AN ECOLOGICAL APPRAISAL OF THE DWARFMISTLETOE PROBLEM AT CRATERS OF THE MOON NATIONAL MONUMENT, IDAHO

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ABSTRACT

Reconnaissance methods were employed to determine the distribution of the dwarfmistletoe, Arceuthobium campylopodum f. cyanocarpum, in the limber pine (Pinus flexilis) stands of Craters of the Moon National Monument, Idaho. The parasite was as widely distributed as the host, with several exceptions. As determined from the critical positions of the uninfected limber pine stands, an overall pattern of infection spread from west to east was evident. Although highly atypical for dwarfmistletoe parasitism, numerous isolated infections were located.

The dwarfmistletoe infection was dated from analyses of core samples extracted from limber pines that exhibited bole abnormalities characteristic of old dwarfmistletoe infections. These analyses indicated that the initial infection occurred at least 209 years ago.

Infection patterns were analyzed within randomly-selected transects. No consistent patterns of infection were detected. Canopy size (as indicated by tree height) was correlated positively with infection intensity. Stand density was not correlated with infection intensity.

The effect of the parasite on the annual radial growth of the pines was determined from analyses of growth ring increments. No correlation was found between infection intensity and annual radial increment of the slow-growing limber pine.

The effectiveness of a dwarfmistletoe eradication program initiated in 1961 and activated in 1962 and 1963 was assessed by determining the levels and types of residual infections in forest stands

that were treated during 1962 and/or 1963. In nearly every treated stand, the percentage of infected trees was below that determined in a pre-eradication survey. Further analysis showed that the percentage of heavily infected trees decreased, while the percentages of lightly and moderately infected trees increased.

Dispersal agents were inadequately assessed in this study, but the relative roles of three agents were postulated. The seed ejection mechanism of the dwarfmistletoe, the unidirectional winds of the Monument, and animals (particularly birds and rodents) apparently contribute to the spread of the parasite and may account for the isolated infections found during the reconnaissance phase of this project.

The effects of limber pine removal on plant community structure and successional dynamics were analyzed with permanent quadrat methods for vegetative analysis. These analyses indicated that on sites where subclimax and climax shrub understories were nearly closed at the time of tree removal, normal plant succession was accelerated by removal of the tree synusia. On these sites no evidence of reforestation by the noncompetitive limber pine, a seral species, was found. Conversely, tree removal from sites supporting relatively open pioneer plant communities retarded the rate of normal succession.

CHAPTER I

INTRODUCTION

Research in forest pathology frequently has been focused upon parasites that infect tree species of great commercial importance. Studies on the dwarfmistletoes infecting the conifers of the western United States have been no exception to this generalization. In practically every phase of dwarfmistletoe research work (i.e., cytology, physiology, taxonomy, etc.) those forms of the various species of the genus Arceuthobium Bieb. which do not infect commercially valuable hosts have been neglected. Similarly, the non-commercial host species have been less extensively studied than those vital to the lumbering industry.

At Craters of the Moon National Monument, Idaho, a parasitic relationship between the dwarfmistletoe, Arceuthobium campylopodum Engelm. f. cyanocarpum (A. Nels.) Gill, and its host, the limber pine, Pinus flexilis James, has been known to exist at least since 1928 when it was first recorded in the literature of the Monument (McElreath, 1928). Probably because of the economic irrelevance of the host species, virtually no studies of the dwarfmistletoe situation at Craters of the Moon National Monument have been undertaken previously.

Since practically no information concerning the dwarfmistletoe infection at Craters of the Moon National Monument was available to National Park Service officials in 1961 when a dwarfmistletoe control program was initiated, and since the ecological implications of such a

program were not analyzed prior to the commencement of the control program, the following study was initiated in 1966. The study was undertaken in a manner which would be useful to the National Park Service, including special considerations of controversial points previously disputed without scientific basis, and as many aspects of the dwarfmistletoe problem as could be assessed accurately from quantitative, statistical, and descriptive ecological methods in the allotted time. Those aspects of the dwarfmistletoe problem at Craters of the Moon National Monument treated in the present study include: a determination of the age of the dwarfmistletoe infection in the limber pine stands of the Monument; a distributional analysis of the dwarfmistletoe infection with ecological implications for distributional patterns within forest stands as well as within the boundaries of the Monument; an appraisal of the dwarfmistletoe infection levels; an analysis of the effects of the parasite upon its host, particularly in terms of annual growth; a comparison of infection levels before and after control measures were exercised in selected forest stands; an assessment of phytosociological changes initiated by host removal in control areas; a brief discussion of the effects of host removal on ecosystem dynamics; and suggestions for further research.

