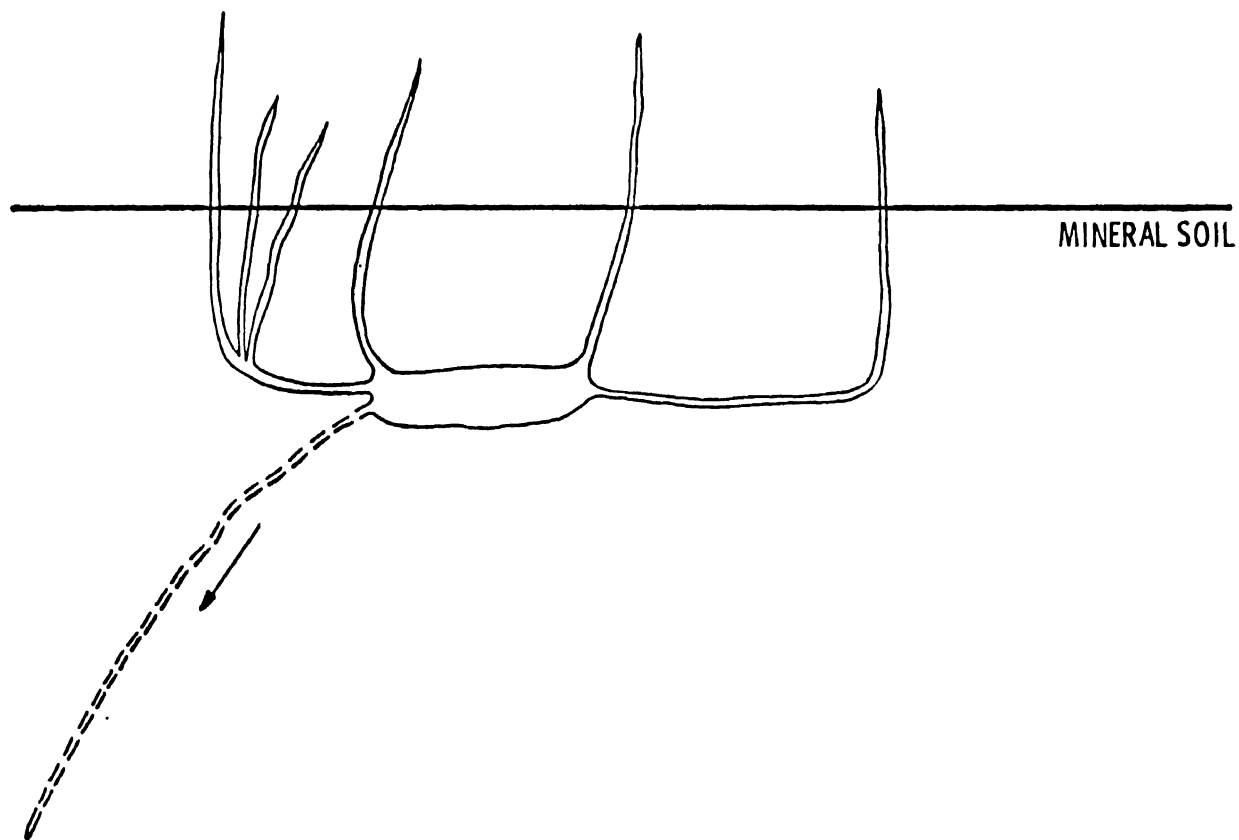


Figure 8. Amelanchier plant with a rootcrown form, excavated from the Pattee Canyon Burn. The root drawn with dotted lines projects outward from the plane of the page.



1 BLOCK - 12 cm



points along their perimeter.

One individual fit Hemmer's taproot description. It had two masses of tissue connected by a narrower section, so that one mass was situated directly above the other in the soil (plate 1). By sectioning this connecting tissue, I determined that at least to 20 cm. depth, the perennating organ of this Amelanchier is still stem tissue. The age of this section was nine years.

In a strict morphological sense, terms such as "rootstock" or "rootcrown" are somewhat misleading. However, they do conjure up an image of a more robust organ than does the term rhizome, so they are perhaps useful for general descriptive purposes.

Plants in both the burned and unburned sites had massive below ground structures, although individual plants were quite variable, ranging from a vertical rhizome type to an extremely elongate horizontal form (figure 9). In the unburned stand, the proportion of rhizome which resided in the mineral soil ranged from less than 5% to 100% with a mean of 44.6%.

The Amelanchier control site showed a greater range of maximum depth measurements, with a shallower minimum and a deeper maximum than the burn site. Removal of the organic fraction did not alter this relationship (figure 10).

Plate 1. Amelanchier excavated from the Pattee Canyon Burn.



Figure 9. Amelanchier plant with a horizontal rhizome. This plant was excavated from the Pattee Canyon Control Ravine. The break in the upper drawing represents the section of rhizome which makes the 90° turn illustrated in the lower drawing.

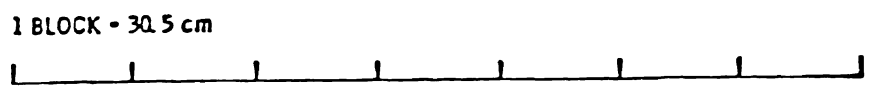
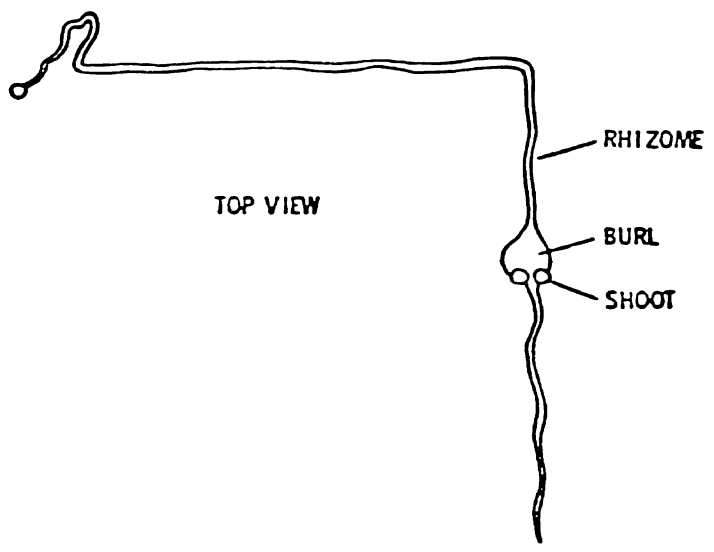
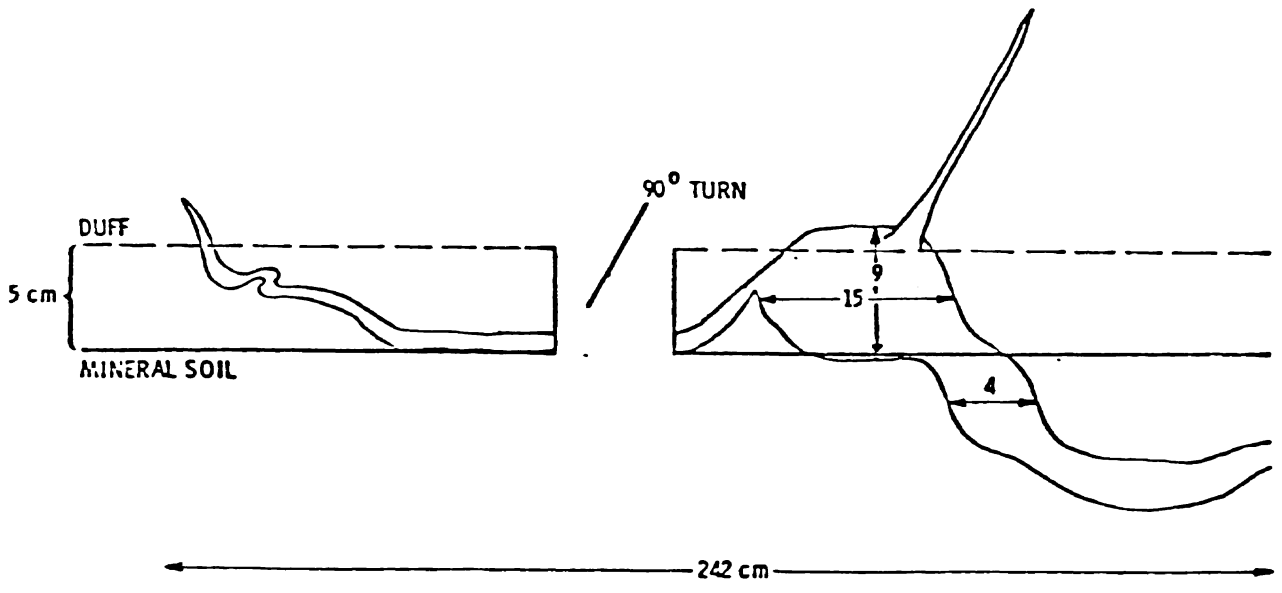
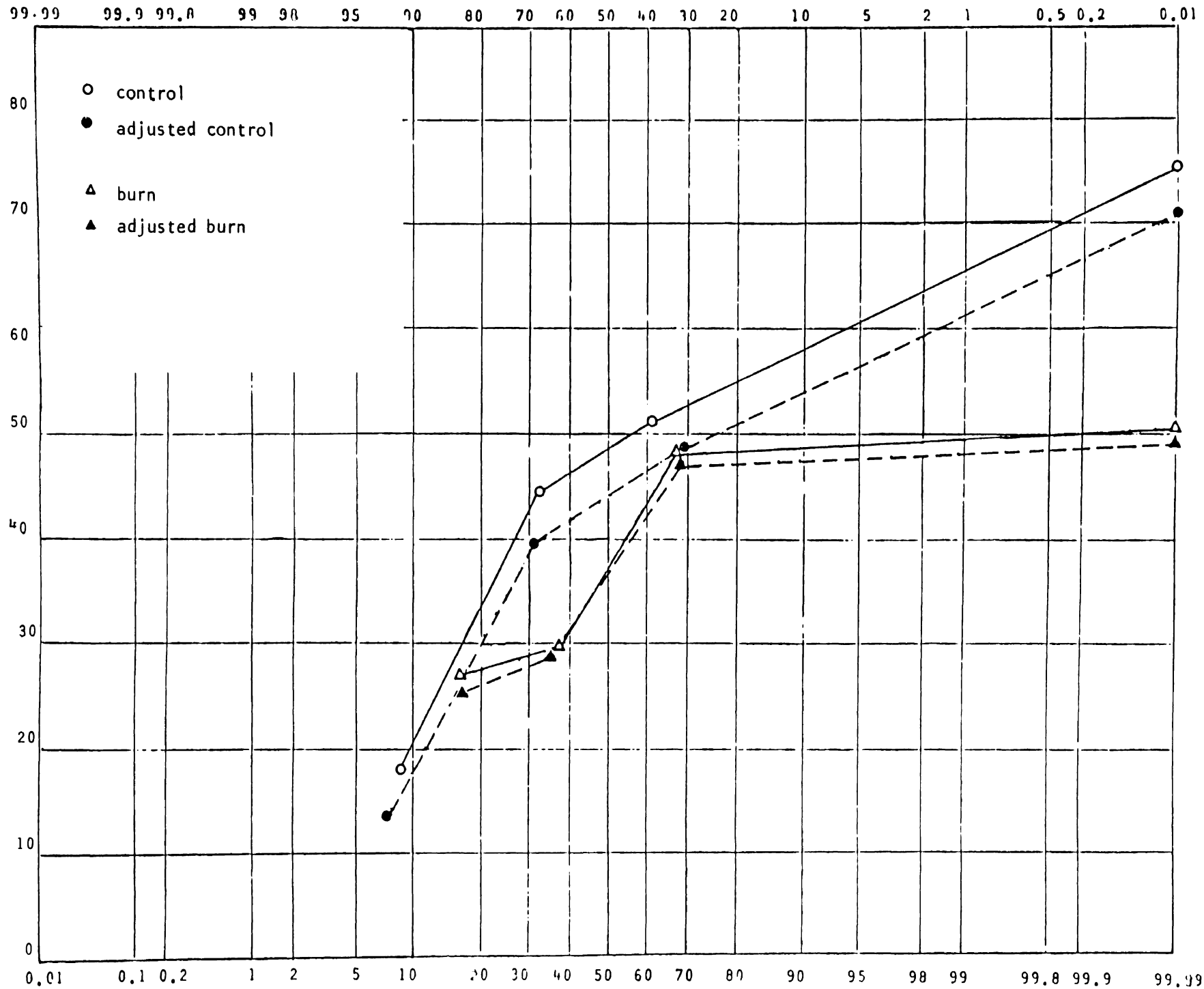


Figure 10. Amelanchier percent cumulative frequency graph for Pattee Canyon specimens.



In the T-test of significance, only the means for the tallest stem measurements were statistically different at an alpha level of .05, with the control site shrubs having taller stems. Only one specimen still had burned tissue evident five years post-fire. Other plants had some dead and broken stems but no obvious charred wood.

Regenerated stems on burned plants originated from the portion of the rootcrown closest to the soil surface. This was true of stems on unburned specimens as well. I also noted suppressed stems in the control plants which had not reached the soil surface were concentrated in this upper tissue region (plate 2).

It was not evident from external examinations made in this study whether buds and primordia are more densely clustered on the top of the rootcrown than on other portions of the perennating organ. Other rosaceous plants, such as apple, can produce cushions of primordia, at least on primary root tissue (Siegler and Bowman, 1939).

Although successful stems tend to be concentrated in this area, there is evidence that other parts of the rhizome are capable of producing stems. Hemmer observed plants regenerating from rhizome sections less than 6 inches (15.24cm.) long with a diameter of 1.27 cm. or greater.

Plate 2. Suppressed shoots on an Amelanchier rhizome excavated from the Pattee Canyon Control Ravine. This plant is also illustrated in figure 9.



I observed one burned plant whose regenerating stems originated from a section of the rhizome mass 30 cm. below the mineral soil surface and 15 cm. below the main tissue mass, which had been killed by fire. There were other segments of the rhizome that were closer to the surface of the soil and had no stems. Either killing the tissue or heating it released these lower buds, while those adjacent to the burned section remained inactivated.

Shrubs, like serviceberry, which produce massive perennating organs are perhaps less easily killed by fire even when their perennating organs are not completely protected by mineral soil. Wood is a poor conductor of heat, and although one area of the mass is fire-killed, it may still act as insulation to the potential budding sites below it.

In some instances it may be disadvantageous to produce large quantities of wood, particularly when the fire frequency is low. Mohamed and Gimingham (1970) found that in heath (Calluna vulgaris (L.)Hull) the ability of stems to resprout was much reduced after 15 years without pruning by fire or grazing. They attributed this partly to a buildup of secondary xylem around and over suppressed buds. Shrubs which are surviving in a reduced state of vigor under maturing tree canopies may, after a period of years, produce fewer new buds annually and continue to develop wood around

buds already present.

Because of its generally clumped form (at least in west-central Montana), serviceberry is a shrub not likely to increase in frequency after a fire. But, individual shrubs often survive successfully, so frequency may not decrease unless shrubs are in poor condition.

There were four shrub species sampled which had horizontally oriented rhizomes generally situated well within the mineral soil layer, namely Physocarpus, Spiraea, Symphoricarpos, and Berberis.

Physocarpus malvaceus

Physocarpus malvaceus has a horizontal perennating system although it, like Amelanchier, is often called a "rootcrown shrub". Sectioning revealed that its perennating organ is a rhizome. According to Hitchcock and Cronquist (1964), ninebark is a

"spreading to erect shrub... (0.5-2m. tall)... [found in] canyon bottoms and rocky hillsides to ponderosa pine and Douglas-fir forest; entirely to the e. of the Cascades, from s.c.B.C. through c. and e. Wash. to c. and e. Oreg., e. to s.w. Alta., Mont., Wyo., and Utah."

Physocarpus was excavated from the same Pattee Canyon ravine sites as Amelanchier. Six specimens were examined in each site.

All plants excavated in this study arose from horizontal rhizomes of varying thickness and length.

I found Physocarpus plants in two different settings-as obviously single or small clumps of stems sprouting from one rhizome (plate 3), or in large groupings, with many stems which originated from a number of interlaced rhizomes. Examples of some of the observed growth forms appear in figure 11. A burned clump and resprout are illustrated in plate 4. Randomly selected stems in the clumps were excavated to the rhizome from which they arose. Sometimes these appeared autonomous from the other rhizomes around them. It is possible that within the grouping an original connecting section of tissue had died, leaving these individual plants, Or, these larger clumps may result from several seedlings establishing in close proximity to each other, as might occur in a rodent cache.

External observations of rhizomes revealed numerous suppressed buds along the entire length of the axis. One half of the plants excavated had stems which arose from more than one section of the rhizome (plate 5). Presumably, the presence of buds throughout the rhizome would permit resprouting at many points given the proper environmental and hormonal cues.

Plate 3. Physocarpus rhizome excavated from the Pattee Canyon Control Ravine. Each block in the grid is 10 cm X 10 cm.



Figure 11. Physocarpus growth forms - six representative specimens.
Note the lack of a "rootcrown" in three of these plants.

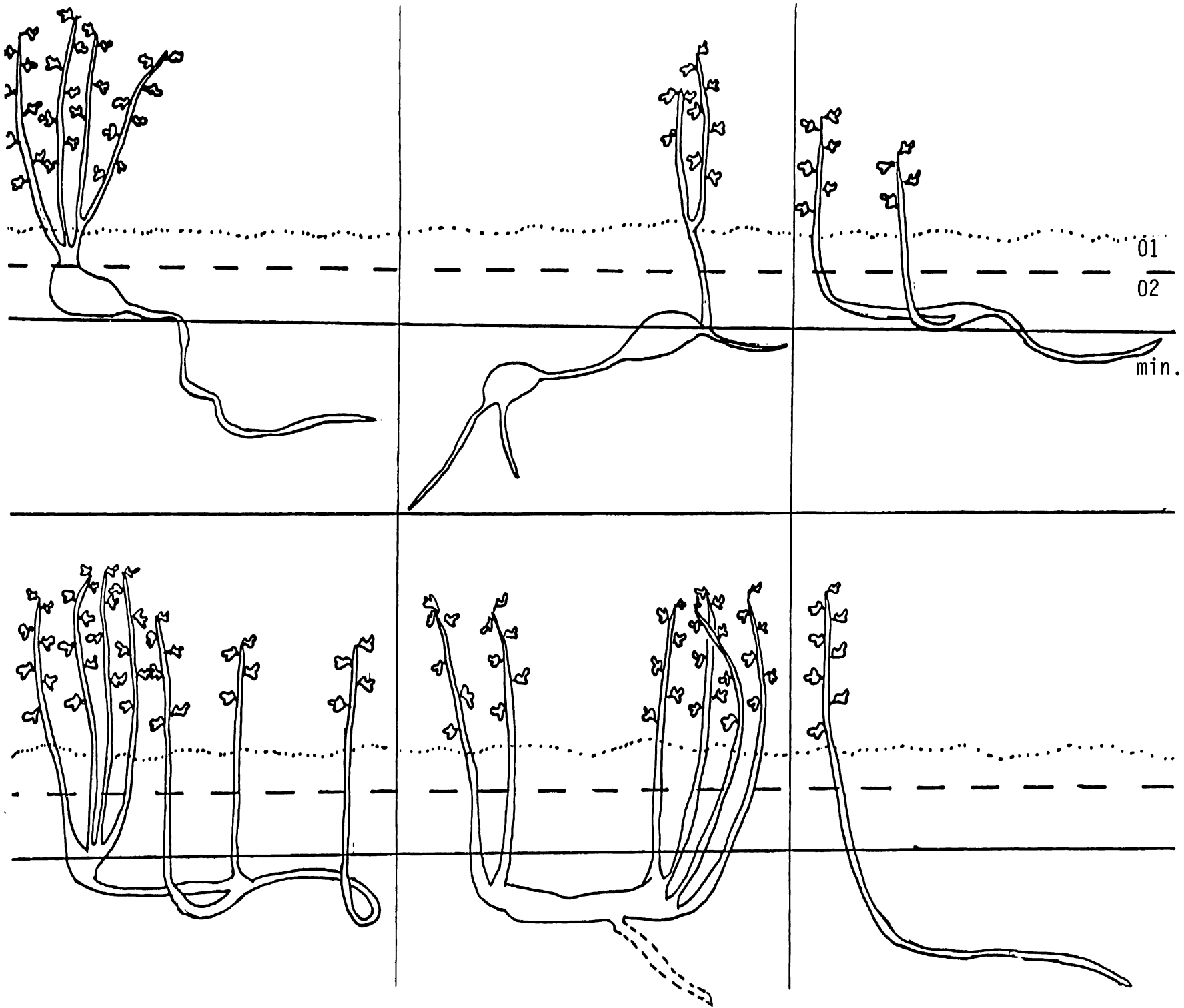
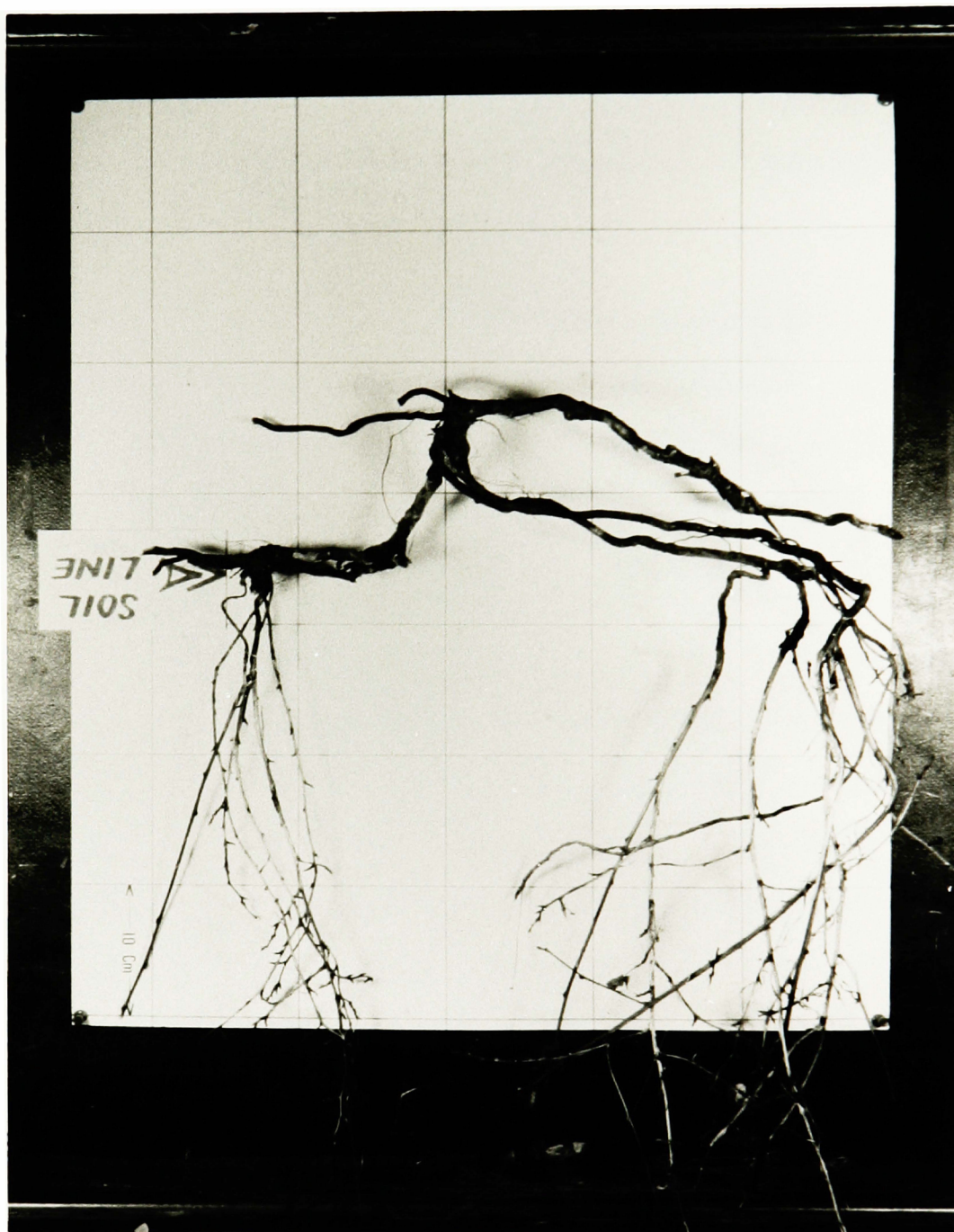


Plate 4. Physocarpus post-fire resprout. (J. Habeck photo)



Plate 5. Physocarpus rhizome excavated from the Pattee Canyon Control
Ravine.



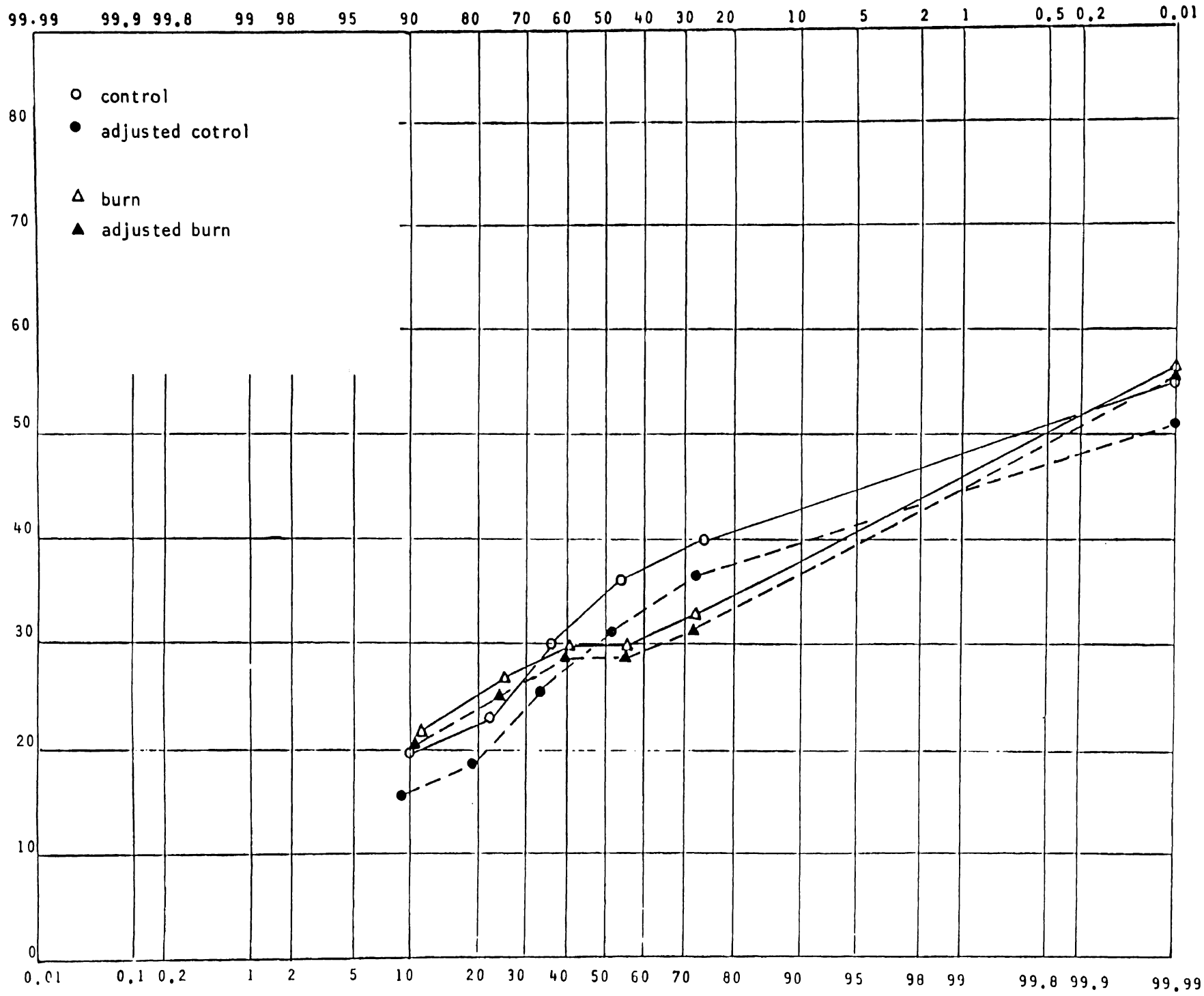
Ninebark has a greater proportion of its perennating organ in mineral soil than does serviceberry. In the control site, 36%-99% of ninebark rhizome resided in mineral soil, with a mean of 82.9%.

Burned and unburned maximum depth values were quite similar in their ranges. Control site values, particularly those adjusted, were somewhat more shallow at the maximum and the minimum although midrange values were deeper than those on the burn (figure 12). The horizontal extent and stem number are significantly different on the burn and control sites. Rhizomes on the burned site, were longer and had more stems.

Although smaller in mass than serviceberry, many ninebark rhizomes have enough woody material to act as insulation for buds on the undersurface of the rhizome. The amount of insulation depends on the age and the degree of secondary tissue development.

Rhizomes serve as a source of buds for regeneration and as a carbohydrate reserve for stem elongation. These larger masses of tissue do not necessarily contain a higher ratio of starch storage cells, but a more massive organ may represent a greater potential reserve.

Figure 12. Physocarpus percent cumulative frequency for Pattee Canyon specimens.



In some Physocarpus, the distribution of secondary tissues was fairly uniform (figure 13) whereas in others, slender segments were interspersed with lumps or knots of tissue (figure 14). No observed environmental condition was an evident cause of these differing morphologies.

Symphoricarpos albus

Symphoricarpos albus is an

"erect branching shrub, (0.5)1-2(3)cm. tall, less conspicuously rhizomatous than S. occidentalis,...[found in] thickets, woodlands, and open slopes, from the lowlands to moderate elevations in the mountains, Alaska panhandle to Quebec, s. to Calif., c. Ida, Colo., Neb., and Va." (Hitchcock and Cronquist, 1964).

Specimens of snowberry were excavated at both Pattee Canyon and Rumble Creek. Snowberry rhizomes are considerably more slender than those of Physocarpus or Amelanchier (figure 15, plate 6). They are well adapted to snaking between rocks. In a number of specimens, slender belowground stems were connected to each other via larger masses of woody tissue, as has been described for ninebark (figure 16). These masses were more common in snowberry than in any other species sampled. In Symphoricarpos they seem to be a central location for bud production and multiple stems were sometimes produced in clumps on these

Figure 13. Physocarpus rhizome excavated from the Pattee Canyon Burn.

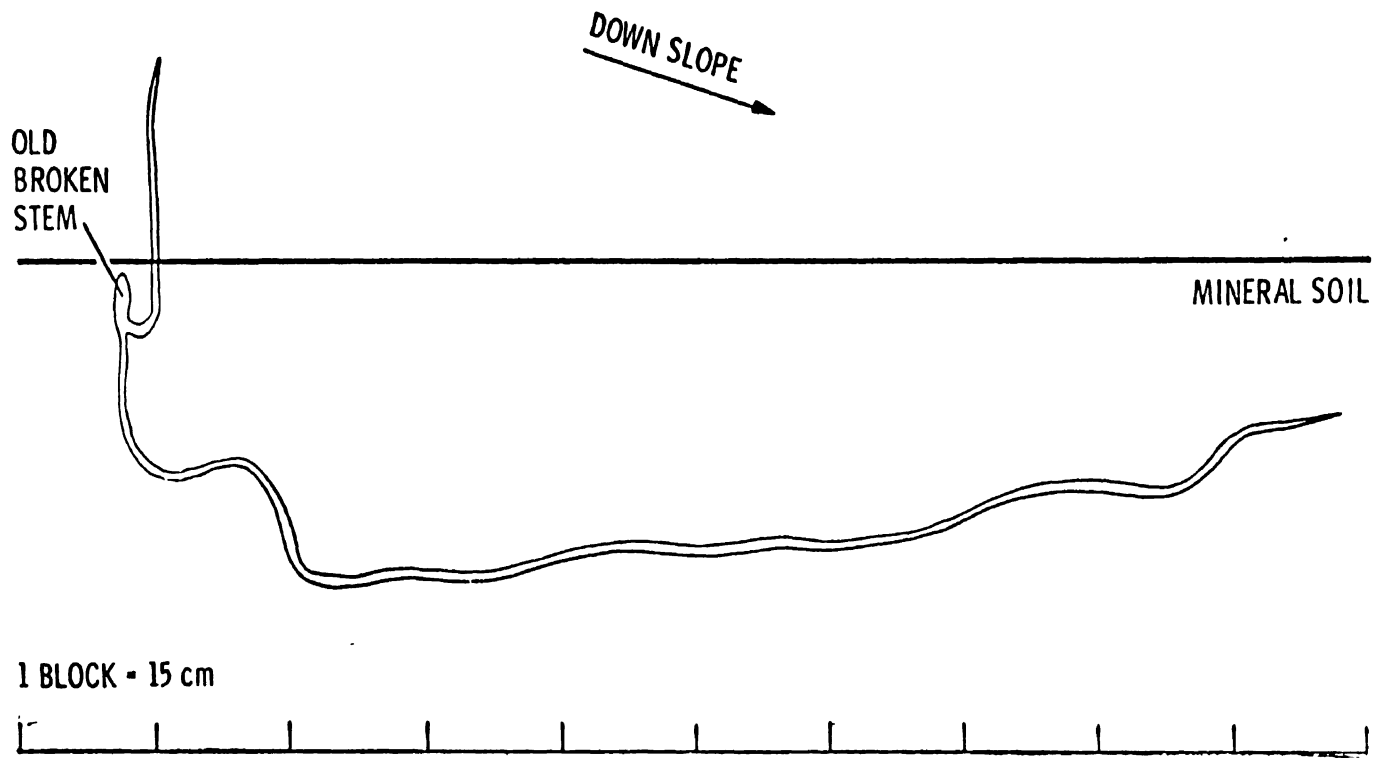


Figure 14. Physocarpus rhizome with enlarged nodes, excavated from the Pattee Canyon Control Ravine.

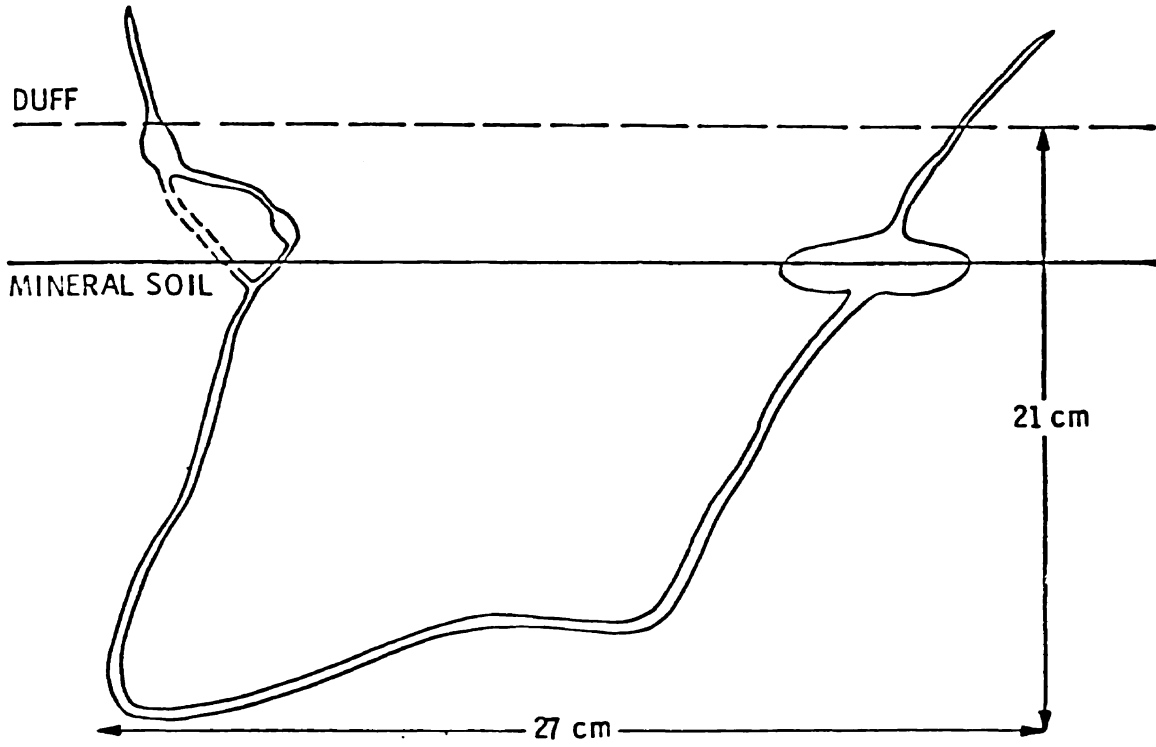


Figure 15. Symphoricarpos rhizomes: a.) a plant excavated from the Pattee Canyon Burn; b.) a plant excavated from the Pattee Canyon Control Ravine. The lower drawing illustrates an individual with an enlarged node - a common feature in Symphoricarpos albus.

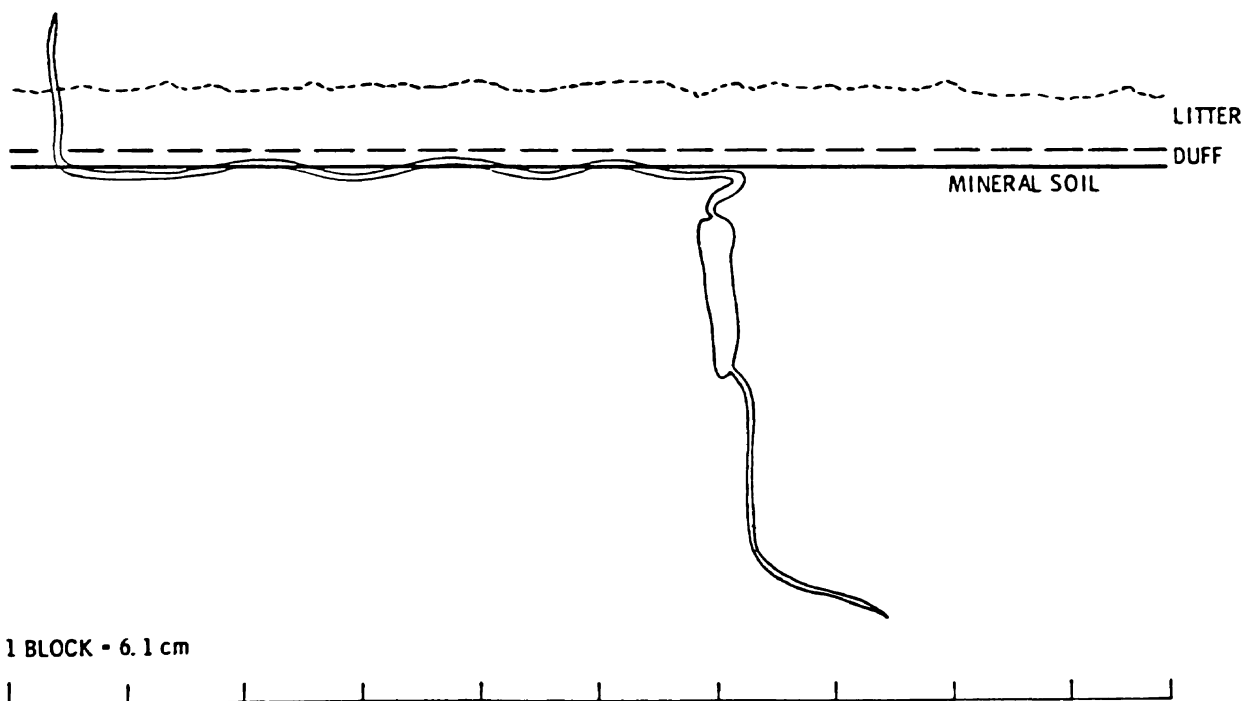
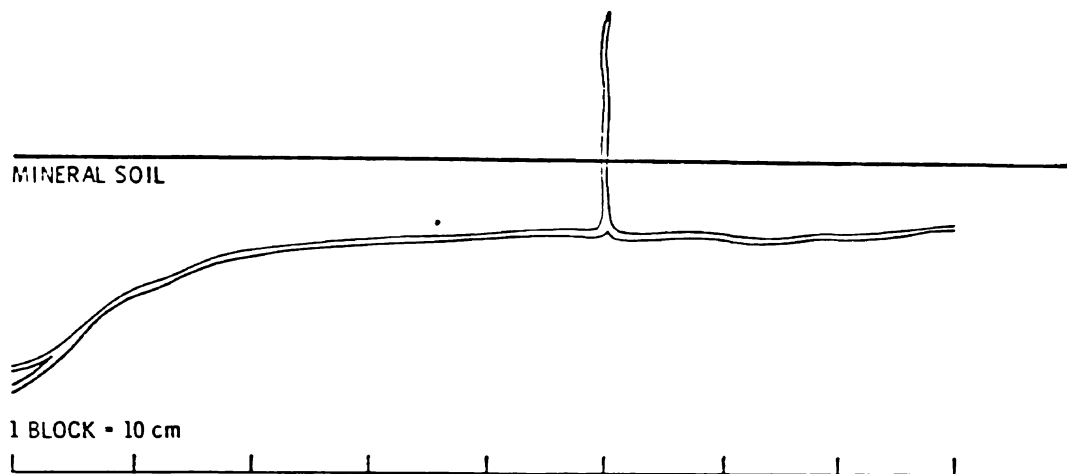
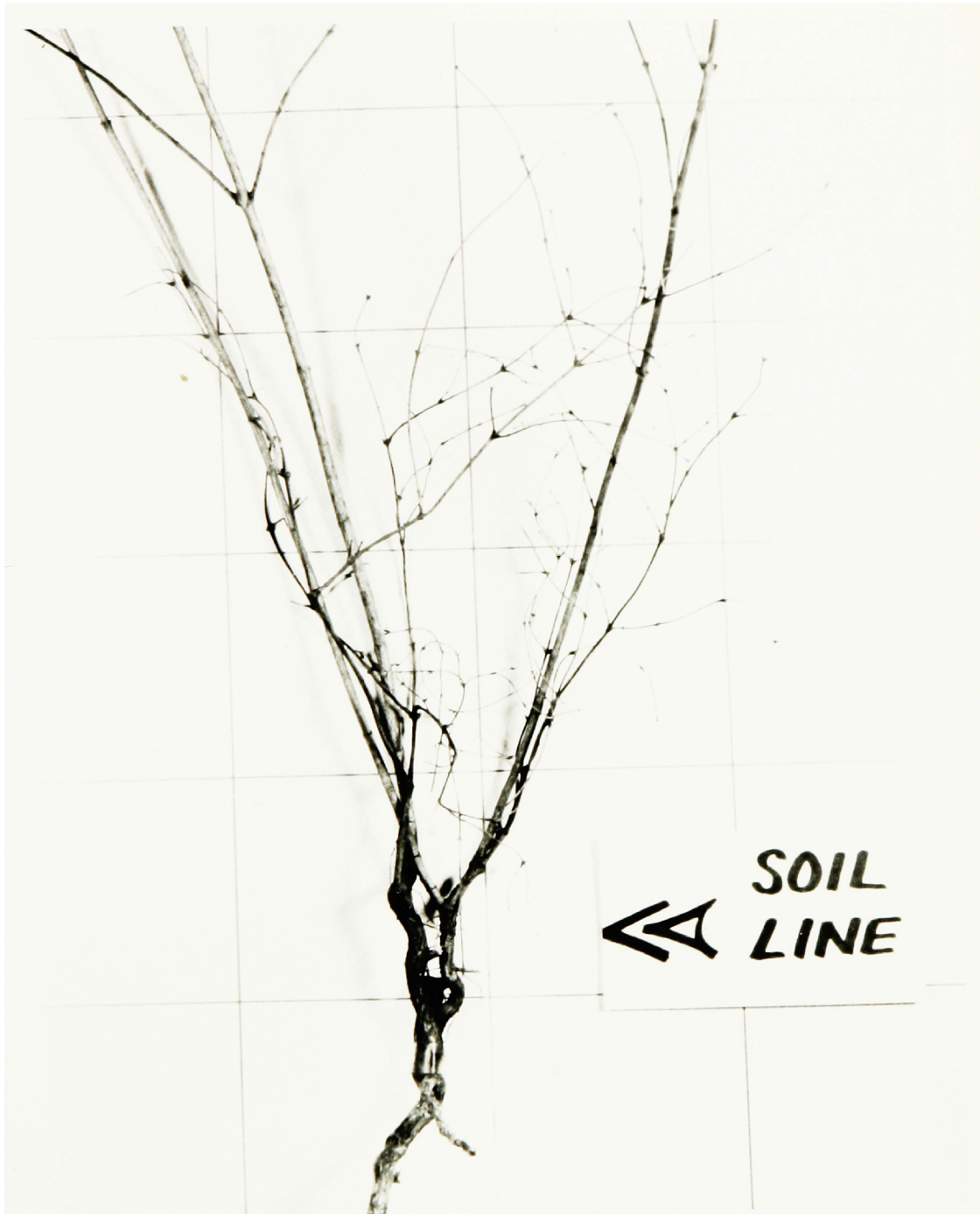
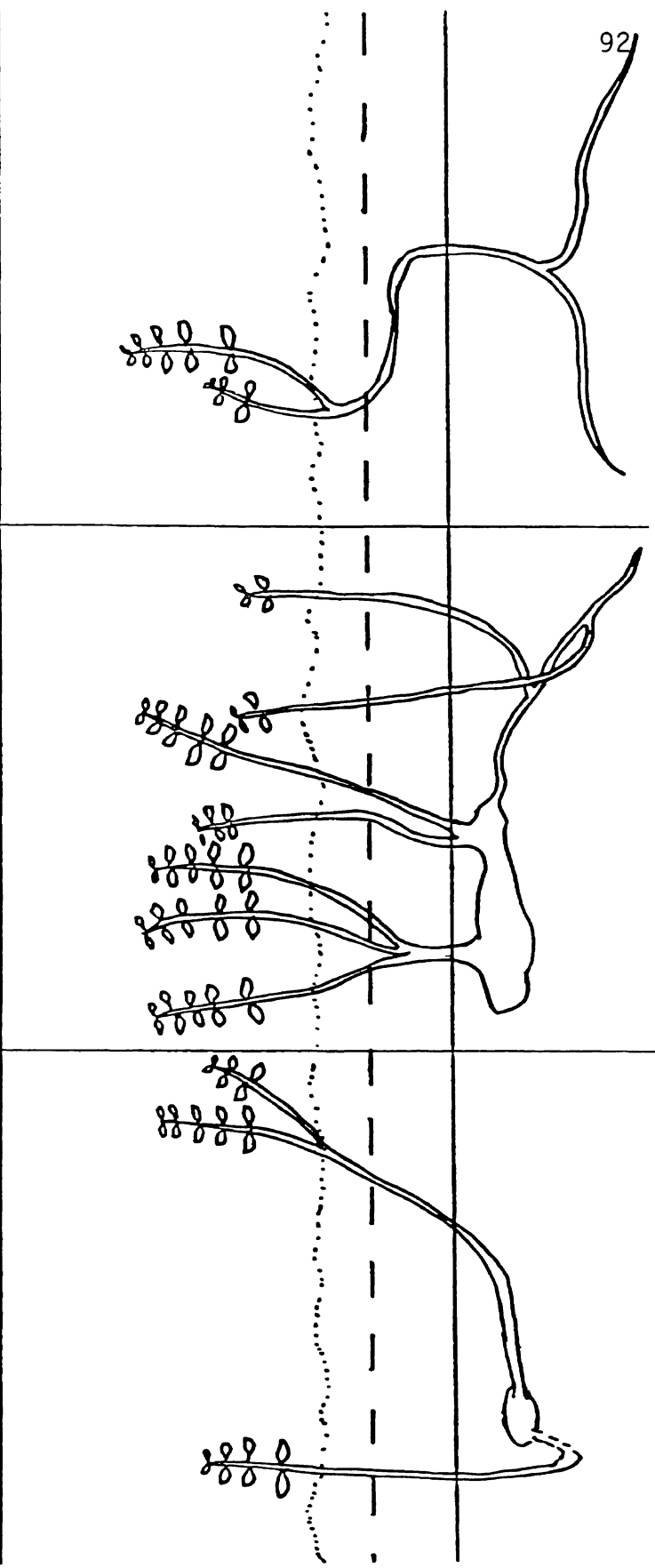
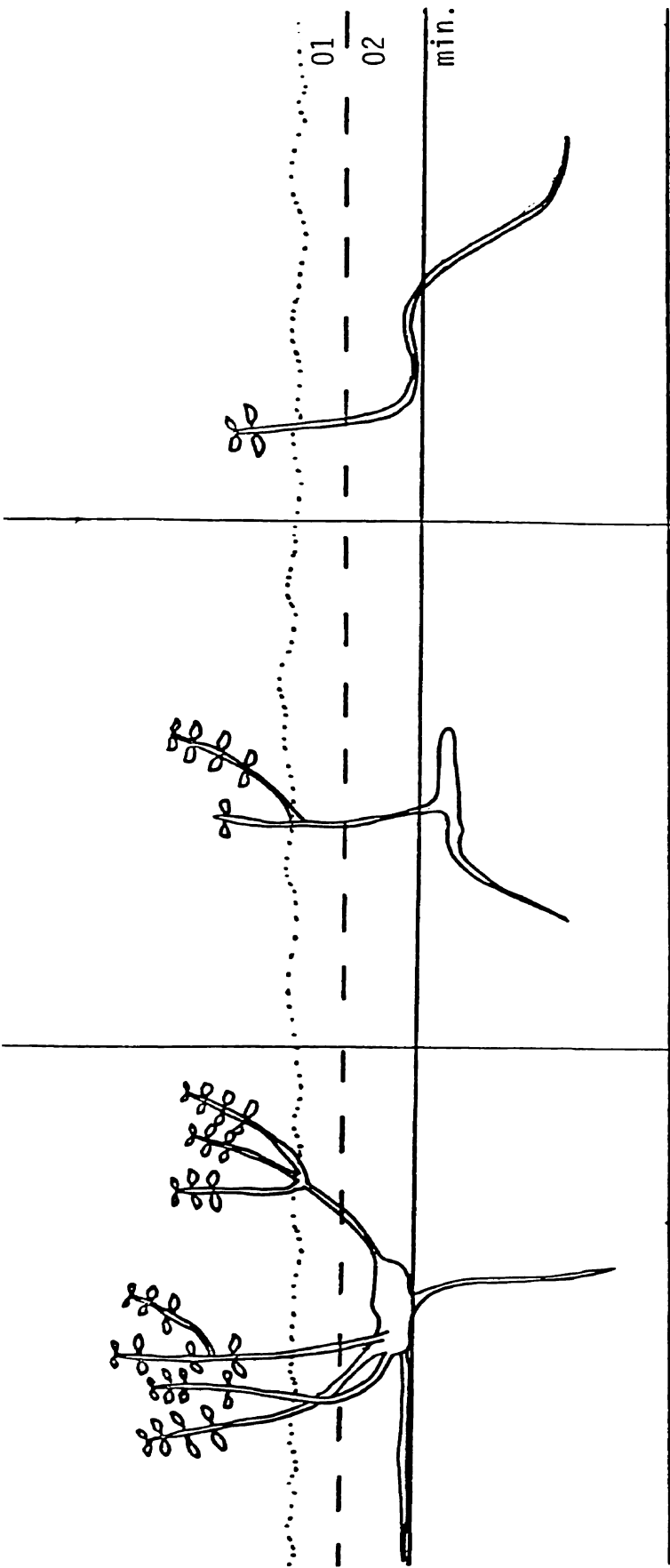