CHAPTER II

REVIEW OF THE LITERATURE

I. DESCRIPTION OF THE STUDY AREA

Craters of the Moon National Monument is located at the base of the Pioneer Mountains 18 miles southwest of Arco, Butte County, Idaho, and has been administered under the protective jurisdiction of the National Park Service since May 2, 1924, when President Coolidge proclaimed it a National Monument. The political boundaries of the Monument encompass approximately 83 square miles of Quaternary basaltic volcanic features produced during three (Stearns, 1963) or four (Murtaugh, 1961) periods of volcanic eruptions that occurred along a recently-active zone of crustal weakness known locally as the Great Rift Zone.

Because of the relatively thick layers of recently-extruded lava, the general elevation of the Monument is higher than that of the adjacent Snake River Plain. Excluding the summits of the Pioneer Mountains, the elevation of the lava fields exhibits a gradual slope from 5900 feet in the northwestern region to 5300 feet in the southeast. The relief is broken in at least fifty-five points by numerous cinder cones which are concentrated in a 2-mile-wide strip running from northwest to southeast for 13 miles (Parsons, 1964). These cones parallel the fissures of the Great Rift Zone, and rise as high as 800 feet above the adjacent plain which itself features many minor

irregularities unique to a lava landscape. On either side of the chain of cones, basaltic lava flows stretch for miles. In many areas the flows have an extremely rough texture and are termed "aa," while in other areas they are much smoother and are termed "pahoehoe" (Stearns, 1963).

Although surrounding weather stations record approximately 10 inches of annual precipitation, this same index at Craters of the Moon has averaged 15.8 inches over the past 9 years. December and January are the months of greatest precipitation, while July and October are the driest ones (see Figure 1, page 5). These unusual precipitation patterns can be explained in terms of orographic precipitation induced by the adjacent Pioneer Mountains and by the unusual convection conditions that prevail in the area throughout the year as a result of the differential heating of the dark basaltic flows and the lighter colored soils of the adjacent mountains and plains. Lindsey (1951) found that differential heating of air masses above large areas of contrasting substrate colors contributed significantly to the unusually high precipitation recorded at Grants Lava Beds, New Mexico, and it is highly probable that the same factors affect the weather patterns at Craters of the Moon.

The mean annual temperature in the area is 42° F., with August having the highest mean monthly temperature of 64.56° F., and January having the lowest mean monthly temperature of 20.03° F. The seasonal fluctuation of air temperatures is summarized in Figure 2 on page 6. The frost-free period, and hence the conventional growing season, averages 104 days although this climatic index is highly variable since