Plate 6. Symphoricarpos plant excavated from the Rumble Creek Burn.



1

Figure 16. Symphoricarpos growth forms - six representative specimens.



swellings. Often though, separate rhizomes were produced which remained subterranean and travelled horizontally in different directions for some distance. From each of these rhizomes a single aboveground stem emerged.

Once an aerial stem has become leafy, its dependence on the larger rhizome mass may be relatively short-lived. In a study conducted on S. occidentalis, Pelton (1953) found good root development on young rhizome segments and believed they could become independent after the first year. Young stems of S. albus have large irregularly shaped leaves compared to the parent clump. This phenomenon was also observed in ninebark and spirea. If new stems become nutritionally independent at a relatively early stage, this increased photosynthetic area may aid in the rapid accumulation of carbohydrates for later growth. Since only young stems have a larger leaf pattern, it may be possible to tally and map incremental clone growth in these species.

Placement of Symphoricarpos rhizomes is mostly in mineral soil. At Rumble Creek the percent residence in mineral soil on the control site ranged from 13%-91% with a mean of 58.7%. At Pattee Canyon, values ranged from 25%-97% with a mean of 81.3%.

When the unadjusted Rumble Creek depth values were compared, burn site values proved to be consistently deeper. The separation between burned site and control values were emphasized by removal of the organic material from the measurements (figure 17). T-test results were close to the alpha .05 level for maximum depth means at Rumble Creek with the burned site having the greater mean depth.

The Pattee Canyon samples showed a somewhat different pattern. Control ravine depths had a greater range of values with a considerably more shallow minimum and a somewhat deeper maximum. Burn depths were less variable and fell in the range of the deeper control samples. Adjusted values also displayed this relationship (figure 18).

Spiraea betulifolia

Spiraea betulifolia plants are

"...strongly rhizomatous, glabrous or subglabrous shrubs mostly (1.5)2.6-6(10) dm. tall, ...[found on] steambanks and lake margins and open to wooded valleys and hillsides, often in rockslides; B.C. southward to n.c. Oreg., from near sealevel to about 4000 ft. elevation in the Cascades, e. and up to 10,000-11,000 ft. elevation from Sask. to S.D. and Wyo; Asia." (Hitchcock and Cronquist, 1964)

Figure 17. Symphoricarpos percent cumulative frequency graph for Rumble Creek specimens.

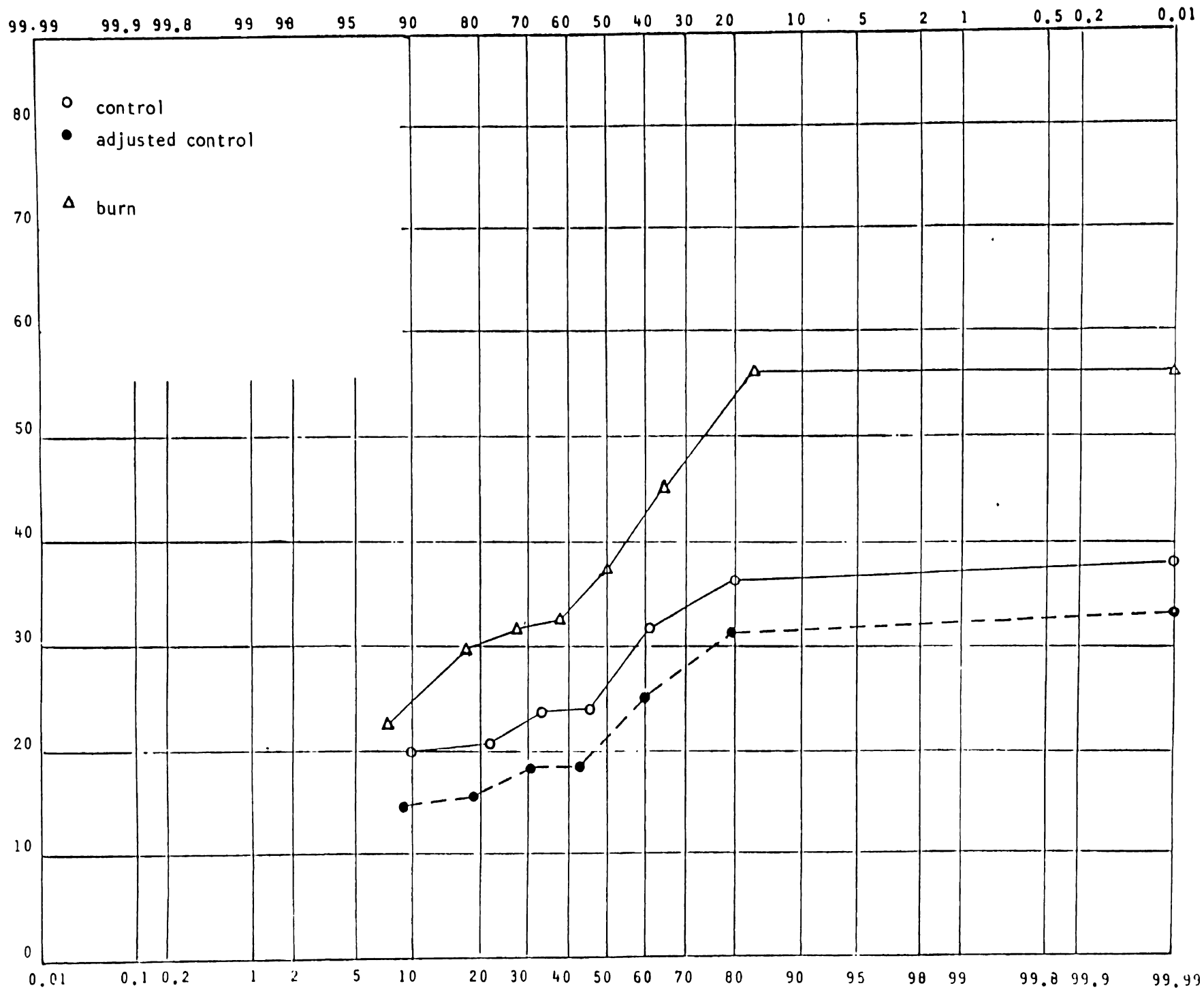
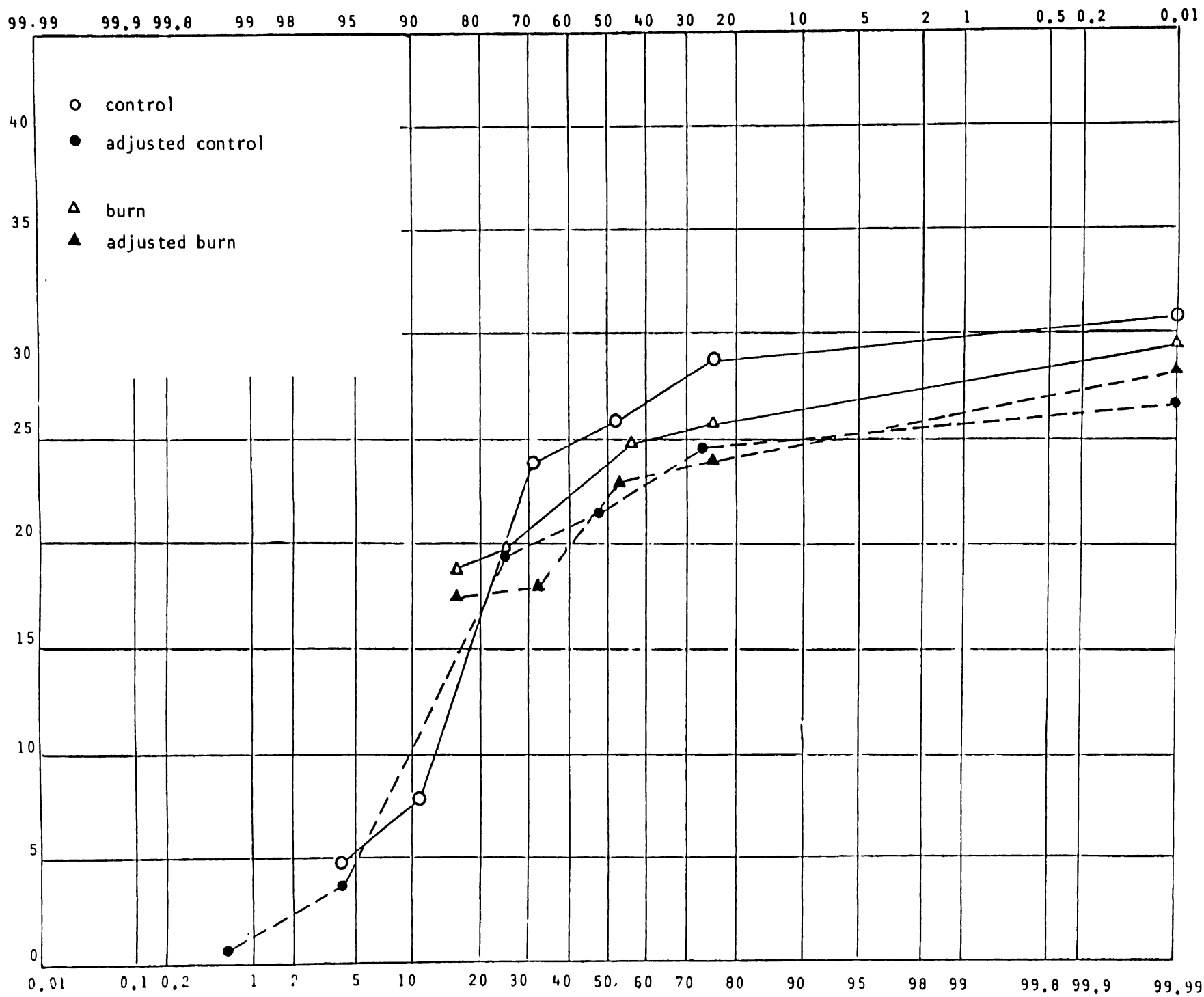


Figure 18. Symphoricarpos percent cumulative frequency graph for Pattee Canyon specimens.



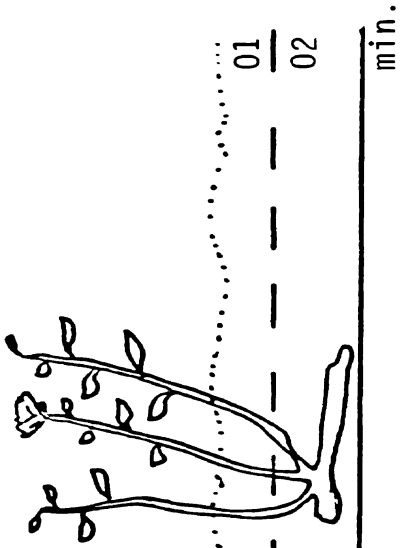
Spiraea is very similar to Symphoricarpos in its habit. It too is well suited to rocky sites by its slender rhizomes (figures 19 and 20). Spirea does not have as many of the pronounced woody swellings present in snowberry and ninebark. They do occur on occasion and some specimens showed areas where thicker portions were produced by the fusion of adjacent segments.

Incipient perennating buds are well distributed along the entire length of the spirea rhizome. Any section is probably capable of generating stems if it is large enough to provide the carbohydrate necessary for sprouting. One plant excavated from the Rumble Creek burn developed from a section 9 cm long and 4 mm in diameter (left hand portion, plate 7). The mature plant measured 19 cm in its horizontal extent. Spiraea also appears capable of some layering from aerial stems. One specimen collected in Pattee Canyon during an earlier study was found to be developing new vertical shoots from a stem appressed to the soil surface.

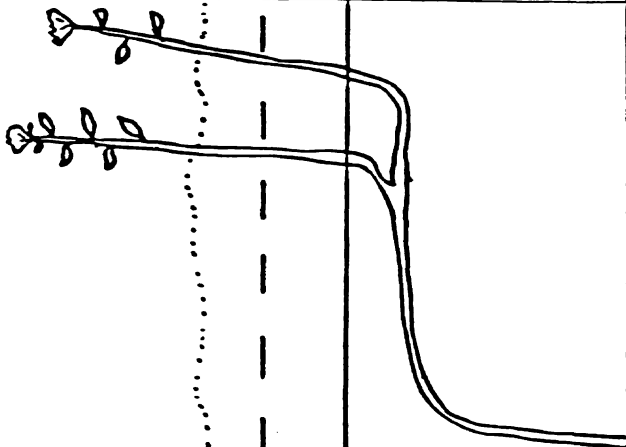
The proportion of spirea perennating tissue residing in the mineral soil is relatively great. In Pattee Canyon, the percent residence ranged from 52%-100% with a mean of 83.2%. At Rumble Creek, the range was somewhat narrower, 30%-62% with a mean of 49.6%.

Figure 19. Spiraea growth forms - six representative specimens. Plant in c. is derived from a broken fragment.

ε.



b.



a.

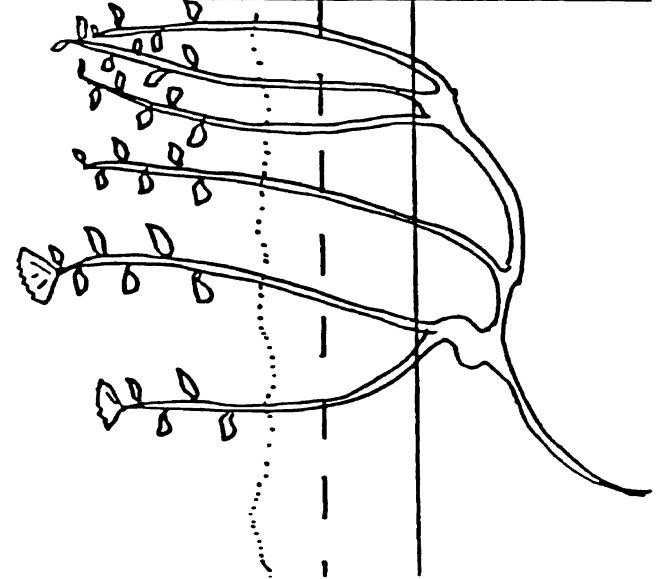
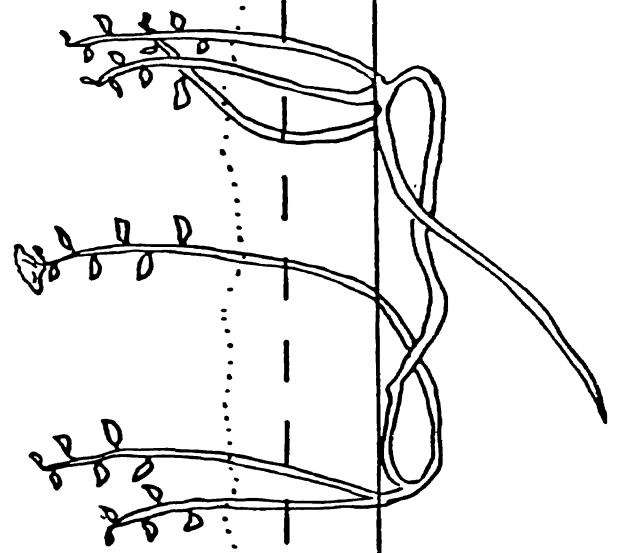
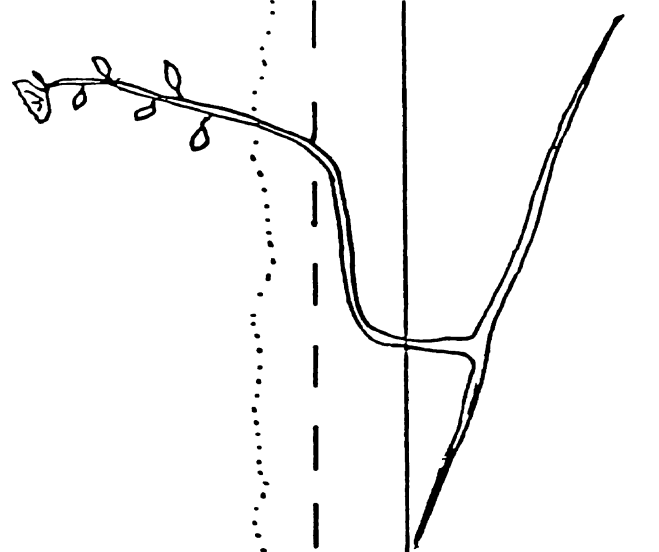
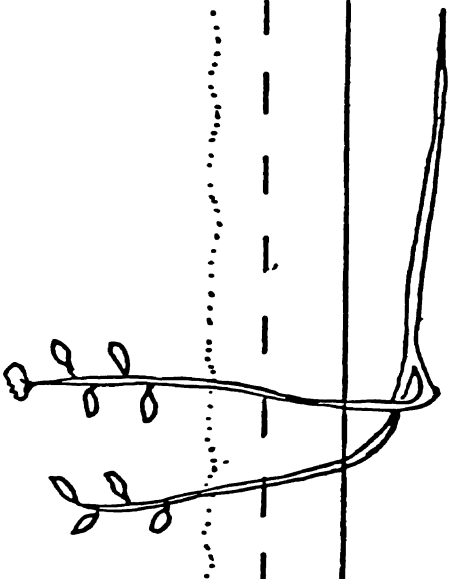


Figure 20. Spiraea rhizomes: a.) Pattee Canyon burn; b.) Rumble Creek Burn.

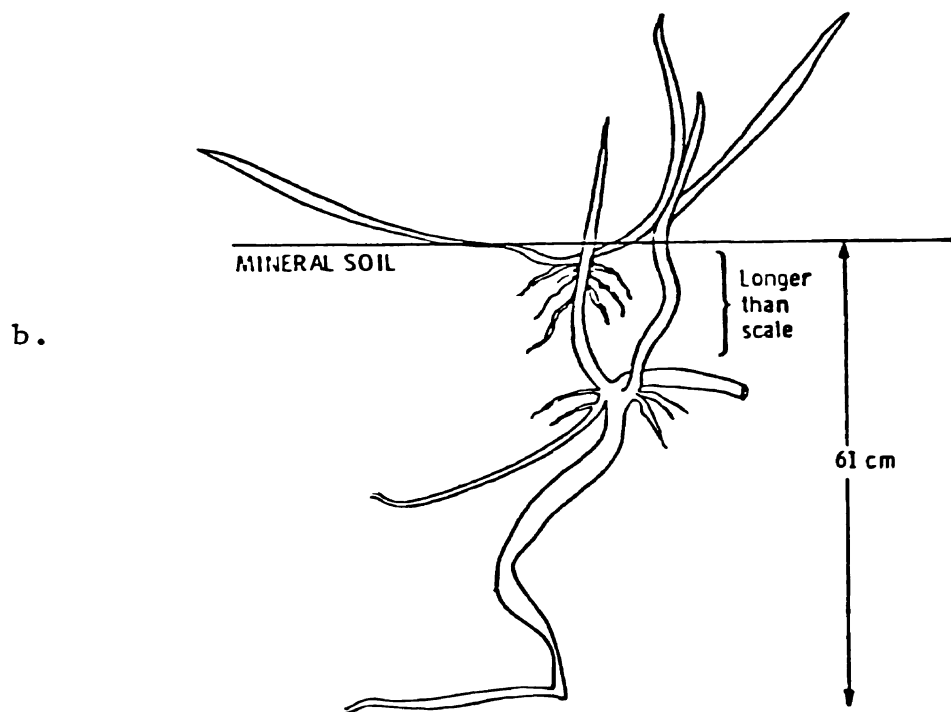
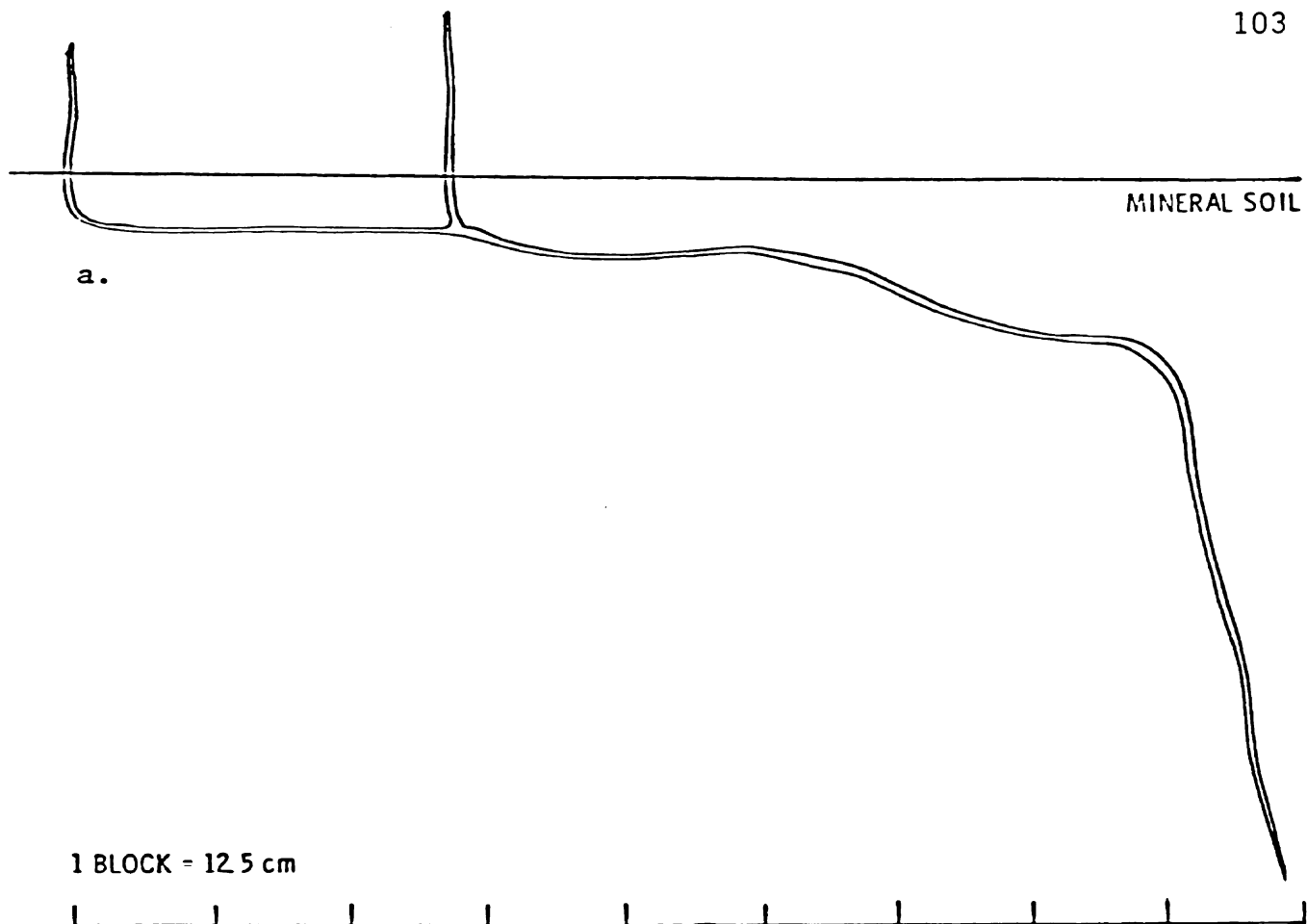
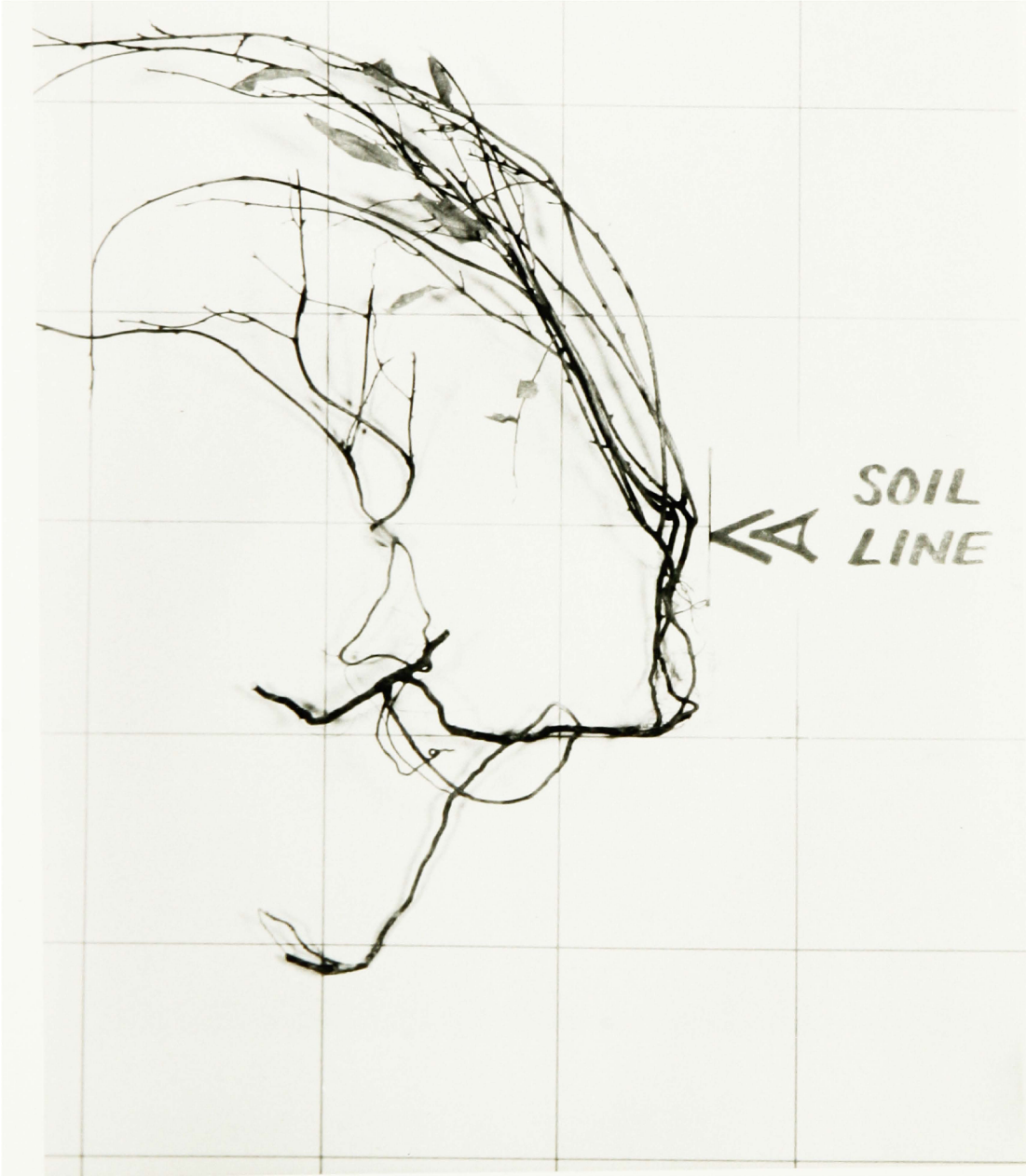


Plate 7. Spiraea rhizome excavated from the Rumble Creek Burn. Small segment on the left of the plant is the originating fragment. Grid blocks are 10 cm X 10 cm.



At Rumble Creek, unadjusted control and burn values were similar (figure 21). Once the organic fraction was removed, however, the overall depths of the control appeared considerably more shallow.

In Pattee Canyon, comparison of unadjusted values indicated that the burn site plants had deeper minimum and maximum values (figure 22). Once the organic fraction was removed, the difference between burn and control minima was eliminated. The separation between the maxima was retained, as was that between the median values.

At Rumble Creek, the burn site mean for stem number was significantly greater at an alpha of .05.

As was the case with serviceberry, sprouts which replaced burned stems were produced immediately behind the fire-killed section (plate 8).

Berberis repens

Berberis repens is in the same perennating category as Symphoricarpos and Spiraea. It also has slender linear rhizomes often located below the mineral soil surface (figure 23) Hitchcock and Cronquist (1964) describe its habit and distribution as

"...always more or less procumbent and widely stoloniferous ...lower foothills to forested slopes; e. Wash. to Alta. and s. to S.D., Tex., N.M., Utah, s. Nev., and n.e. Calif., in

Figure 21. Spiraea percent cumulative frequency graph for Rumble Creek specimens.

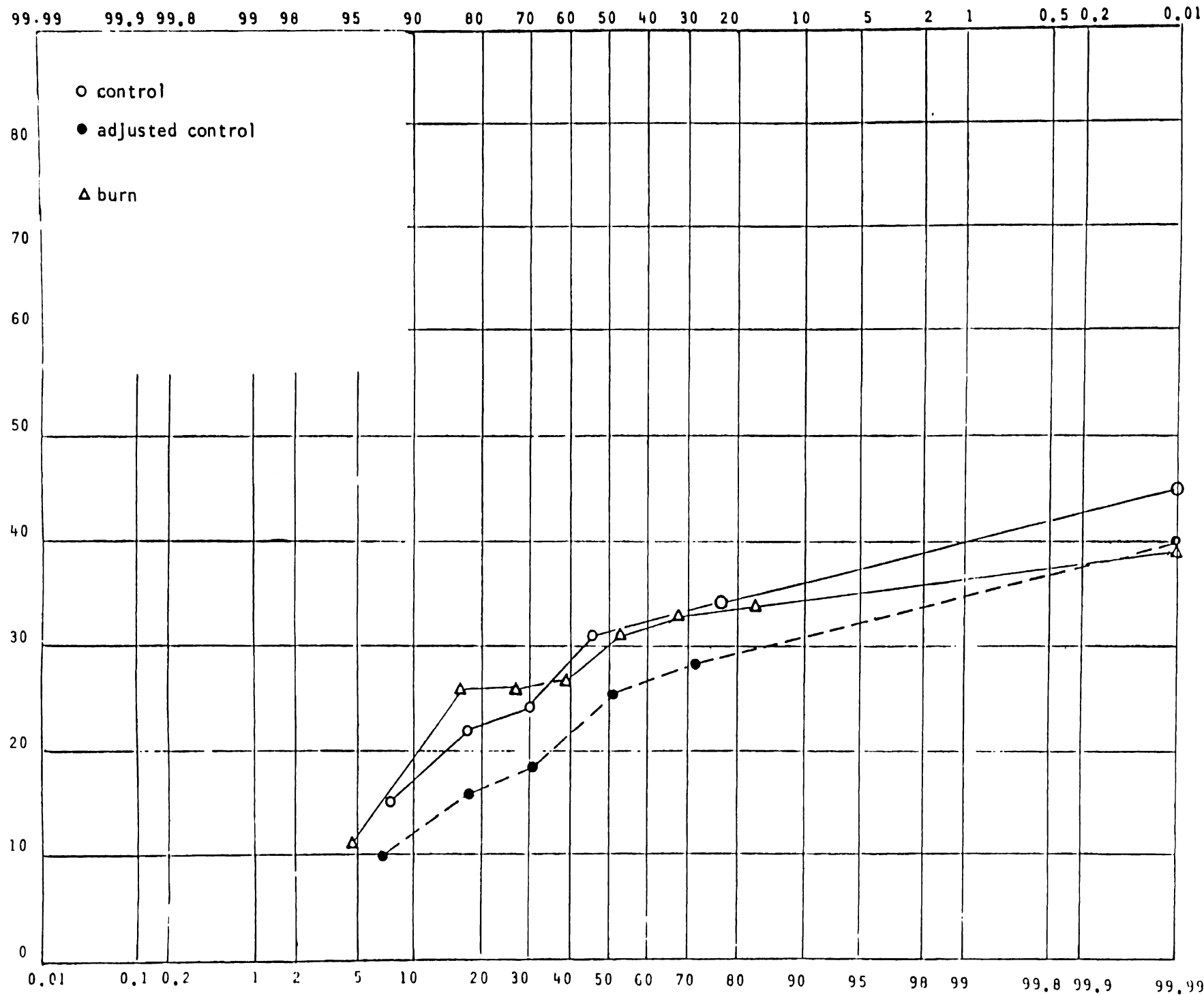


Figure 22. Spiraea percent cumulative frequency graph for Pattee Canyon specimens.

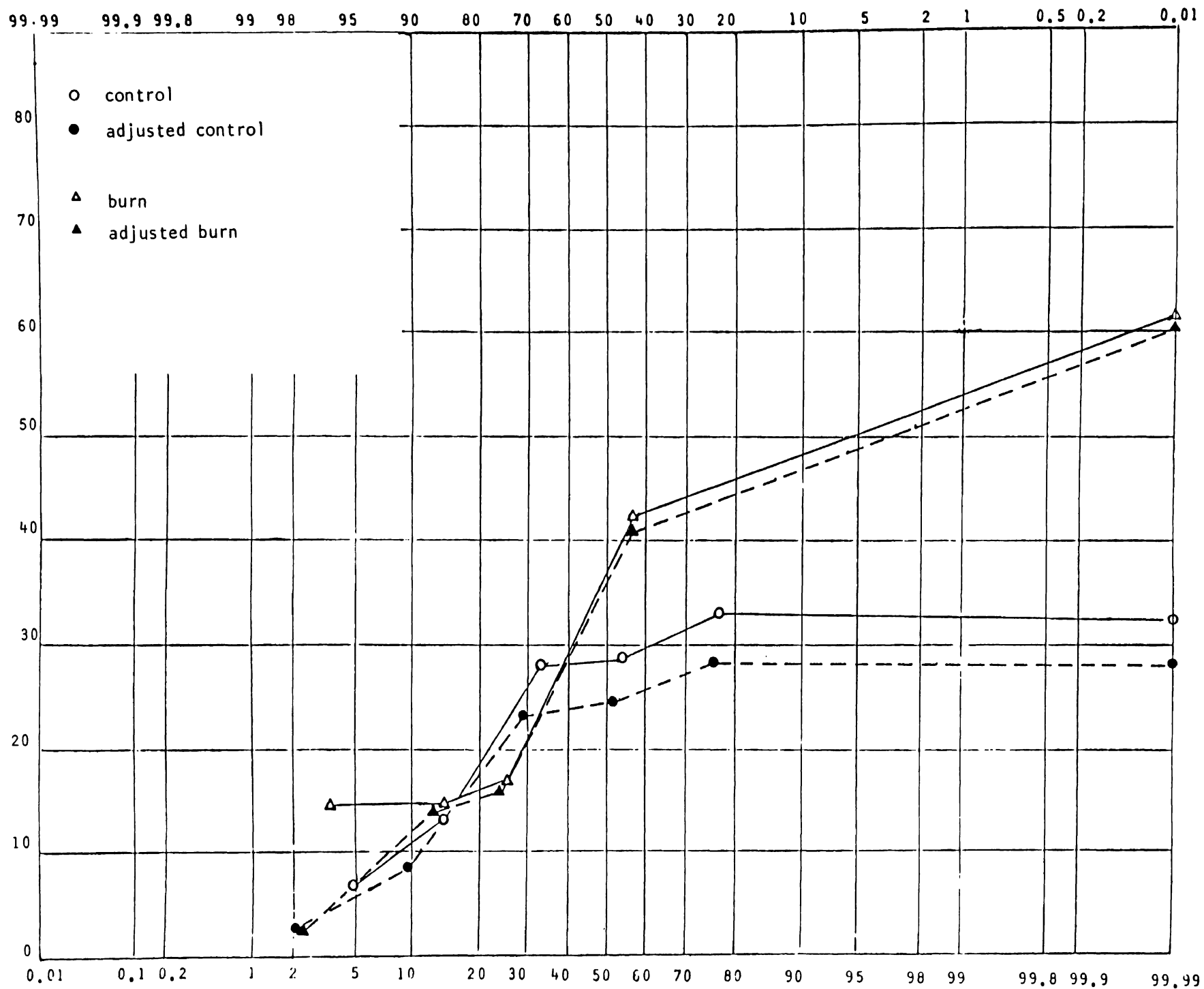


Plate 8. Spiraea rhizome with a burned stub, excavated from the Rumble
Creek Burn.

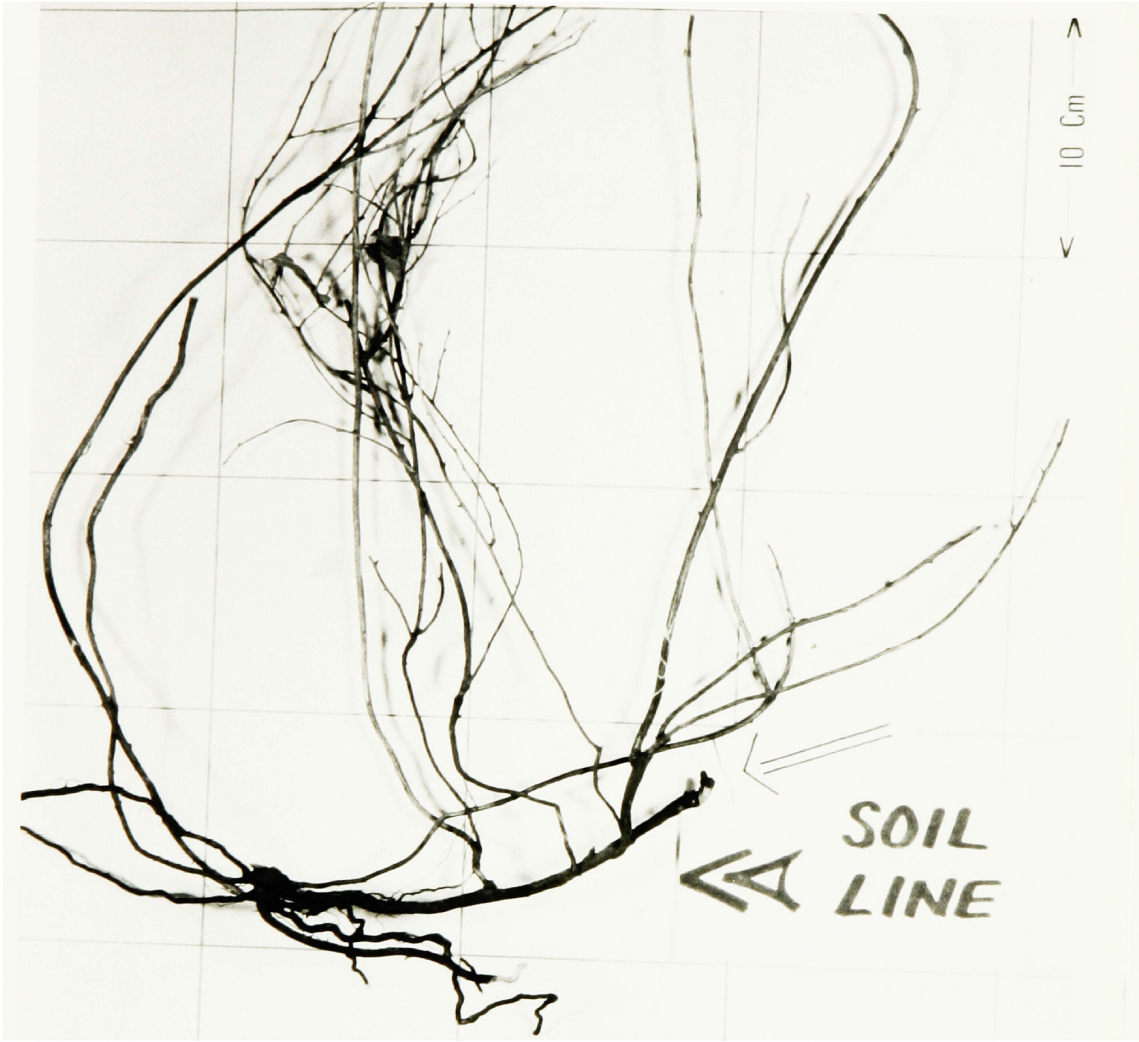
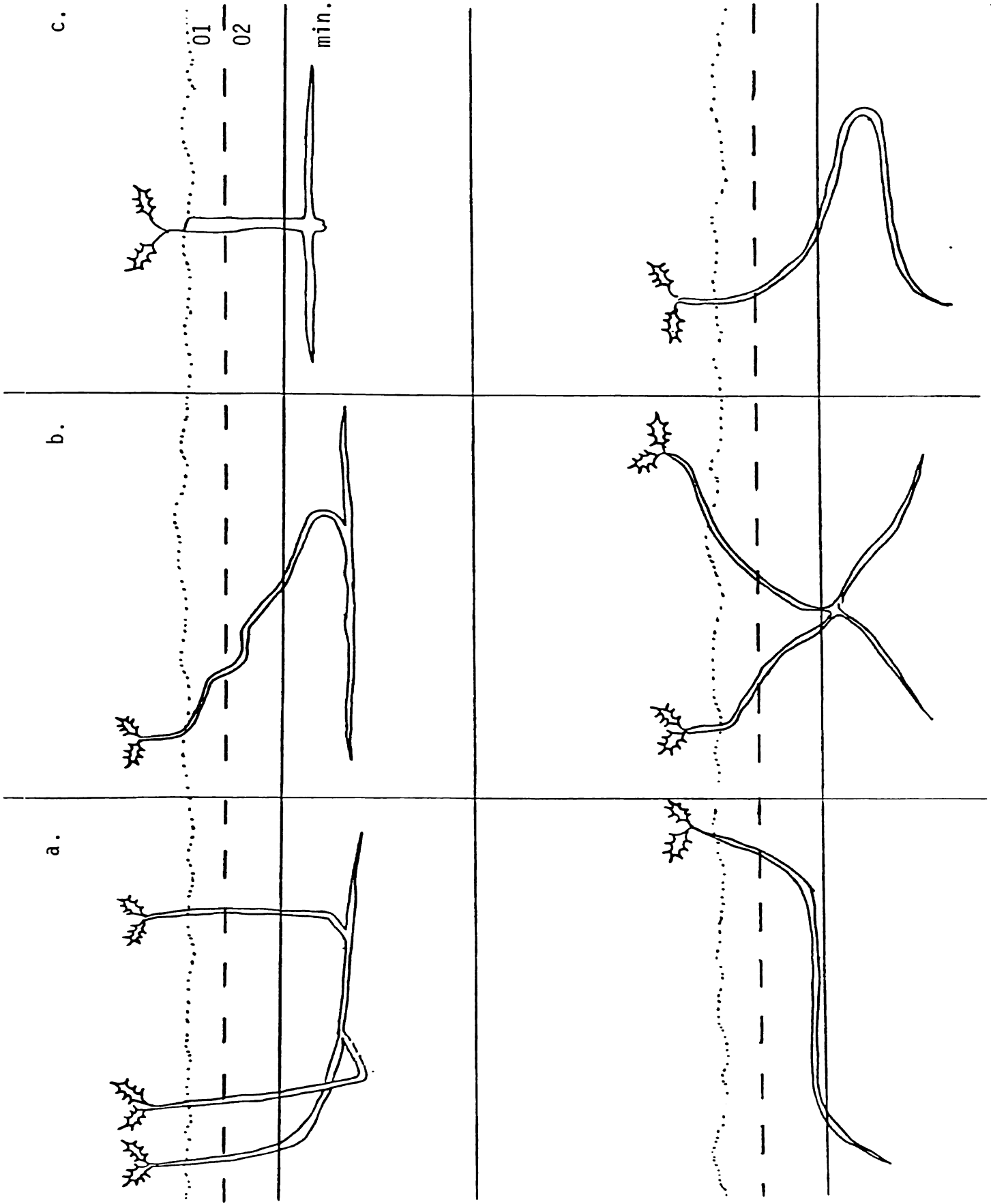


Figure 23. Berberis growth forms - six representative specimens.
Plant in c. originated from a broken fragment.