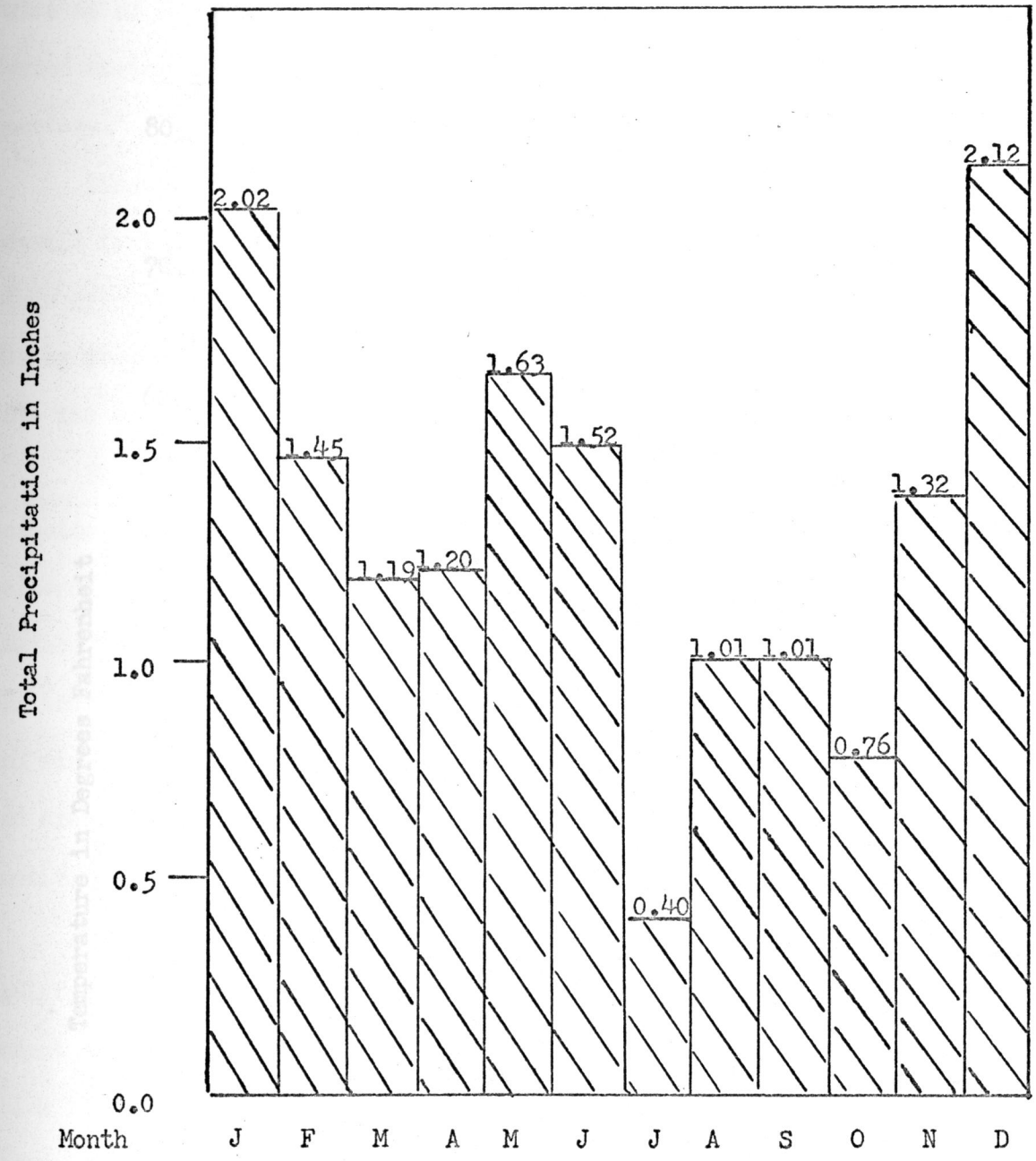


Figure 1. Mean monthly total precipitation and annual distribution of precipitation for Craters of the Moon National Monument. Monthly means obtained from weather records maintained at Monument headquarters from December 1958 to June 1967.