Oreg.,w. to Deschutes and Wasco Cos."

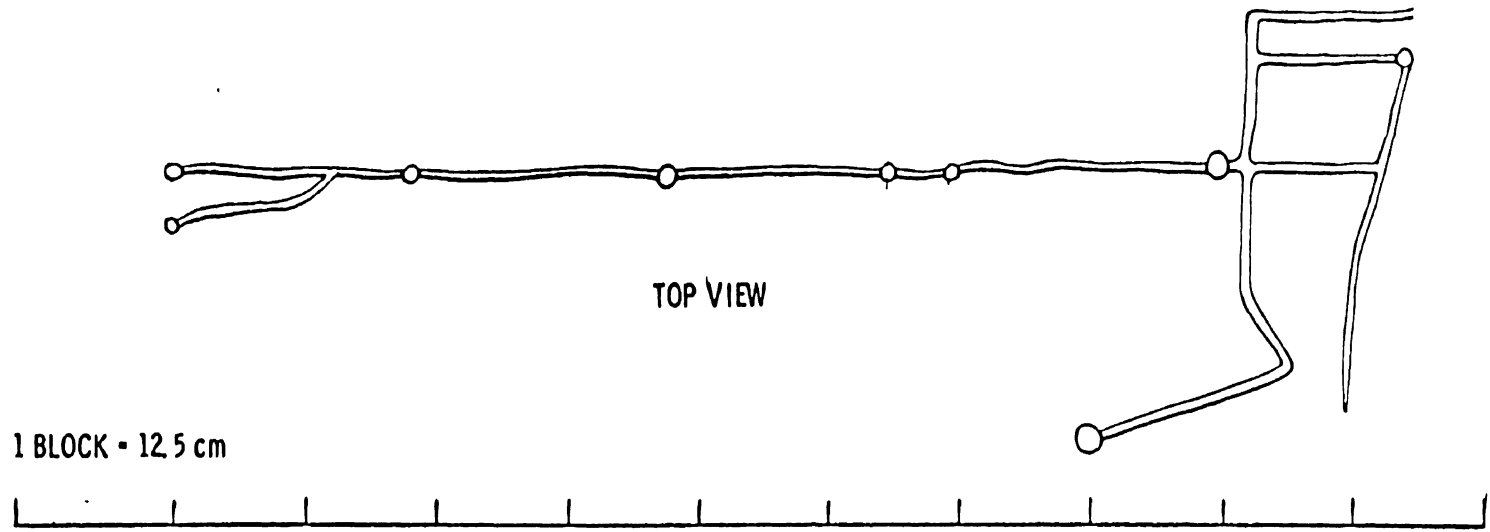
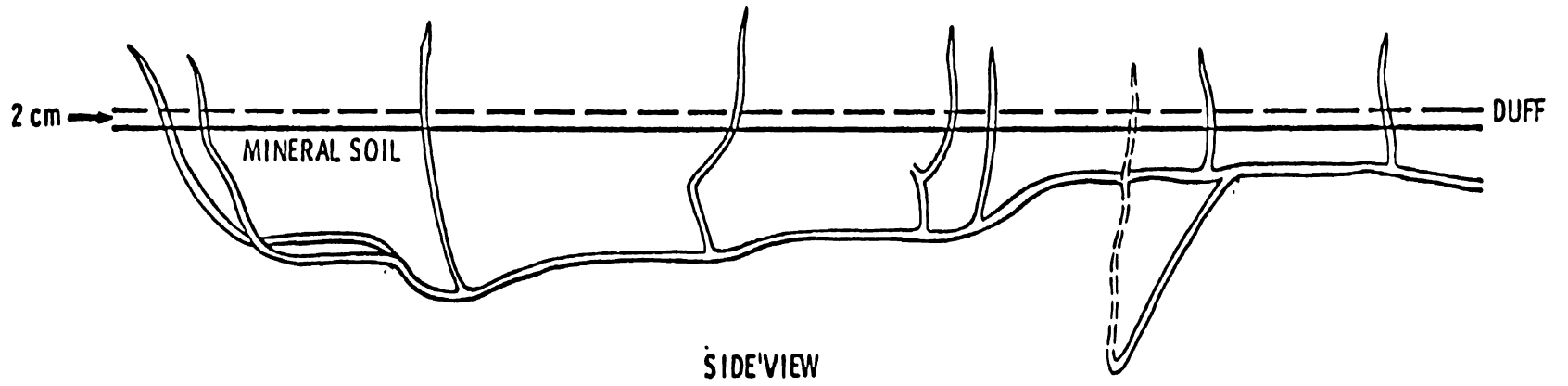
The rhizomes of Oregon grape are bright yellow and somewhat easier to trace through the soil than those of Spiraea or Symphoricarpos. Well-developed plants have rhizomes which may branch quite frequently (figure 24), although the above ground stems in the sample specimens usually remained unbranched and sparse.

Berberis rhizomes can sprout from relatively great depth even without the stimulus of fire. In the Pattee Canyon control ravine, one active rhizome branch originated from 15 cm. below the soil surface and was nearly emergent.

Oregon grape is an important winter browse species in the Swan Valley (Mundinger 1979). In a study of white-tailed deer winter range in Wisconsin, Habeck (1959) hypothesized that the pawing actions by deer could break up the rhizomes of some browse species and actually increase their frequency. Such a frequency increase might be possible for Oregon grape either under browse pressure or under a fire regime.

Most Berberis sampled had the greater fraction of their perennating organs in mineral soil. Two specimens on the Rumble Creek burn control had lesser proportions in mineral soil-18% and 36%. Including all six specimens for which proportions were estimated, the values ranged from 18%-91%

Figure 24. Berberis plant excavated from the Pattee Canyon Control Ravine.



with a mean of 63%. At Pattee Canyon, the overall percentage protected by mineral soil was greater: 57%-96% with a mean of 84.4%.

The depths of Rumble Creek unadjusted control plants was greater across the range of values than those of burn samples. The differences were reduced by adjusting values and at the lower end of the ranges, values are quite similar (figure 25). Pattee Canyon samples showed consistently more shallow depth values in the control ravine, for both adjusted and unadjusted data (figure 26).

Maximum depth means were significantly different for burn and control at the Rumble Creek sites. Control site depths were greater. Plants with a larger proportion of their length in the organic material were seated near the mineral soil surface with some segments below this interface. This was also true of snowberry. Portions of the rhizomes of these plants which are above this mineral soil surface are susceptible to fire. If these sections are killed, the remaining intervening portions below the mineral soil line can survive to form separate plants. Plants were sampled on the Rumble Creek burn which originated from partially burned rhizome fragments. Whether the above scenario was actually responsible for their condition could not be determined.

Figure 25. Berberis percent cumulative frequency graph for Rumble Creek specimens.

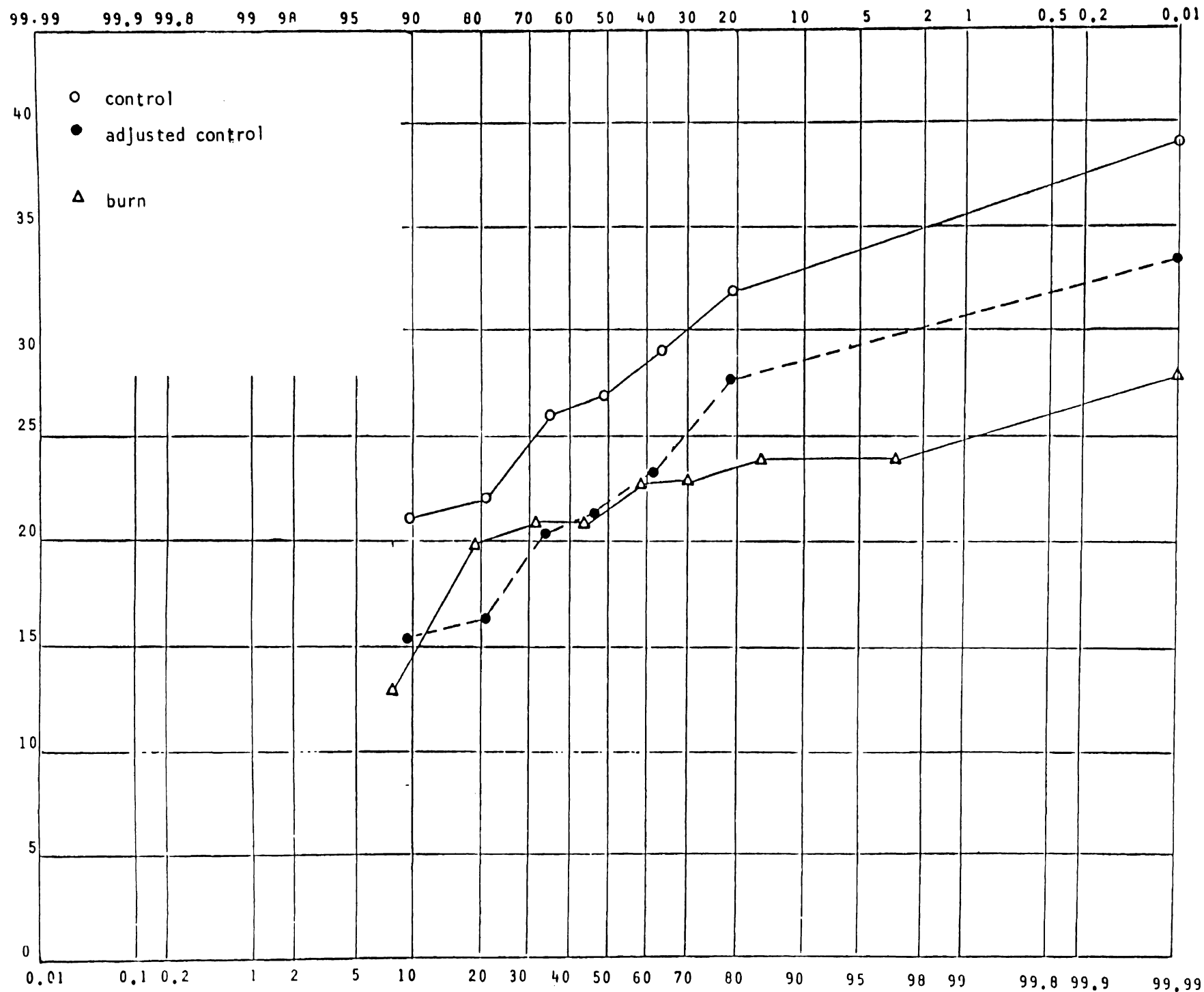
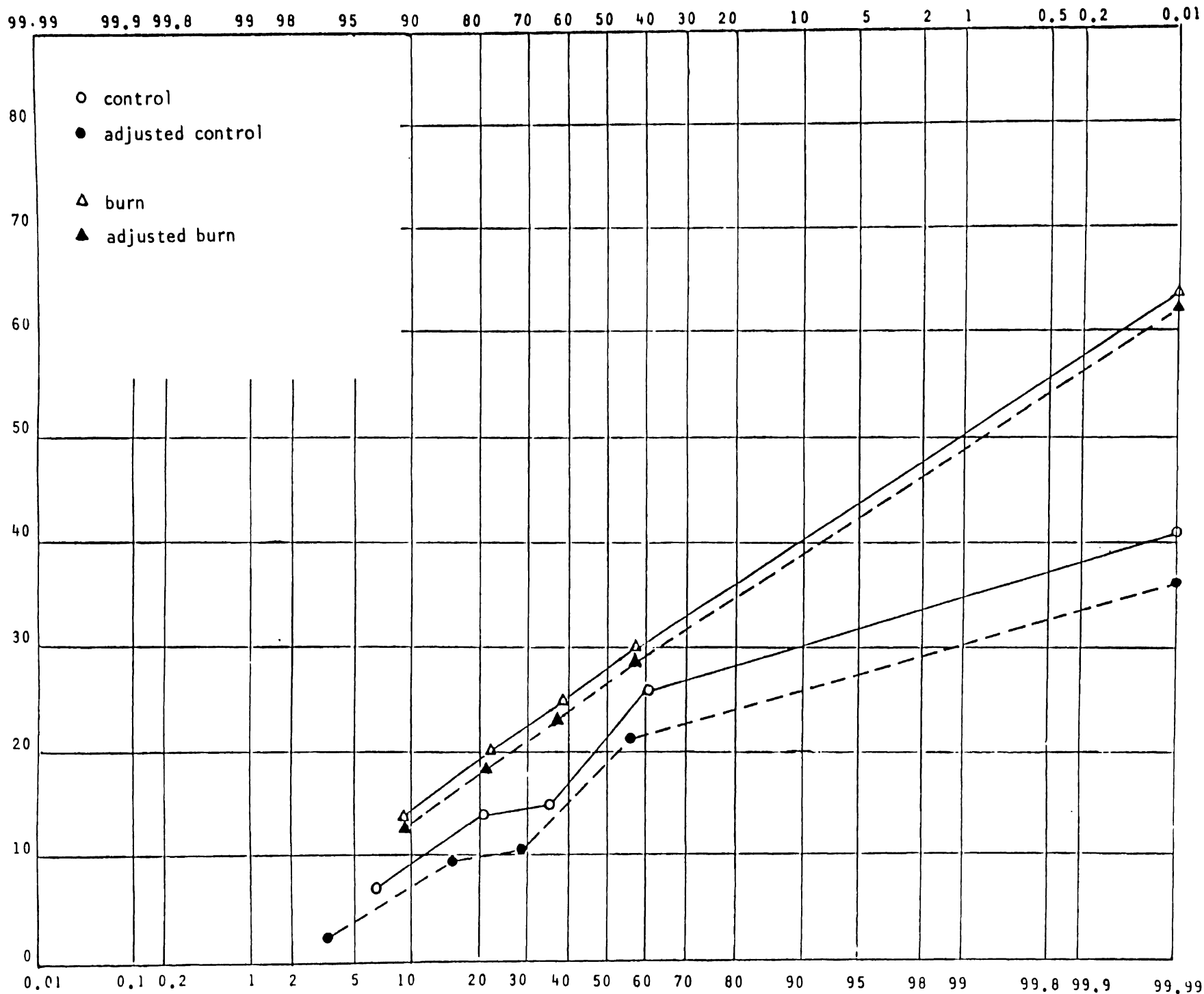


Figure 26. Berberis percent cumulative frequency graph for Pattee Canyon specimens.



General observations made during this study indicated that Berberis has a greater rate of seedling success than other species sampled. Seedlings were seen in both the Pattee Canyon and Rumble Creek control sites. Berberis plants were considered to be of seedling origin if they lacked a rhizome.

Arctostaphylos uva-ursi

The habit and distribution of Arctostaphylos uva-ursi according to Hitchcock and Cronquist (1964) :

a "[p]rostrate shrub with trailing and rooting stems sometimes forming mats several meters broad, the tips often ascending and 5-15 cm. tall ..coastal Calif. n. and more widespread from Oreg., to Alas. to N.M., Ill., the Middle Atlantic states, and Labrador; Eurasia."

Arctostaphylos was sampled on two unburned sites in Pattee Canyon. One was a forested upland site somewhat higher in elevation than the ravines previously described. The other site was located in a stand below the northeast corner of the burn along the Larch Camp Road.

Arctostaphylos is not a highly successful fire endurer (sensu Rowe). Plants excavated in this study had their perennating stems restricted to the organic fraction of the soil. Of 10 plants excavated, only one had a significant portion of its length (60%) in mineral soil. The ranges for

percent residence in mineral soil for the upper site was 0%-60% and that at the lower site 0%-25% with means of 8% and 15.1% respectively.

With the exception of one specimen, all maximum depths for Arctostaphylos fell in the zero to 12 cm. range. In the adjusted distributions on both the upper and lower sites, some values fell below the zero line. These are individuals which would be completely removed by fire if the equivalent of the mean organic material was burned off (figure 27). Log-transformed data indicate a significant difference between the two sites at the .05 alpha level for maximum depth measurements.

McLean (1969) reported that bearberry begins producing roots along its trailing stems after the second year, and that when a portion of this stem is severed from the main plant body "a substantial main root develops" (p122). One specimen in this study originated from a broken stem section 12 cm. long producing a plant 33 cm. in extent. McLean also stated that some researchers have found a "rootcrown" structure from which regeneration might occur. No such organs were observed in the Pattee Canyon plants. Vegetative regeneration is rare, if it occurs at all, after a fire as severe as that in Pattee Canyon. Removing the organic fraction of the soil effectively removes the perennating stems as well (figure 28). Lutz (1956) reported

Figure 27. Arctostaphylos percent cumulative frequency graph for Pattee Canyon specimens.

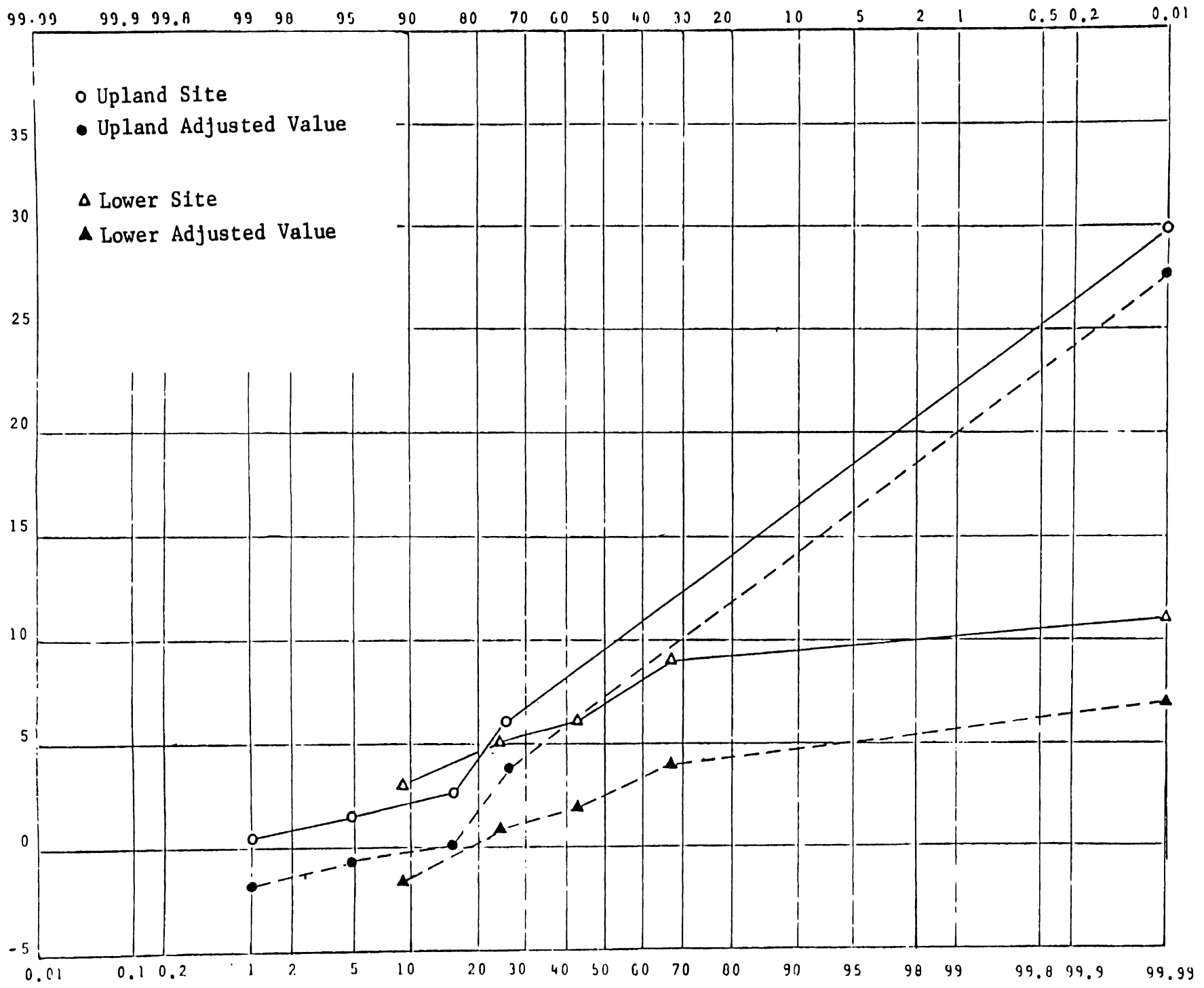
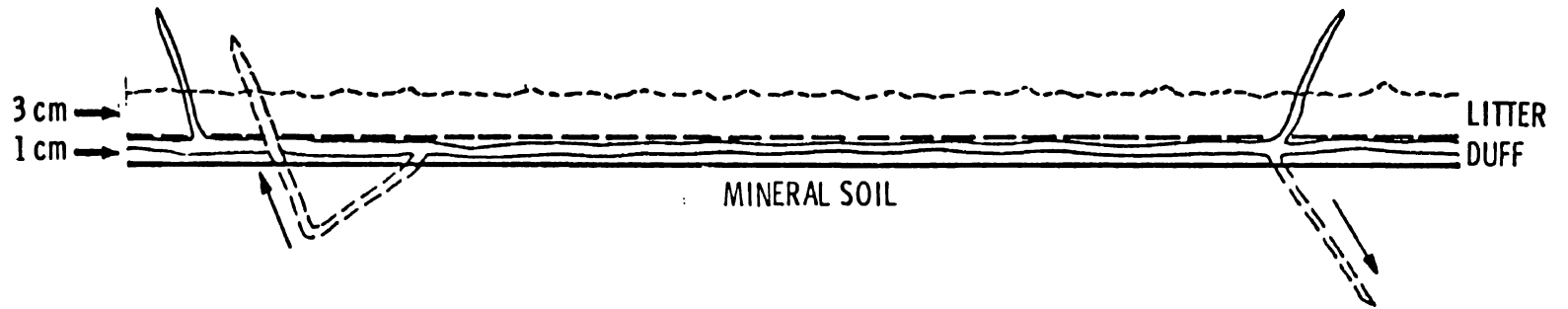
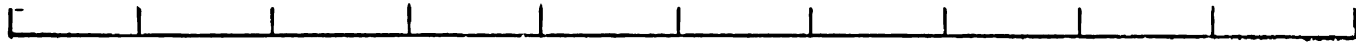


Figure 28. Arctostaphylos plant excavated from the Pattee Canyon Upland Site.



1 BLOCK • 10 cm



that bearberry is capable of regenerating from soil stored seed on burns in Alaska. On the Pattee Canyon burn, such post-fire seedlings were not observed. Arno and Simmerman (1982) note that Arctostaphylos is a successful reinvader of burned sites from unburned areas.

A number of bearberry plants were observed in association with rotting logs or growing over old stumps (figure 29). The moisture regime in this decomposing wood may be conducive to mycorrhizal development (Antibus, 1983, pers. comm.).

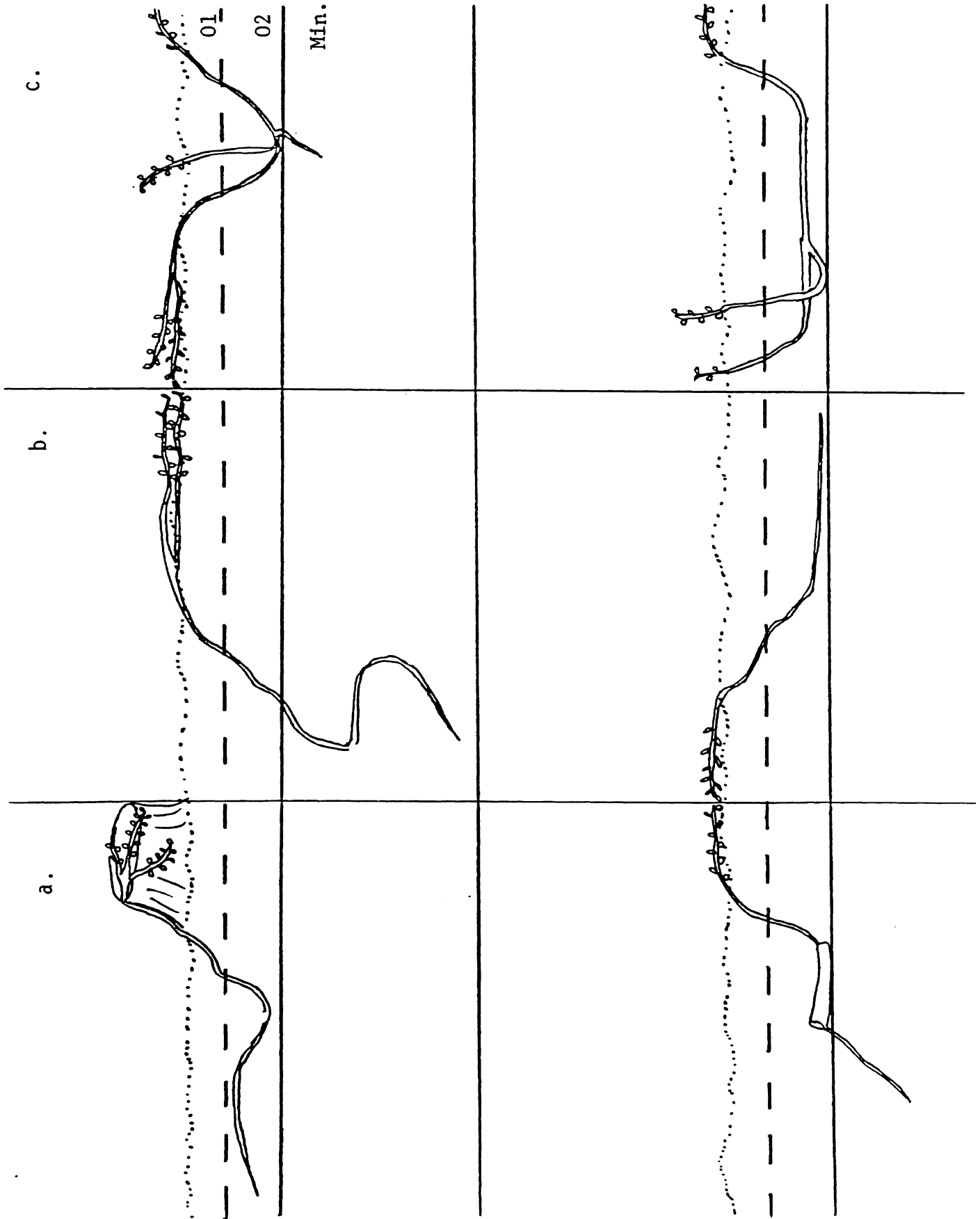
Linnaea borealis

Linnaea borealis was collected on two unburned sites. The Pattee Canyon control ravine and the upland stand where Arctostaphylos was also collected. According to Hitchcock and Cronquist (1964) Linnaea has

"...stems slender but woody, [is] elongate, trailing and creeping,... [and is found in] open or dense woods and brush at various elevations throughout our range; circumpolar, extending s. in America to Calif., Ariz., N.M., S.D., Ind., and W. Va...."

Linnaea is often associated with mesic forest stands that experience a relatively low fire frequency. This is consistent with its habit of growing in well-developed organic material and its apparent lack of any specific fire

Figure 29. Arctostaphylos growth forms - six representative specimens. Plant a. is growing up and over a rotting stump - a common occurrence in Arctostaphylos.

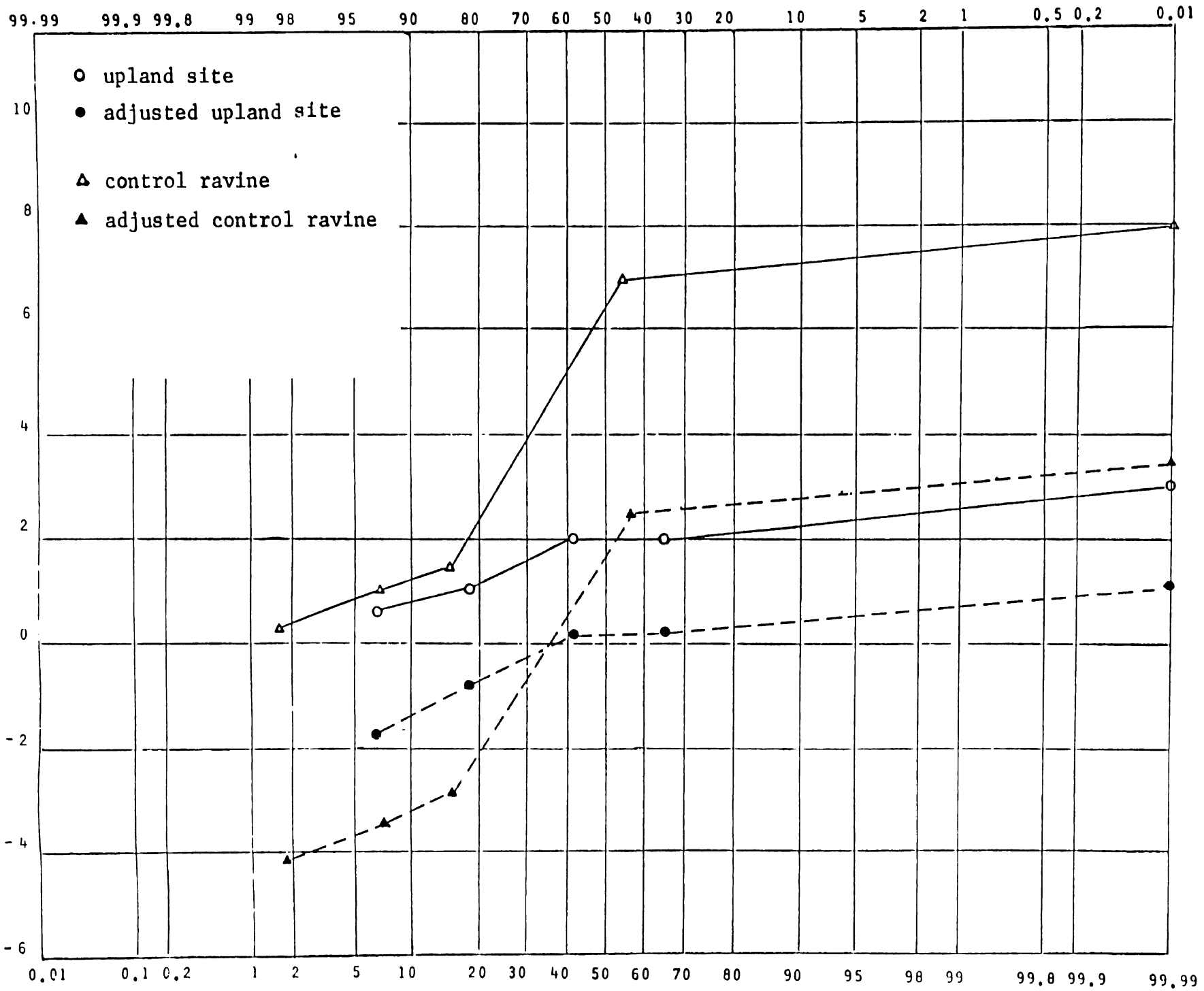


adaptations. McLean (1969) cites Kujala's 1926 finding that some twinflower plants have a sort of "rootcrown" (of undetermined tissue). Lutz (1956) reported Sarvas' (1937) statement that Linnaea is unable to resprout from belowground structures after fire.

All specimens excavated in this study were located in the O1 and O2 fractions of the soil. Plants were: a) rhizomatous- with their horizontal stems under the O1 surface, b) stoloniferous -with the procumbent stems resting on or marginally in the O1, or c) a combination of both. In the Pattee Canyon ravine site, 0-34% of the twinflower stems resided in the O1 fraction with a mean of 25%. In the upland site, 0%-100% of the stems' length was in the O1 with a mean of 36%.

Like Arctostaphylos, when twinflower depth measurements are adjusted , lower range individuals are effectively removed from the site (figure 30). Also like Arctostaphylos, excavated plants and those not sampled but seen grew preferentially in decayed wood. It was possible to identify the location of older decayed logs by the pattern of Linnaea growth. This was particularly true on the upland site.

Figure 30. Linnaea percent cumulative frequency graph for Pattee Canyon specimens.



Xerophyllum tenax

Xerophyllum tenax is a

"...perennial herb with dense clumps of elongate, persistent, wiry grass-like leaves arising from a short thick rhizome, any particular offshoot plant not flowering for several years... [with a] Rhizome 1-2 cm. thick...[growing in] open woods and clearings; B.C. to s. to Calif., e. to the Rocky Mts. from B.C. to Ida. and Mont., from near sea level on the Olympic Peninsula up to over 7000 ft. in the Rocky Mts." (Hitchcock and Cronquist, 1964)

Xerophyllum is a monocot, and thus has a different pattern of growth than the other plants sampled in this study. The meristematic region of beargrass is restricted to the leaf rosette base, rather than being distributed throughout the rhizome.

Beargrass exhibits differential fire response. Daubenmire and Daubenmire (1968) reported that beargrass often recovered well after fire. Arno and Simmerman (1982) noted a post fire and post scarification decrease in four western Montana habitat types. Stickney (1983, pers. comm.) found that on controlled burns at Miller Creek, Montana Xerophyllum survived spring burns in areas where the duff was moister.

The basal leaves of beargrass provide some protection to the meristem if the leaves are moist and the amount of heat actually transferred to the meristem is ameliorated. Under dry conditions, these same leaves can act as an added fuel source and increase the heat delivered to the base of the rosette. At Rumble Creek, surviving plants were restricted to the burn perimeter in places where there was some organic material left.

The beargrass plants excavated were relatively uniform in soil depth. Meristematic regions tended to lie on the O₂-mineral soil interface, or slightly above it (plate 9). The rhizomes themselves were seated in the mineral soil. Since the only part of the rhizome capable of producing new growth is the meristem within the leaf bases, it is the depth of this region that is critical to plant survival. Percentage of the total rhizome residing in mineral soil ranged from 0%-100% with a mean of 73%.

The range of maximum depth values differed between sites. The minimum was shallower and the maximum was deeper on the burn. The overall pattern observed was for burn-site plants to lie deeper in the soil (figure 31).

Persistent leaf-base scars gave beargrass rhizomes a barred appearance. Roots, except for the cluster immediately below the current year's growth, looked dry and

Plate 9. Xerophyllum plants excavated from the Rumble Creek Burn.

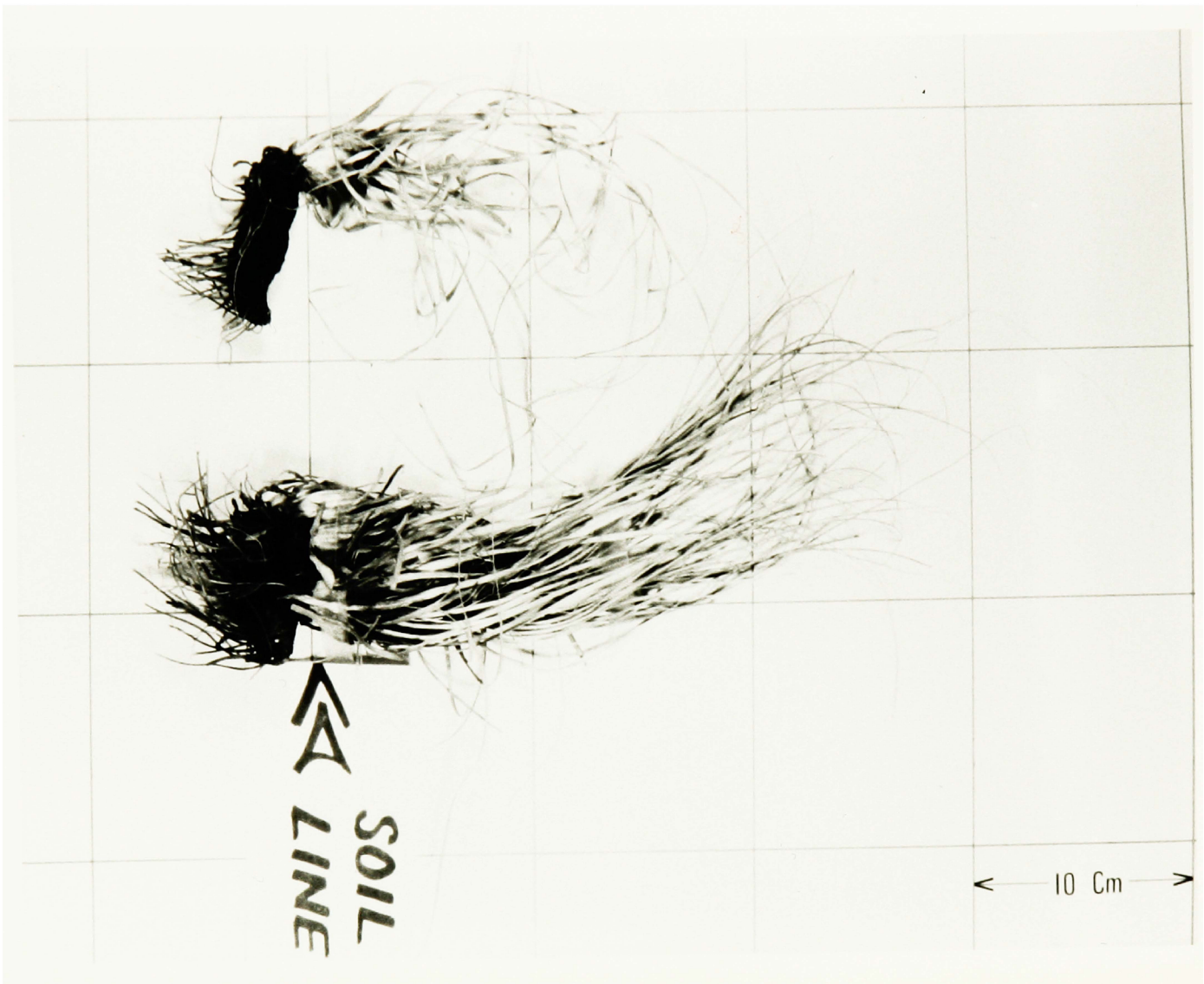
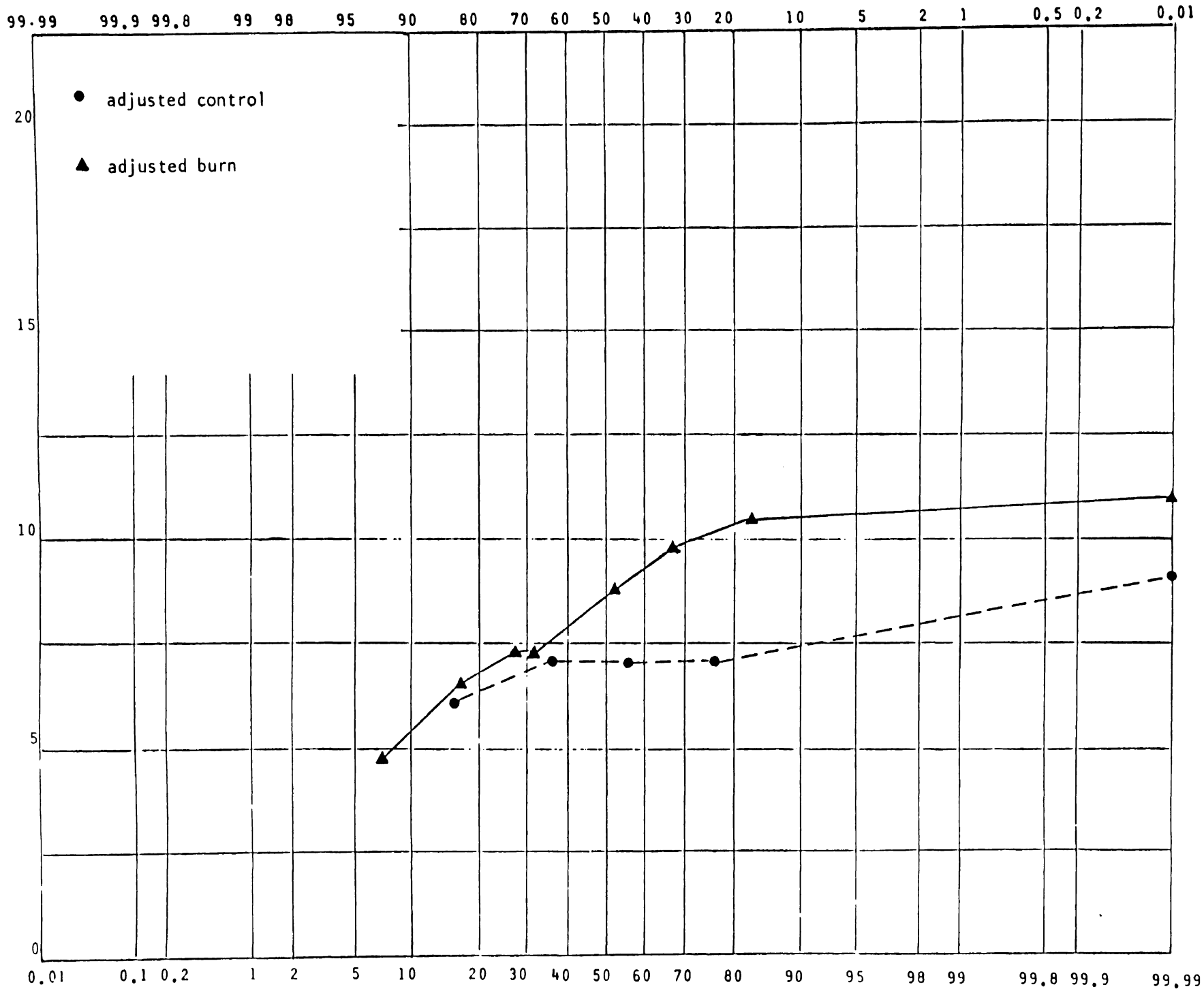


Figure 31. Xerophyllum percent cumulative frequency graph for Rumble Creek specimens.



inactive. These anchor the plant securely in the soil—a fact discovered in my attempts to excavate them. The presumed active roots had relatively thick and moist tissue with a somewhat wrinkled appearance—possibly like the contractile roots known from other liliaceous plants (Esau, 1977)

Apparently, some Xerophyllum plants are seated above the mineral soil line. The specimen in plate 10 comes from the Sundance Fire, a severe wildfire on the Kaniksu Forest of northern Idaho in 1967 (Stickney, pers. comm., 1983). The fire burned off all organic material in many instances. The free-standing rhizomes illustrated here were probably seated in the organic horizons.

Xerophyllum can grow in extensive clumps or as individual rhizomes. According to Holtum (1955), in his discussion of monocot growth patterns, branch-producing buds are formed at nodes, and each of these is capable of its own horizontal growth. With this pattern, a plant with an indefinite lifespan is produced, although each stem generated lives a limited time.

I think all but one of the plants excavated on the burn site was a fire-survivor. The one possible exception was a specimen which had well-developed roots but no rhizome.

Plate 10. Xerophyllum rhizome exposed by the Sundance Fire of 1967.
(P. Stickney photo)



Chapter 7

Discussion

Since this study was partially designed to be an exploration of methods, a criticism of the techniques is appropriate here.

The tools used in this study were basic—a trowel and a surveying pin for loosening dirt. I used a shovel when excavating larger shrubs like serviceberry, but the small and easily broken rhizomes of spirea, snowberry and Oregon grape were too delicate for such a large tool, particularly when the rhizomes were in rocky soil.

After the field season, main rhizome measurements and maximum depth measurements were evaluated to assess which was the better predictor of potential plant survival. With the exception of beargrass, all species examined were capable of producing buds on areas deeper than that measured by the definition "main rhizome". Also, many specimens did not have a sharply defined point where the rhizome became horizontal, so this measurement was somewhat arbitrary. As a result, the maximum depth measurement was chosen as the variable for comparison. This measure is inherently a liberal one since it is not known whether the lowest portion of the rhizome of all plants is capable of regeneration. As

was indicated earlier, making accurate organic horizon measurements was difficult. Maximum depth measurements from which the mean depths of the O1 and O2 horizons have been subtracted have been presented as a suggested method of compensating for duff variability on a site. A comparison of mineral soil protection on burned and unburned sites is provided by the recalculated depth values. These recalculated values are an indirect way of estimating mineral soil protection. Ideally, a trench parallel to the rhizome should be dug, and the soil above the rhizome in the exposed face measured. In the excavations I performed, this technique was impractical. Rhizomes grow in unpredictable directions. Digging a trench parallel to the looping path they take through the soil is extremely difficult.