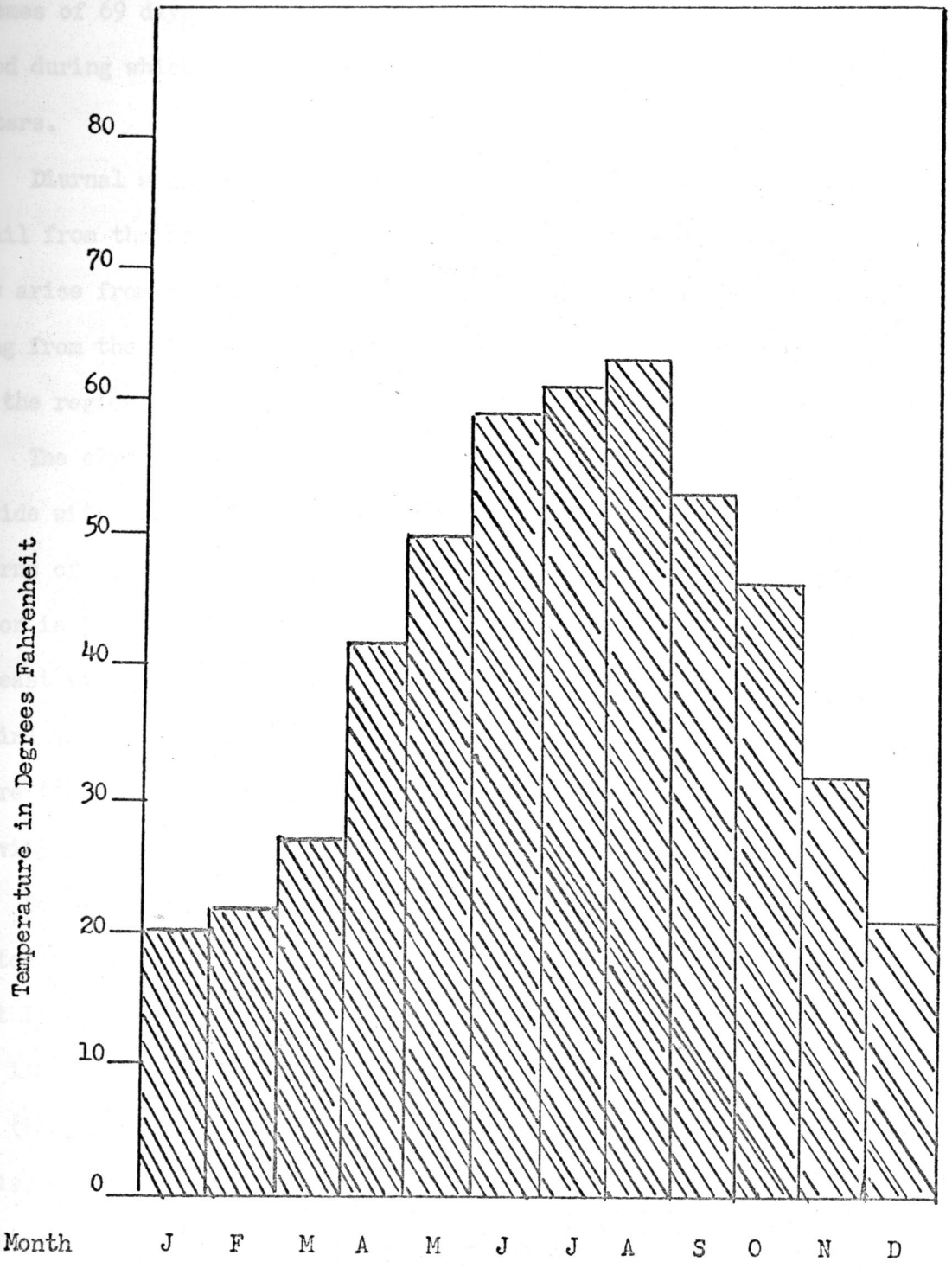


Figure 2. Mean monthly temperatures and annual temperature distribution for Craters of the Moon National Monument. Monthly means obtained from weather records maintained at Monument headquarters from December 1958 to June 1967.

extremes of 69 days and 160 days have been recorded in the 9-year period during which weather records have been kept at Monument headquarters.

Diurnal winds of velocities of 15 to 30 miles per hour frequently prevail from the southwest during all seasons (Eggler, 1941). These winds arise from convection currents generated as the warmer air masses rising from the blackened basalt are displaced by the cooler air moving into the region from the adjacent Snake River Plain.

The climatic data collected at Monument headquarters generally coincide with Blaisdell's (1959) findings since the distributional patterns of precipitation and temperature indicate that annual precipitation is the most variable climatic factor while mean temperature is the least variable. Apparently periodicity, prevailing temperatures, and wind conditions contribute to the effectiveness of the precipitation and are the most significant factors in influencing vegetative productivity and composition.

Soils generally exhibit immature development except in certain isolated relict areas, termed "kipukas," which were not inundated by the recent lava flows (Parsons, 1964). Thin layers of soil buried beneath thick layers of basaltic cinder are composed largely of Snake River loess (Passey, Hugie, and Williams, 1964). With the exceptions of the kipukas, unweathered basalt is universally present, indicating the geologically young age of the parent material.

Although Craters of the Moon has been a National Monument since 1924, published studies of the ecology of this unique area are rare. Eggler's (1941) classic descriptive discussion of primary

plant succession on the lava flows of the Monument constitutes the only publication based on research conducted in those areas of the Monument that support limber pine stands. Other research projects have been completed on the Carey Kipuka, an area in the southwestern corner of the Monument which was recently annexed to Park Service lands (Passey, Hugie, and Williams, 1964; and Tisdale, Hironaka, and Fosberg, 1965).