Excavating shrubs requires removing substantial quantities of soil, especially if the species are large (e.g. ninebark or serviceberry). Maximum depth measurements were taken from the bottom of a pit to the nearest surface of undisturbed soil. This undisturbed area was sometimes well over 30 cm horizontal distance from the rhizome. My assumption was that the relative quantities of organic and mineral soil may well vary over that distance. This assumption led me to use mean soil fractions to estimate mineral soil protection. Future investigators may or may not find this to be the optimal way to make such

estimates. Post-excavation O1 and O2 soil measurements can be made at a point close to the deepest portion of the rhizome. Care should be taken to avoid pockets of organic material unless this accumulation represents the probable quantity over the rhizome. My soil measurements were taken before excavation at a set point (the stem base) in order to avoid possible bias. This was probably an unnecessary precaution. Accuracy might be improved if some selection of measurement points is made.

The percent cumulative frequency graphs provide a means for comparing the depth distributions of populations on burned and unburned sites. Between species comparisons are also possible. Use of these graphs permits some degree of prediction of population depth distribution. If at the fiftieth percentile, a depth of 20 cm. is interpolated, one can expect half the population to have maximum rhizome depths greater than 20 cm. and half less than this.

The unique morphologies of plants should be considered in any further sampling or prediction. Xerophyllum, with its intercalary meristem, is more susceptible to fire damage than its maximum depth measurements indicate. Conversely, Amelanchier may have a large proportion of its rhizome mass in the O horizons, yet its woodiness and its ability to sprout from areas below the rootcrown convey to it a degree of immunity to fire injury.

The species excavated in this study may be ranked by their fire-survival characteristics. I propose the following order:

Lowest	<u>Linnaea</u>
	<u>Arctostaphylos</u>
	<u>Xerophyllum</u>
	<u>Symphoricarpos</u> and <u>Berberis</u>
	<u>Amelanchier</u>
Highest	<u>Spiraea</u> and <u>Physocarpus</u>

This ranking is based on my observations of the morphology and soil placement of these species, added to their fire-response as reported by other investigators (Stickney, 1980; Crane, 1983). The high and low ranks are better defined than are those in between. Symphoricarpos, Berberis, and Spiraea have the same life-form and have substantial portions of their rhizomes in mineral soil. Stickney (1980) reported a marked post-fire increase of Spiraea, especially when compared with the other two species. This pushed Spiraea into a higher fire-survival category.

Amelanchier has comparatively massive rhizomes and generally survives fire well. Its placement at a higher fire-survival rank than Symphoricarpos and Berberis is tentative. It appears to sprout most prolifically from the

top of its "rootcrown", making it potentially more vulnerable to fire damage than Physocarpus.

Further work is needed to make a study of this sort truly predictive. These results showed a relatively high degree of variability in measurements. Variability may reflect the true nature of the populations sampled, or be merely an artifact of the necessarily small sample size.

The importance substrate has on the observed variability is intuitively obvious. Plants whose rhizomes encounter rocks or other obstacles will develop a different belowground and aboveground pattern of growth than those whose spread has not been impeded. These physical factors probably have more impact on the plant's morphological features than does habitat type. Hemmer (1975) noted the role substrate played in the production of different growth forms in serviceberry. A thorough survey of other species across a series of substrates should be made to determine the relative importance of such exogenous factors to a plant's growth form in comparison to endogenous genetic influences.

Shrubs have evolved a growth habit in which only a partial apical dominance is expressed, giving them a multistemmed form. There are hormonal and environmental interactions which permit several stems to arise together,

while leaving other buds along the rhizome repressed. In this study, most regenerating stems occurred on portions of the rhizome nearest the soil surface. Light may be an important causal factor in stem developmental processes (Schier, 1983).

Fire frequency, along with fire severity and lifeform influences the survival of shrubs. Sites where a heavy organic mantle has accumulated are sites on which shrubs are susceptible to fire damage for two reasons:

- 1) The added fuel is likely to produce a fire of greater severity

- 2) Shrubs which establish from seedlings, or new rhizome branches which develop during the fire-free interval are likely to do so above the mineral soil line.

Some evidence of this latter phenomenon was evident on the control sites at Rumble Creek. On the Rumble Creek control, there was a tendency for plants to establish in decayed wood, with either all or a large proportion of their perennating organs in the O1 and O2 horizons. The current distribution of shrubs on the burn at Rumble Creek is a relative concentration of individuals on the perimeter. Very few shrubs have regenerated from rhizomes in the

central portion of the burn where conditions were most severe. If the preburn populations had a soil distribution like that of the control plants, the current situation may be accounted for. The fire burned down to the mineral soil in many places around the perimeter, but the heat pulse delivered to the perennating parts seated at relatively shallow depths in the mineral fraction would be less than that at the center of the burn. The potential role of fire frequency on shrub survival should be further examined.

Chapter 8

Summary

A suite of eight understory shrubs was excavated and examined for their fire-surviving potential. They were: Arctostaphylos uva-ursi, Amelanchier alnifolia, Berberis repens, Linnaea borealis, Physocarpus malvaceus, Spiraea betulifolia, Symphoricarpos albus, and Xerophyllum tenax.

The excavations were conducted on paired burned and unburned stands in the Swan Valley and Pattee Canyon, both in western Montana. The vegetation of the Swan Valley site was classified as a Pseudotsuga menziesii/Symphoricarpos albus habitat type. Vegetation on the Pattee Canyon site was in the Pseudotsuga menziesii/Physocarpus malvaceus habitat type, Physocarpus malvaceus phase (habitat types according to Pfister, et al., 1977).

The perennating organs of all species excavated were rhizomes rather than roots. Measurements made on these rhizomes included their maximum length, depth, and diameter, as well as the depth of their main rhizome mass and percent residence in mineral soil. Of these measurements, maximum depth was chosen as the best predictor of potential plant survival after fire.

No significant difference was found between burned and unburned plots for most measurements at an alpha level of .05. This lack of difference may reflect the nature of these populations, or be an artifact of the relatively small sample size. Sampling was limited in this study by the amount of time required to carefully excavate each plant.

Maximum depths were graphed as percent cumulative frequencies. With these graphs, the proportion of plants with rhizomes at a specified depth can be interpolated, and different sites or species compared.

Results indicate that morphology, as well as rhizome depth are important for estimates of potential fire survival. Soil texture may strongly influence the latter character.

Based on the observations of this study, the following fire-survival ranking is suggested, from lowest potential for survival to the highest:

Lowest	<u>Linnaea borealis</u>
	<u>Arctostaphylos uva-ursi</u>
	<u>Xerophyllum tenax</u>
	<u>Berberis repens</u> and <u>Symphoricarpos albus</u>
	<u>Amelanchier alnifolia</u>
Highest	<u>Spiraea betulifolia</u> and <u>Physocarpus malvaceus</u>

The length of the fire-free interval may also affect the potential fire-survival of these plants. A long period without fire may permit an accumulation of organic material on the mineral soil surface. Plants which establish in an O1 or O2 (litter or duff) horizon will be susceptible to burning when fire occurs again.

LITERATURE CITED

- Adams, A.B., and V.D. Adams.1983.Patterns of plant recovery on the debris avalanche from Mt. St. Helens. presented at the 53rd annual Meeting of the Northwest Scientific Assoc. March 24-26,1983, Olympia, Washington
- Alden,W.C.1953.Physiography and glacial geology of western Montana and adjacent areas. U.S. Geol. Survey Prof. Pap. no. 231. 200 pp.
- Antibus, R.1983.Mycologist, Dept. of Botany .University of Montana Missoula, Montana.
- Antos, J.A.1977.Grand fir (Abies grandis (Dougl.)Forbes) forests of the Swan Valley, Montana. M.A. thesis. University of Montana. Missoula, Montana. 220 pp
- Bamber, R.K. and K.J. Mullette.1978.Studies of the lignotubers of Eucalyptus gummifera (Gaertn. and Hochr.) II anatomy. Aust. J. Bot. 26:15-22.
- Belehradek, J.1935. Temperature and living matter. Protoplasma Monog. 8. 277 pp
- Benson, L.1951.Plant Classification. D. C. Heath and Co. 688 pp.
- Cattelino, P. U. ,I. R . Noble, R. O. Slatyer and S .R. Kessell.1979. Predicting the multiple pathways of plant succession. Environ. Mgt. 3:41-50.
- Chapman, R. R. and G. E. Crow.1981.Application of Raunkiaer's lifeform system to plant species survival after fire. Bull. Torr. Bot. Club. 108(4):472-478.
- Crane, M.F.,J.R. Habeck, and W.C. Fischer.1983.Early postfire revegetation in a western Montana Douglas-fir forest. USDA For. Serv. Resch. Pap. INT-319 Intermountain Forest and Range Expt. Sta. Ogden, Ut. 29 pp.
- Daubenmire R. and J. Daubenmire.1968. Forest vegetation of eastern Washington and northern Idaho. Wash. Agr. Exp. Sta. Tech. Bull. 60. Coll. of Agric. Wash. State Univ., Pullman, Wash. 104 pp.

- Dutton, B.1982.Soil Scientist. U.S. Soil Cons. Serv. Missoula, Montana.
- Flinn, M.A.1980.Heat penetration and early postfire regeneration of some understory species in the Acadian Forest. Ph.D. diss., Univ. of New Brunswick. 86 pp.
- Flinn, M.A. and J. Pringle.1983.Heat Tolerance of Rhizomes of Several Understory Species. Can. J. Bot. 61(2):452-457.
- Flinn, M.A. and R. Wein.1977.Depth of underground plant organs and theoretical survival after fire. Can. J. Bot. 55:2550-2554.
- Gardener, C.J.1980. Tolerance of perennating Stylosanthes plants to fire. Aust. J. Exp. Agric. Husb. 20:587-593.
- Gill, A.M.1981.Adaptive responses of Australian vascular plant species to fire. IN Fire and the Australian Biota. A.M. Gill, H. Groves, and I.R. Noble eds. Aust. Acad. of Sci., Canberra, Australia. 582 pp.
- Grime, J.P.1979.Plant Strategies and Vegetation Processes. John Wiley and Sons, Ltd. New York. 222 pp.
- Habeck, J.R.1959.A vegetational study of the central Wisconsin winter deer range. J. of Wildlife Mgt. 23(3):273-278.
- Habeck, J.R. and R. Mutch.1973.Fire-dependent forests in the northern Rocky Mountains. Quat. Resch. 3:408-424.
- Hare, R.C.1961.Heat effects on living plants. Occasional Pap. no. 183. So. For. Expt. Sta. USDA. 32pp.
- Hayden, A.1919.The ecologic subterranean anatomy of some plants of a province in central Iowa. Am. J. Bot. 6:87-105.
- Hemmer, D.1975.Serviceberry:ecology, distribution and relationships to big game. M.A. thesis. Univ. of Montana, Missoula, Montana.
- Heywood, F.1938.Soil temperatures during forest fires in the longleaf pine region. J.For. 36:478-491.

- Hitchcock, C.L., A. Cronquist, M. Ownbey, and J.W. Thompson. 1964. Vascular Plants of the Pacific Northwest. Part 1. University of Washington Press. Seattle, Wa. 914 pp
- Hitchcock, C.L., A. Cronquist, M. Ownbey, and J.W. Thompson. 1964. Vascular Plants of the Pacific Northwest. Part 2. University of Washington Press. Seattle, Wa. 597 pp
- Hitchcock, C.L., A. Cronquist, M. Ownbey, and J.W. Thompson. 1964. Vascular Plants of the Pacific Northwest. Part 3. University of Washington Press. Seattle, Wa. 614 pp
- Hitchcock, C.L., A. Cronquist, M. Ownbey, and J.W. Thompson. 1964. Vascular Plants of the Pacific Northwest. Part 4. University of Washington Press. Seattle, Wa. 510 pp
- Holch, A.E. 1941. Root habits of certain plants of the foothills and alpine belts of Rocky Mountain National Park. Ecol. Monog. 11(2):327-345.
- Holtum, R.E. 1955. Growth habits of monocotyledons-variations on a theme. Phytomorphology 5:399-413.
- Horton, K.W. and E.J. Hopkins. 1965. Influence of fire on aspen suckering. Dept. of For. Pub. No. 1095. For. Res. Br. Contrib. No. 664. Dept. of For., Canada. 19 pp.
- Johns, W.M. 1964. Geologic investigations in the Kootenai-Flathead Area, Northwest Montana: No. 6, southeastern Flathead county and northeastern Lake County, Montana. Bur. of Mines and Geol. Bull. 42 60 pp.
- Johns, W.M. 1970. Geology and mineral deposits of Lincoln and Flathead Counties, Montana. Montana Bur. of Mines and Geol. Bull. 79. 182 pp.
- Jones, M.B. and H.M. Laude 1960. The relationships between sprouting in chamise and the physiological condition of the plant. J. Range Mgt. 13:210-214.
- Keeley, J.E. 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. Ecol. 58(4):820-829.

- Keeley, J.E. 1981. Reproductive cycles and fire regimes. IN Fire Regimes and Ecosystem Properties., Proc.; H. Mooney, T. Bonnicksen, N. Christensen, J. Lotan, W. Reiners Tech. Coordinators. USDA For. Serv. Gen. Tech. Rept. WO-26 pp. 231-277.
- Keller, M.C. 1980. Post-fire recovery within ravine forest communities of Pattee Canyon, Missoula Montana. M.A. thesis. Univ. of Montana. Missoula, Montana. 136 pp.
- Kender, W.A. 1967. Rhizome development in the lowbush blueberry as influenced by temperature and photoperiod. Am. Hort. Sci. 90:144-148.
- Komarek, E.V. 1964. The natural history of lightning. Proc. Tall Timbers Fire Ecol. Conf. 3:139-183.
- Kormanik, P.P. and C.L. Brown. 1967. Rootbuds and the development of root suckers in sweet gum. For. Sci. 13:338-348.
- Kujala, V. 1926. Einfluss von Waldbränden auf die Waldvegetation in Nordfinland. Metsatieteellise Koelaitokoen Julkaiseja 10:1-36.
- Kummerow, J. and R. Mangan. 1981. Root systems in Quercus dumosa Nutt. dominated chaparral in southern California. Acta Oecologia Oecol. Plant. 2(16):177-188.
- Leakey, R.R.B. and R.J. Chancellor. 1977a. Regeneration from rhizome fragments of Agropyron repens. I. The seasonality of shoot growth and rhizome reserves in single-node fragments. Ann. Appl. Biol. 87:423-431.
- Leakey, R.R.B. and R.J. Chancellor. 1977b. Regeneration from rhizome fragments of Agropyron repens II. The breaking of late spring dormancy and the influence of chilling and node position on growth from single-node fragments. Ann. Appl. Biol. 87:433-441
- Leakey, R.R.B. and R.J. Chancellor. 1978. Regeneration from rhizome fragments of Agropyron repens (L.) Beauv. III. Effects of nitrogen and temperature on the development of dominance amongst shoots on multi-node fragments. Ann. Bot. 42:197-204.

- Leege, T.A. and W.D. Hickey. 1971. Sprouting of northern Idaho shrubs after prescribed burning. *J. Wildlife Mgt.* 35(3):508-515.
- Lonner, T.N. 1972. Age distributions and some relationships of key browse plants on big game ranges in Montana. Montana Fish and Game Dept. Job Compl. Rept Proj. W-120-R-2-3. 79 pp.
- Lutz, H.J. 1956. Ecological effects of forest fires in the interior of Alaska. USDA Agric. Tech. Bull. No. 1133. pp. 1-121.
- Lyon, L.J. and P.F. Stickney. 1976. Early vegetal succession following large Rocky Mountain wildfires. Proc. Tall Timbers Fire Ecol. Conf. No. 14, and The Intermountain Fire Research Council, Fire and Land Management Symposium. pp. 355-375.
- Maini, J.S. and K.W. Horton. 1966a. Vegetative propagation of Populus spp. I. Influence of temperature on the formation and initial growth of aspen suckers. *Can. J. Bot.* 44:1183-1189.
- McLean, A. 1969. Fire resistance of forest species as influenced by root systems. *J. Range Mgt.* 22:120-122.
- Meyer, B.S., D.B. Anderson, R.H. Bohning and D.G. Fratianne. 1973. Introduction to Plant Physiology. D. Van Nostrand Co. N.Y., Cincinnati, Toronto, London, Melbourne. 565 pp.
- Miller, M. 1976. Shrub sprouting response to fire in a Douglasfir/western larch ecosystem. M.A. thesis. Univ. of Montana. Missoula, Montana. 124 pp.
- Miller, M. 1977. Response of blue huckleberry to prescribed fires in a western Montana larch-fir forest. USDA For. Serv., Intermountain Forest and Range Experiment Station. Ogden, Ut. Res. Pap. INT-188. 33 pp
- Minore, D. 1975. Observations on the Rhizomes and Roots of Vaccinium membranaceum. USDA For. Ser., Pacific Northwest Forest and Range Experiment Station. Portland, Oregon. Res. Note PNW-261. 5pp.

- Mohamed, T.F. and C.H. Gimingham. 1970. The morphology of vegetative regeneration in Calluna vulgaris. New Phytol. 69:743-750.
- Montana Dept. of Natural Resources and Conservation, For. Div. 1978. Swan River State Forest Management Plan. Final E.I.S. Helena, Montana. 107 pp.
- Mount, A.B. 1969. Eucalypt ecology related to fire. Proc. Tall Timbers Fire Ecol. Conf. 9:109-118.
- Mueller, I.M. 1941. An experimental study of rhizomes of certain prairie plants. Ecol. Monog. 14:165-188.
- Mundinger, J.G. 1979. Population ecology and habitat relationships of white-tailed deer in coniferous forests of northwestern Montana. IN Montana Deer Studies, Job Prog. Rept. Montana Dept. of Fish and Game. Helena, Montana. Fed. Aid Proj. W-120-R-10. pp. 5-65.
- Naveh, Z. 1975. The evolutionary significance of fire in the Mediterranean Region. Vegetatio 29(3):199-208.
- Noble, I.R. and R.O. Slatyer. 1977. Post-fire succession of plants in Mediterranean ecosystems. IN Proc. Symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems. USDA For. Serv. Gen. Tech. Rept.. WO-3:27-36.
- Noste, N.V. 1981. Progress Report on using fire to improve wildlife habitat: The O'Keefe Creek prescribed fire study. prepared for the Fire in Multiple Use Management Research Development and Application Program. Intermountain Forest and Range Experiment Station. Northern Forest Fire Lab. Missoula, Montana.
- Noste, N.V. 1982. Research Forester, US For. Serv. Northern Forest Fire Lab. Missoula, Montana.
- Pelton, J. 1953. Studies on the life history of Symphoricarpos occidentalis Hook. in Minnesota. Ecol Monog. 23:17-39.
- Pfister, R.D., B.L. Kovalchik, S.F. Arno, R.C. Presby. 1977. Forest habitat types of western Montana. USDA For. Serv. Gen. Tech. Rept. INT-34. Intermountain For. and Range Expt. Sta. Ogden, Ut. 174 pp.

- Purdie, R. W. 1977. Early stages of regeneration after burning of dry sclerophyll vegetation. I. Regeneration of the understory by vegetative means. *Aust. J. Bot.* 25:21-34.
- Purdie, R.W. and R.O. Slatyer. 1976. Vegetation succession in sclerophyll woodland communities in south-eastern Australia. *Aust. J. Ecol.* 1:223-236.
- Raju, M.V.S., R.T. Coupland, T.A. Steeves. 1966. On the occurrence of root buds on perennial plants in Saskatchewan. *Can. J. Bot.* 44:33-47.
- Raunkiaer, C. 1934. The Lifeforms of Plants and Statistical Plant Geography. Clarendon Press, Oxford. 632 pp.
- Rowe, J.S. 1979. Concepts of fire effects on plant individuals and species. paper read at Symposium on Fire in Northern Circumpolar Ecosystems. Fredericton, New Brunswick. Oct. 22-24.
- Rundel, P.W. 1981. Fire as an ecological factor. IN Physiological Plant Ecology I: Responses to the Physical Environment. pp. 501-528. Springer-Verlag. Berlin, Heidelberg, New York.
- Salisbury, F.B. and C.W. Ross. 1978. Plant Physiology, second ed. Wadsworth Pub. Co, Inc. Belmont, Ca. 436 pp.
- Sarvas, R. 1937. [Beobachtungen über die Entwicklung der Vegetation auf den Waldbrandflächen Nord-Finnlands] Havaintoja Kasvillisuuden Kehetykkoesta Pohjois-Suomen Kuloaloilla. *Silva Fenn.* 44, 64 pp.
- Schier, G.A. and R.B. Campbell. 1976. Differences among Populus species in ability to form adventitious shoots and roots. *Can J. For. Res.* 6:253-261.
- Schier, G.A. 1983. Vegetative regeneration of Gambel oak and chokecherry from excised rhizomes. *For. Sci.* 29(3):499-502
- Schuler, J.H. 1968. The composition and distribution of Douglas-fir forest communities in the Pattee Canyon area, Missoula, Montana. M.A. thesis. Univ. of Montana. Missoula, Montana. 84 pp.

- Shearer, R.C.1975.Seedbed characteristics in western larch forests after prescribed burning. USDA For. Serv. Resch. Pap. INT-167 Intermountain For. and Range Expt. Sta. Ogden, Ut. 26 pp
- Siegler, E.A. and J.J. Bowman.1939.Anatomical studies of root and shoot primordia in 1-year apple roots. J. of Agric. Resch. 58:795-803.
- Sokal, R.R. and J.F. Rohlf.1981.Biometry, second ed. W.H. Freeman and Co. San Francisco. 859 pp.
- Stickney, P.F.1980.Database for post-fire succession, first 6 to 9 years, in Montana larch-fir forests. Gen. Tech. Rept. INT-62. Intermountain For. and Range Expt. Sta. Ogden, Ut.
- Stickney, P.F.1983. Plant Ecologist. USDA For. Serv. Forestry Sciences Lab. U. of Montana campus. Missoula, Montana.
- van der Valk, A.G.1981. Succession in wetlands: a Gleasonian approach. Ecol. 62(3):688-696.
- Vogel, R.J.1971. Fire and the northern Wisconsin pine barrens. Proc. Ann. Tall Timbers Fire Ecol. Conf. 10:175-209.
- Weaver, J.E. and F.E. Clements.1938.Plant Ecology ed. 2. McGraw Hill Inc. 601 pp.
- Wellner, C.A.1970.Fire history in the northern Rocky Mountains. IN The role of fire in the intermountain west. Symp. Proc. Intermountain Fire Research Council and School of Forestry. Univ. of Montana. Missoula, Montana. pp. 42-64.
- Willard, E.E.1971. Some factors involved in activation of sprouting in little rabbitbrush and snowberry on summer range. Ph.D. diss. Utah State Univ. Logan, Utah 145 pp.

APPENDIX

MEASUREMENTS OF ORGANIC SOIL HORIZONS

Location	Soil Horizon	Mean	95% Confidence Interval
Pattee Canyon Burn	01	1.6 cm	± 3.4 cm
	02	0.2 cm	± 0.7 cm
Pattee Canyon Control Ravine	01	2.9 cm	± 3.3 cm
	02	1.5 cm	± 1.7 cm
Pattee Canyon Upland Site	01	1.2 cm	± 1.4 cm
	02	1.2 cm	± 2.5 cm
Pattee Canyon Lower Site	01	3.2 cm	± 2.1 cm
	02	1.0 cm	± 1.2 cm
Rumble Creek Burn	01	0.1 cm	± 0.2 cm
	02	0.5 cm	± 0.8 cm
Rumble Creek Control	01	2.2 cm	± 3.4 cm
	02	3.4 cm	± 4.8 cm

SPECIES: Amelanchier alnifolia

SAMPLE AREA: Pattee Canyon

SAMPLE SIZE: burn = 4 control = 4

Measurement (cm)	Site	Range	Mean linear(log)	Std. Dev. linear(log)
Maximum depth	burn	27-50	39.0(37.5)	12.1(1.3)
	control	18-76	48.2(42.7)	24.0(1.8)
Main rhizome depth	burn	6-49	15.5(6.4)	22.4(4.9)
	control	2-26	13.7(9.5)	10.4(3.1)
Horizontal extent	burn	24- 61	53.7(47.9)	28.5(1.7)
	control	22-242	105.0(74.8)	95.7(2.6)
Maximum diameter	burn	8-24	15.5(13.8)	8.1(1.7)
	control	3.5-15	10.3(8.9)	5.6(1.9)
Number of stems	burn	2-40	14.2(8.1)	17.4(3.4)
	control	2- 5	3.7(3.5)	1.5(1.5)
Number of clumps	burn	1-3	1.7(1.5)	0.9(1.7)
	control	1-2	1.2(1.2)	0.5(1.4)
Tallest stem	burn	60-180	137.0(126.2)	54.0(1.6)
	control	205-458	310.5(297.6)	106.8(1.4)

SPECIES: Arctostaphylos uva-ursi

SAMPLE AREA: Pattee Canyon

SAMPLE SIZE: upland = 5 lower slope = 5

Measurement (cm)	Site	Range	Mean linear(log)	Std. Dev. linear(log)
Maximum depth	upland	0.5-30	8.1(3.2)	12.4(4.7)
	lower	3-11	6.6(6.0)	3.0(1.6)
Main rhizome depth	upland	0.5-2.5	1.1(0.9)	0.8(2.0)
	lower	3-7	4.1(7.4)	1.9(4.5)
Horizontal extent	upland	30-288	174.4(116.8)	129.7(3.1)
	lower	33-290	138.6(107.8)	102.0(2.3)
Maximum diameter	upland	0.5-0.9	2.2(1.1)	3.5(3.2)
	lower	0.4-8	0.5(0.5)	0.2(1.5)
Number of stems	upland	1- 6	2.4(1.9)	2.0(2.1)
	lower	1-20	5.2(2.4)	8.2(3.4)
Number of clumps	upland	—	—	—
	lower	—	—	—
Above ground length	upland	17-86	47.2(39.9)	27.9(2.0)
	lower	9-25	16.8(16.0)	5.7(1.4)

SPECIES: Berberis repens

SAMPLE AREA: Pattee Canyon

SAMPLE SIZE: burn = 5 control = 5

Measurement (cm)	Site	Range	Mean linear(log)	Std. Dev. linear(log)
Maximum depth	burn	14-65	28.8(23.3)	21.7(2.1)
	control	7-26	20.6(17.3)	31.2(2.0)
Main rhizome depth	burn	5-20	9.6(8.4)	6.0(1.7)
	control	1.5-26	13.1(14.2)	10.2(4.6)
Horizontal extent	burn	45- 85	64.0(62.5)	15.1(1.3)
	control	2-122	91.2(14.3)	27.5(3.0)
Maximum diameter	burn	0.3-0.6	0.4(0.4)	0.1(1.3)
	control	0.1-0.7	0.4(0.3)	0.2(2.2)
Number of stems	burn	1-6	2.6(1.9)	2.3(2.4)
	control	1-9	4.2(2.9)	3.4(2.8)
Number of clumps	burn	1-3	1.6(1.4)	0.8(1.7)
	control	1-9	4.0(2.8)	3.4(2.7)
Tallest stem	burn	4-23	11.0(19.4)	6.4(1.2)
	control	7-26	14.8(16.4)	5.7(1.8)

SPECIES: Berberis repens

SAMPLE AREA: Rumble Creek

SAMPLE SIZE: burn = 9 control = 7

Measurement (cm)	Site	Range	Mean linear (log)	Std. Dev. linear (log)
Maximum depth	burn	13-28	21.8(21.5)	4.0(1.2)
	control	21-38	27.8(27.3)	5.8(1.2)
Main rhizome depth	burn	3-28	15.4(20.0)	8.8(3.1)
	control	1.5-38	16.3(18.1)	15.0(5.1)
Horizontal extent	burn	11-46	31.5(62.6)	14.2(5.1)
	control	8-71	40.7(34.3)	21.0(2.1)
Maximum diameter	burn	0.25-2.0	0.5(0.4)	0.5(1.8)
	control	0.20-0.5	0.3(0.3)	0.1(1.4)
Number of stems	burn	1-5	2.3(2.0)	1.3(1.8)
	control	1-3	2.7(2.5)	1.1(1.6)
Number of clumps	burn	1-2	2.0(1.8)	0.8(1.6)
	control	1-2	2.1(2.0)	0.6(1.4)
Tallest stem	burn	4-23	11.0(26.6)	6.4(8.3)
	control	7-26	14.8(14.0)	5.7(1.5)

SPECIES: Linnaea borealis

SAMPLE AREA: Pattee Canyon

SAMPLE SIZE: ravine = 5 upland = 5

Measurement (cm)	Site	Range	Mean linear(log)	Std. Dev. linear(log)
Maximum depth	upland	0.6-3	1.7(1.9)	0.9(4.0)
	ravine	0.3-7	3.5(1.5)	3.6(1.9)
Main rhizome depth	upland	0-3	0.9(3.2)	1.2(9.4)
	ravine*	0.3-7	2.4(1.1)	3.0(1.9)
Horizontal extent	upland	25-300	129.8(91.2)	102.9(1.7)
	ravine	45-183	102.4(97.1)	54.5(2.5)
Maximum diameter	upland	0.1-0.2	0.1(0.1)	0.06(0.0)
	ravine	0.1	0.1(0.1)	0.0(1.5)
Number of stems	upland	1	1	0
	ravine	1	1	0
Number of clumps	upland	1	1	0
	ravine	1	1	0
Above ground length	upland	0-90	67.0(13.6)	71.0(4.5)
	ravine	0-45.5	22.6(16.3)	16.9(13.0)

* Sample size = 4.

SPECIES: Physocarpus malvaceus

SAMPLE AREA: Pattee Canyon

SAMPLE SIZE: burn = 6 control = 6

Measurement (cm)	Site	Range	Mean linear(log)	Std. Dev. linear(log)
Maximum depth	burn	22-25	33.0(13.6)	11.8(1.4)
	control	23-55	34.1(32.2)	12.8(1.4)
Main rhizome depth	burn	1-20	8.5(6.0)	6.8(2.8)
	control	3-23	11.3(8.9)	7.8(2.2)
Horizontal extent	burn	85-143	103.8(100.3)	29.2(1.3)
	control	44- 91	70.5(67.4)	21.3(1.4)
Maximum diameter	burn	1- 6	2.7(2.2)	1.9(2.0)
	control	1-13	3.9(2.7)	4.5(2.3)
Number of stems	burn	4-22	10.5(9.0)	6.4(1.8)
	control	2- 8	3.6(3.1)	2.4(1.8)
Number of clumps	burn	1-4	2.0(1.7)	1.2(1.9)
	control	1	1.0(0.0)	0.0(0.0)
Tallest stem	burn	57-110	81.0(78.8)	20.3(1.3)
	control	59-153	103.6(99.3)	32.7(1.4)

SPECIES: Spiraea betulifolia

SAMPLE AREA: Pattee Canyon

SAMPLE SIZE: burn = 6 control = 5

Measurement (cm)	Site	Range	Mean linear(log)	Std. Dev. linear(log)
Maximum depth	burn	5-62	28.4(20.2)	23.4(2.7)
	control	7-33	23.8(20.8)	11.0(1.9)
Main rhizome depth	burn	2.5-12	6.7(5.9)	3.4(1.8)
	control	3-29	11.2(7.5)	11.0(2.6)
Horizontal extent	burn	6-103	50.2(35.3)	37.2(3.0)
	control	23-103	56.6(49.2)	32.1(1.8)
Maximum diameter	burn	0.3-0.5	0.4(0.4)	0.08(1.2)
	control	0.1-0.8	0.4(0.3)	0.2(2.0)
Number of stems	burn	1-12	4.0(2.7)	4.5(2.5)
	control	1- 6	3.1(2.6)	1.9(2.1)
Number of clumps	burn	1-4	1.8(1.5)	1.3(1.9)
	control	1-2	1.5(1.4)	0.5(1.5)
Tallest stem	burn	30-54	41.8(41.0)	9.1(1.2)
	control	24-55	42.3(40.8)	11.7(1.4)

SPECIES: Spiraea betulifolia

SAMPLE AREA: Rumble Creek

SAMPLE SIZE: burn = 9 control = 6

Measurement (cm)	Site	Range	Mean linear(log)	Std. Dev. linear(log)
Maximum depth	burn	11-39	28.6(27.3)	7.8(1.4)
	control	15-45	28.5(26.9)	10.5(1.5)
Main rhizome depth	burn	3-46	14.8(11.6)	12.6(2.1)
	control	_____	_____	_____
Horizontal extent	burn	13-79	51.8(65.0)	22.0(3.2)
	control	22-69	49.5(45.3)	21.0(1.6)
Maximum diameter	burn	0.1-1.0	0.4(0.4)	0.2(1.9)
	control	0.2-0.5	0.3(0.3)	0.1(1.4)
Number of stems	burn	3-7	5.5(5.3)	1.6(1.4)
	control	1-4	2.1(1.8)	1.4(2.0)
Number of clumps	burn	1-4	1.7(1.5)	1.0(1.7)
	control	1-2	1.1(1.1)	0.4(1.3)
Tallest stem	burn	22-64	42.2(57.3)	13.5(3.1)
	control	2-54	28.8(37.3)	18.4(7.3)

SPECIES: Symphoricarpos albus

SAMPLE AREA: Pattee Canyon

SAMPLE SIZE: burn = 5 control = 6

Measurement (cm)	Site	Range	Mean linear (log)	Std. Dev. linear (log)
Maximum depth	burn	19-30	24.0(25.7)	4.5(1.2)
	control	5-31	20.5(16.8)	11.1(2.2)
Main rhizome depth	burn	2-14	7.4(6.2)	4.3(2.0)
	control	1- 5	3.2(2.8)	1.6(1.9)
Horizontal extent	burn	16-100	55.2(45.8)	33.2(2.1)
	control	46-193	94.3(82.0)	57.8(1.8)
Maximum diameter	burn	0.35-2.0	1.2(1.0)	0.6(2.0)
	control	1.0 -3.5	1.8(3.2)	1.0(5.8)
Number of stems	burn	1-16	6.8(4.0)	6.3(3.7)
	control	1- 8	4.0(3.0)	2.9(2.5)
Number of clumps	burn	1-2	1.4(1.3)	0.5(1.5)
	control	1-4	2.1(1.9)	1.1(1.8)
Tallest stem	burn	35-50	42.8(42.5)	5.6(1.1)
	control	22-72	44.0(40.8)	18.8(1.5)

SPECIES: Symphoricarpos albus

SAMPLE AREA: Rumble Creek

SAMPLE SIZE: burn = 8 control = 7

Measurement (cm)	Site	Range	Mean linear(log)	Std. Dev. linear(log)
Maximum depth	burn	23-57	39.5(37.8)	12.6(1.4)
	control	20-39	28.1(27.3)	7.7(1.3)
Main rhizome depth	burn	0.6-18	9.4(5.5)	7.3(3.6)
	control*	3.5-18	11.8(28.8)	8.2(4.1)
Horizontal extent	burn	38- 72	55.2(53.2)	16.9(1.3)
	control	31-123	61.7(56.0)	31.2(1.6)
Maximum diameter	burn	0.9-3.0	1.2(1.9)	0.8(5.3)
	control	0.4-6.0	1.9(1.4)	1.8(2.3)
Number of stems	burn	2-10	4.3(3.9)	2.5(1.6)
	control	1- 8	3.0(2.3)	2.4(2.1)
Number of clumps	burn	1-2	1.1(1.1)	0.3(1.3)
	control	1-2	1.1(1.1)	0.3(1.3)
Tallest stem	burn	31-71	50.8(71.3)	15.0(3.0)
	control	31-67	44.1(42.5)	13.3(1.3)

* Sample size = 4.

SPECIES: Xerophyllum tenax

SAMPLE AREA: Rumble Creek

SAMPLE SIZE: burn = 5 control = 5

Measurement (cm)	Site	Range	Mean linear(log)	Std. Dev. linear(log)
Maximum depth	burn	5-11	8.5(9.8)	2.1(1.3)
	control	8-18	11.3(9.6)	3.8(1.1)
Main rhizome depth	burn	2- 8	5.6(5.3)	1.9(1.5)
	control	5-15	8.4(6.7)	3.7(1.1)
Horizontal extent	burn	3- 8	6.6(6.3)	1.9(1.4)
	control	5.5-15	8.2(6.3)	4.0(1.3)
Maximum diameter	burn	2-4	2.7(2.7)	0.7(1.3)
	control	0.3-5	2.9(1.8)	1.7(3.2)
Number of stems	burn	—	—	—
	control	—	—	—
Number of clumps	burn	1-4	2.4(2.1)	1.2(1.8)
	control	1-3	2.2(1.9)	0.8(1.6)
Basal diameter	burn	2-6.5	3.7(3.5)	1.5(1.5)
	control	2-5	3.4(3.1)	1.1(1.4)

PERCENT CUMULATIVE FREQUENCY OF MAXIMUM RHIZOME DEPTH

Amelanchier alnifolia

Site	Unadjusted Maximum Depth	% Frequency	Adjusted Maximum Depth	% Frequency
Pattee	27	17	25.2	17
Canyon	30	36	28.2	36
Burned	49	68	47.2	68
Ravine	50	100	48.2	100
Pattee	18	09	13.6	08
Canyon	45	33	40.6	31
Control	54	61	49.6	60
Ravine	76	100	71.6	100

PERCENT CUMULATIVE FREQUENCY OF MAXIMUM RHIZOME DEPTH

Arctostaphylos uva-ursi

Site	Unadjusted Maximum Depth	% Frequency	Adjusted Maximum Depth	% Frequency
Pattee Canyon Upland	0.5 1.5 2.5 6.0 30.0	01 05 16 26 100	-1.9 -0.9 +0.1 +3.6 +27.6	01 05 16 26 100
Pattee Canyon Lower Site	3.0 5.0 6.0 8.0 11.0	09 24 42 67 100	-1.2 +0.8 +1.8 +3.8 +6.8	09 24 42 67 100

PERCENT CUMULATIVE FREQUENCY OF MAXIMUM RHIZOME DEPTH

Berberis repens

Site	Unadjusted Maximum Depth	% Frequency	Adjusted Maximum Depth	% Frequency
Pattee Canyon	14	09	12.24	08
Burned Ravine	20	22	18.2	21
	25	38	23.2	37
	30	58	28.2	56
	65	100	63.2	100
Pattee Canyon Control Ravine	7	07	2.6	03
	14	20	9.6	15
	15	35	10.6	28
	26	60	21.6	55
	41	100	36.6	100
Rumble Creek Burn	13	07		
	20	17		
	21	27		
	21	38		
	23	50		
	23	61		
	24	74		
	24	86		
	28	100		
Rumble Creek Control	21	11	15.4	10
	22	22	16.4	20
	26	35	20.4	33
	27	49	21.4	47
	29	64	23.4	62
	32	80	27.4	79
	38	100	33.4	100

PERCENT CUMULATIVE FREQUENCY OF MAXIMUM RHIZOME DEPTH

Linnaea borealis

Site	Unadjusted Maximum Depth	% Frequency	Adjusted Maximum Depth	% Frequency
Pattee Canyon Ravine	0.3	02	-4.11	02
	1.0	07	-3.4	07
	1.5	16	-2.9	16
	7.0	55	+2.6	55
	8.0	100	+3.6	100
Pattee Canyon Upland	0.6	07	-1.8	07
	1.0	19	-0.8	19
	2.0	42	+0.2	42
	2.0	65	+0.2	65
	3.0	100	+1.2	100

PERCENT CUMULATIVE FREQUENCY OF MAXIMUM RHIZOME DEPTH

Physocarpus malvaceus

Site	Unadjusted Maximum Depth	% Frequency	Adjusted Maximum Depth	% Frequency
Pattee	20	10	15.6	09
Canyon	23	21	18.6	19
Burn	30	36	25.6	33
	36	53	31.6	51
	41	73	36.6	72
	55	100	50.6	100
Pattee	22	11	22.2	11
Canyon	27	25	25.2	24
Control	30	40	28.2	39
	30	56	28.2	54
	33	72	31.2	71
	56	100	54.2	100

PERCENT CUMULATIVE FREQUENCY OF MAXIMUM RHIZOME DEPTH

Spiraea betulifolia

Site	Unadjusted Maximum Depth	% Frequency	Adjusted Maximum Depth	% Frequency
Pattee Canyon Burned Ravine	5 15 17 43 62	04 14 26 56 100	3.2 13.2 15.2 41.2 60.2	02 12 24 55 100
Pattee Canyon Control Ravine	7 13 28 29 33 33	05 14 34 54 77 100	2.6 8.6 23.6 24.6 28.6 28.6	02 10 30 51 76 100
Rumble Creek Burn	11 26 26 27 31 31 33 33 39	04 14 24 35 47 59 72 85 100		
Rumble Creek Control	15 21 24 31 34 45	09 21 35 54 74 100	9.4 15.4 18.4 25.4 28.4 39.4	07 18 32 50 71 100

PERCENT CUMULATIVE FREQUENCY OF MAXIMUM RHIZOME DEPTH

Symphoricarpos albus

Site	Unadjusted Maximum Depth	% Frequency	Adjusted Maximum Depth	% Frequency
Pattee	19	16	17.2	16
Canyon	20	37	18.2	32
Burned	25	53	23.2	53
Ravine	26	75	24.2	75
	30	100	28.2	100
Pattee	5	04	0.6	00.6
Canyon	8	11	3.6	4
Control	24	30	19.6	25
Ravine	26	51	21.6	47
	29	75	24.6	72
	31	100	26.6	100
Rumble	23	07		
Creek	30	17		
Burn	32	27		
	33	37		
	38	49		
	46	64		
	57	82		
	57	100		
Rumble	20	10	14.4	09
Creek	21	21	15.4	19
Control	24	33	18.4	31
	24	45	18.4	42
	31	61	25.4	59
	37	80	31.4	79
	39	100	33.4	100

PERCENT CUMULATIVE FREQUENCY OF MAXIMUM RHIZOME DEPTH

Xerophyllum tenax

Site	Unadjusted Maximum Depth	% Freq.	01	02	Adjusted Maximum Depth	% Freq.
Rumble Creek Burn	5	07	0.1	0.2	4.7(4.7)	07
	7	18	0.1	0.1	6.8(5.9)	16
	7	28	0.1	1.0	5.9(6.8)	27
	8	40	0.0	0.0	8.0(7.0)	38
	8.5	52	1.0	0.5	7.0(8.0)	50
	10.5	68	0.0	0.1	10.4(10.4)	66
	11	84	0.0	0.1	10.9(10.9)	82
	11	100	0.0	0.1	10.9(10.9)	100
Rumble Creek Control	8	14	0.0	0.5	7.5(6.0)	16
	9	31	1.0	0.5	7.5(7.5)	36
	10	49	2.0	2.0	6.0(7.5)	56
	10.5	68	2.0	1.0	7.5(7.5)	76
	18	100	1.0	8.0	9.0(9.0)	100

MEAN PERCENT COVER

SPECIES	Rumble Creek Control	Rumble Creek Burn	Pattee Can. Control	Pattee Can. Burn	Pattee Can. Upland	Pattee Can. Lower
<i>Acer glabrum</i>	<1.0	1.0	10.5	<1.0		
<i>Amelanchier alnifolia</i>	1.8		1.5	1.4	2.5	3.0
<i>Antennaria microphylla</i>			<1.0	<1.0		
<i>Arctostaphylos uva-ursi</i>					<1.0	1.3
<i>Arnica cordifolia</i>			<1.0	<1.0	<1.0	
<i>Arnica latifolia</i>					3.5	
<i>Arnica sp.</i>			<1.0	<1.0	<1.0	
<i>Aster conspicuus</i>			<1.0	4.1		
<i>Aster sp.</i>	<1.0					
<i>Astragalus sp.</i>				<1.0		
<i>Berberis repens</i>	2.3	+	6.2	1.2		8.2
<i>Bromus inermis</i>				<1.0		
<i>Calamagrostis rubescens</i>			2.2	35.3		16.6
<i>Carex geyeri</i>		1.4			22.5	
<i>Chimaphila umbellata</i>	<1.0				<1.0	
<i>Clematis columbiana</i>	<1.0		<1.0	<1.0		
<i>Dactylis glomerata</i>				<1.0		
<i>Epilobium angustifolium</i>		32.6		<1.0		
<i>Epilobium miniatum</i>		1.5		<1.0		
<i>Festuca sp.</i>				1.5		
<i>Fragaria vesca</i>			<1.0	<1.0	<1.0	1.7
<i>Fragaria virginiana</i>		<1.0			<1.0	2.9
<i>Galium triflorum</i>			2.6	<1.0		
<i>Goodyera oblongifolia</i>	<1.0				<1.0	
<i>Heuchera parviflora</i>				<1.0		
<i>Linnaea borealis</i>			1.8		5.5	

MEAN PERCENT COVER

SPECIES	Rumble Creek Control	Rumble Creek Burn	Pattee Can. Control	Pattee Can. Burn	Pattee Can. Upland	Pattee Can. Lower
<i>Lupinus sp.</i>					<1.0	
<i>Osmorhiza chilensis</i>	<1.0	<1.0	<1.0	<1.0		
<i>Pachystima myrsinites</i>	1.4	<1.0				
<i>Pedicularis racemosa</i>					<1.0	
<i>Penstemon sp.</i>				<1.0		
<i>Physocarpus malvaceus</i>			5.3	7.8		9.0
<i>Pinus contorta</i>		<1.0				
<i>Prunus virginiana</i>	<1.0					
<i>Pseudotsuga menziesii</i>	<1.0	<1.0		<1.0	2.5	
<i>Pyrola secunda</i>			<1.0		1.2	
<i>Ribes cereum</i>				1.8		
<i>Rosa gymnocarpa</i>	5.0	<1.0		<1.0	3.5	<1.0
<i>Rosa woodsii</i>				<1.0		
<i>Rosa sp.</i>		<1.0		<1.0	2.0	<1.0
<i>Rubus parviflorus</i>	<1.0		3.7	<1.0		
<i>Salix scouleriana</i>		1.2				
<i>Spiraea betulifolia</i>	5.6	3.9	11.9	4.5	<1.0	4.5
<i>Symphoricarpos albus</i>	11.4	2.7	6.2	2.3		12.7
<i>Thalictrum sp.</i>	<1.0	<1.0		<1.0		
<i>Vaccinium globulare</i>				5.9	23.5	
<i>Verbascum thapsus</i>		<1.0				
<i>Xerophyllum tenax</i>	1.2	+				
<i>litter</i>					5.5	34.7
<i>moss/lichen</i>				2.2	12.0	1.5
<i>slash</i>				6.5	6.5	2.5
<i>soil/rock</i>	55.5	45.5	15.3	15.5	2.5	