Eggler (1941) discussed the composition and variation in plant communities by describing several habitats on the basis of substrate texture. He also elucidated successional trends for plants of the lava flows by comparing their relative abundance on flows of different ages, classed the limber pine as a "species whose density increases and then decreases with greater flow age," and indicated that the limber pine replaced the pioneer herb communities on cinder cones. In addition, he studied mortality rates in limber pine seedlings on North Crater and found that only 2.8% of the seedlings survived during a single summer. Although Eggler noted that nearly all of the limber pines of the Snake River Plain grew in the immediate vicinity of Craters of the Moon National Monument, he offered no explanations for the absence of the tree on the older flows outside, as well as inside, the Monument boundaries.

II. THE DWARFMISTLETOE GENUS, ARCEUTHOBIUM BIEB.

The literature on dwarfmistletoes has been reviewed extensively by Gill and Hawksworth (1961). Although the literature is voluminous, most of the research to date has been confined to taxonomic treatments;

cytological, morphological, and anatomical studies; host responses; and distributional studies of the various species and forms of the parasite. Physiological research has been centered on the nutrient requirements of the parasitic plants and on the translocation pathways of assimilates between host and parasite. Conspicuously absent in the literature is research-validated information on dispersal agents other than detailed studies of the seed ejection mechanism of the dwarfmistletoe fruits. Little research has been conducted on dwarfmistletoes that infect non-commercial coniferous species of the western United States since it has been the damaging effects of infections on commercial species that have focused attention on the genus Arceuthobium. For more than half a century the dwarfmistletoes of the western United States have been recognized as the second most damaging disease of coniferous forests (Weir, 1916).

Taxonomically, the dwarfmistletoe genus Arceuthobium is placed in the family Loranthaceae. Characteristics of this genus include scale-like leaves, dioecious plants with trimerous male flowers and two-parted female flowers (Munz and Keck, 1959), and a unique "explosive" fruit (Kuijt, 1960) consisting of two base-fused orthotropous ovules (Cohen, 1962) in an inferior ovary. Separation of the species and forms is based largely on anatomical differences as well as upon host preferences and variable phenologies (Kimmey and Graham, 1960).

A typical dwarfmistletoe life cycle is briefly summarized as follows: after expulsion of the seeds, which in most species occurs in the fall, precipitation sufficient to wash the disseminules from the needles to the bark of young twigs is required (Roth, 1959; and

Hawksworth, 1965) before germination of the seeds can occur. After the seeds have been washed to the bark, they become attached firmly to the peripheral tissues of the host through the mucilaginous viscin coating and enter a dormancy period of approximately 6 months (Beckman, 1964). Depending upon the species and the environmental conditions that prevail during the period of dormancy, the seeds generally germinate in the spring.

Germination is followed by penetration of the host tissues by the root or endophytic system of the parasite. After penetration has been completed, the shoot apex dies and further development of the shoot tissues occurs from cells of the root promeristem (Cohen, 1963). The endophytic system may become systemic and not visually detectable for several years (Kimmey and Graham, 1960) or may become conspicuous in the first or second year after germination as the grayish-yellow shoots emerge from the host tissue. Depending on species, 1 to 4 years are required before the reproductive tissues are mature enough for pollination to occur. After entomophilous pollination (Kuijt, 1955) has occurred, two seasons pass before the fruits mature, except in Arceuthobium pusillum Peck (Gill and Bedwell, 1949).

Kuijt (1960) listed the distinctive anatomical characteristics of the genus among which are a ringlike archesporium in the anther, the absence of sieve tube elements in the phloem; certain peculiarities in the xylem, the immature absorptive system, and shoot emergence patterns. Cohen's (1963) study of the ontogeny of the parasite showed that shoot development actually occurs from the root promeristem since the shoot apex dies soon after the endophytic system has become established in

the host tissues. Another anatomical peculiarity is the lack of true ovules which may be attributed to the absence of integuments. In contrast with the gynoecial anatomy of other higher plants, the embryo sacs of the dwarfmistletoes are surrounded by undifferentiated tissue, called the mamelon or ovarian papilla (Kuijt, 1960) which fills the single locule. Despite the absence of true ovules, the disseminules are referred to as seeds.

Intrinsically associated with the anatomical features of the Arceuthobium fruit is the unique seed discharge mechanism that accounts for the spread of the parasite in relatively closed forest stands and makes control of the parasite difficult. In the second year after pollination, the fruits mature (Gill and Bedwell, 1949). During maturation, the pedicel elongates and recurves so that the distal end of the fruit points downward. At the proximal end of the berry an abscission zone develops between the pedicel and the pericarp and as the abscission of the fruit occurs, hydrostatic pressure within the viscin cells surrounding the seed forces a contraction of the exocarp which ejects the seed through the base of the fruit (Hinds, Hawksworth, and McGinnies, 1963). As the seed is ejected, the viscin cells are ruptured and, as a result, the disseminule is coated with a sticky substance called viscin. The viscin layer of the seed facilitates its adhesion to the branches of the host. In most of the dwarfmistletoes, the force sustaining the ejection of the seeds is sufficient to propel them for distances of 30 feet (Peace, 1962) so the ejection mechanism is highly efficient in dispersing the species around original infection loci.

Of the dispersal agents, the dwarfmistletoe's seed expulsion mechanism has been studied most extensively. The dispersal distances and velocities of the disseminules following ejection have been determined photographically and the importance of the ejection mechanism in local dispersal of the parasite postulated (Hinds and Hawksworth, 1965). Results of the photographic studies of Hinds and Hawksworth (1965) indicated that the seeds of Arceuthobium campylopodum f. cyanocarpum attain velocities of 2100 cm/sec during dispersal.

The literature on other dispersal agents of the parasite is controversial and detailed research work validating observations has not been undertaken to date. Birds are known to be important vectors of the mistletoes of Europe (Gill and Hawksworth, 1961), but their role in the dissemination of the dwarfmistletoe seeds appears to be of minor importance (Kimmey and Graham, 1960). Kimmey (1957) stated that birds and other animals did not eat the dwarfmistletoe seeds and therefore could not be important in spreading dwarfmistletoe infections. On the other hand, Weir (1916) found dwarfmistletoe seeds in grouse crops analyzed late in the season when the fruits were ripe. Neither Kimmey nor Weir considered the possibility of dispersal through the external adhesion of the sticky seeds to birds or mammals.

Wind is another dispersal agent the importance of which has not been substantiated by research. Weir (1916) found larch mistletoe seeds carried to distances of 1/4 mile from the nearest infection source by the wind. Several other researchers (Kimmey, 1957; Roth, 1953; and Weir, 1916) noted the importance of wind in determining the pattern of the spread of infection within forest stands.

Infection can also occur through natural root grafts. Kuijt (1964) demonstrated vegetative propagation with Arceuthobium americanum Nutt. ex Engelm. and its host Pinus contorta Dougl., and Arceuthobium douglasii Engelm. and Pseudotsuga menziesii Franco.

A highly productive area of dwarfmistletoe research has been that of taxonomically-based host specificity. Kimmey and Graham (1960) listed the host preferences of the major species and forms of the Northern Rocky Mountain and Intermountain Regions of the United States Department of Agriculture Forest Service. Host preferences of the various dwarfmistletoes include: Arceuthobium americanum, lodgepole pine; A. douglasii, Douglas fir; A. campylopodum Engelm. f. campylopodum Engelm., ponderosa pine; A. campylopodum Engelm. f. laricis (Piper) Gill, western and subalpine larches; and A. vaginatum (H.B.K.) Eichler, Rocky mountain form of ponderosa pine. Munz and Keck (1959) recorded the host preferences of the Californian dwarfmistletoes in their monumental A California Flora and listed Pinus flexilis, P. albicaulis Engelm., P. aristata Engelm., and P. balfouriana Grev. & Balf. as hosts of A. campylopodum f. cyanocarpum, the form of the parasite found at Craters of the Moon National Monument. Miller and Bynum (1965) observed A. campylopodum f. cyanocarpum parasitizing Pinus balfouriana adjacent to Pinus monticola Dougl. stands infected with the same parasite. Unpublished studies on host preferences (Hawksworth and Wiens, personal correspondence) indicated that most forms of the parasite will occasionally attack trees other than their principal hosts and that A. campylopodum f. cyanocarpum infects the western white pine, Pinus monticola. Completion of these host preference studies by Hawksworth

and Wiens will probably result in major revisions in the current taxonomy of the genus Arceuthobium and many forms may be elevated to the rank of species as a result.

The physiological requirements of the western dwarfmistletoe, A. campylopodum f. campylopodum, have been studied in depth by Beckman (1964) who determined the critical requirements for each phase of the life cycle of A. campylopodum and concluded that environmental conditions prevailing during the 30 days following seed ejection were primarily responsible for low seed viability and low infection levels. He found that the dormancy period was apparently controlled by a chemical inhibitor associated with the endocarp; that the retention of viability during dormancy was correlated with temperature; and that light intensity significantly stimulated germination. Kimmey and Graham (1960) also noted that the growth and development of the parasite could be stimulated by added light.

The physiological basis of parasitism between the dwarfmistletoes and their hosts has been a highly productive area of research to date. Weir's (1916) hypothesis that the green mistletoes (i.e., the genus Phoradendron Nutt.) were primarily "water" parasites while the dwarfmistletoes were both "water" and "photosynthate" parasites has been tested by numerous plant pathologists. Hull and Leonard (1964), in comparing chlorophyll levels between host foliage and aerial shoots of Arceuthobium, found that the chlorophyll concentration in the parasite amounted to only 0.1 to 0.2 the quantity found in an equivalent mass of host foliage. Rediske and Shea (1961) demonstrated that photosynthesis occurred in dwarfmistletoe shoots under controlled conditions and that

photosynthates were actually translocated from the shoots of the parasite to the host tissues. Leonard and Hull (1965), working with isotopically labeled assimilates, demonstrated that the reciprocal relationship (i.e., translocation from host to parasite) existed between the dwarfmistletoes and their hosts but not between the green mistletoes and their hosts.

The effects of the dwarfmistletoes upon their hosts have been widely discussed in the literature. That only the heart rot fungi of western conifers cause greater economic damage than the dwarfmistletoes has been recognized (Weir, 1916; Kimmey and Graham, 1960; and Peace, 1962). The deleterious effects of the parasite are diverse, ranging from reduction in seed production and in growth in diameter to the unique stimulation of "witches' broom" growth abnormalities in the host. Kimmey and Graham (1960) summarized the damaging effects of the parasite as follows: "(1) increased mortality; (2) growth reduction; (3) increased susceptibility to decay fungi; and (4) seed reduction." Generally, dwarfmistletoe infections alone are not responsible for the death of the host species (Gill and Bedwell, 1949). Rather, a complex of factors, including the dwarfmistletoe, contributes to the gradual decline of forest stands and magnifies the economic significance of the parasite per se.

Reduction of annual growth in diameter and height has been studied by Shea (1964). In Pinus ponderosa Laws. he found that the severity of dwarfmistletoe infection and reduction in growth increment were correlated inversely and that in young trees the production of witches' brooms was associated with decreased vertical growth (height).

Weir (1916) determined annual diametrical growth reduction in infected stands of Pinus contorta, P. ponderosa, Larix occidentalis Nutt., and Pseudotsuga menziesii over a 40-year period. Additional research on the effects of dwarfmistletoe infection on growth was completed by Childs and Wilcox (1966) who reported growth responses in terms of crown conditions.

The actual mechanism by which the parasite reduces host growth has not yet been explained completely. Rediske and Shea (1961) and Hull and Leonard (1964) attributed damage to blockage of the host's translocation pathway for photosynthates, the phloem, by the parasite. The latter team found that the greatest drain of carbohydrates from the host occurred in spring and was, consequently, seasonally variable.

Although the hypothesis that the dwarfmistletoes retard growth by acting as a sink for mineral nutrients has been set forth (Kuijt, 1955), more recent research (McDowell, 1964) tends to invalidate its implications. To date, no evidence has been found that supports the hypothesis that mineral deficiencies develop in the foliage tissue of the host as a result of mineral translocation from host tissue to parasite tissue.

Abnormal growth patterns in the host also may be produced in response to Arceuthobium infections. Uniquely among the mistletoes, Arceuthobium may induce proliferation of branching at points of infection on the host (Peace, 1962). These massive regions of branching are commonly called witches' brooms. As in the case of growth reduction, the mechanism of witches' broom production in the host is not well understood and, unfortunately, most studies have been concerned not

with the actual causes of the brooming but with descriptions of the damage caused. Weir (1916) attributed higher frequencies of breakage of host branches by high winds or heavy snows to the greater surface area provided by the brooms. Although not in strict reference to brooming, Kimmey (1957) ascribed higher susceptibilities to bark beetle attacks, wood decay, and breakage to heavily infected hosts.

Patterns of infection within commercially important forest stands have been delimited by numerous researchers. Needles of the host trees apparently serve as the primary receptors of the seeds (Roth, 1959; Scharpf, 1964; and Hawksworth, 1965). After the initial infections have occurred the factors of stand history and age composition become significant (Shea and Orr, 1963).

Roth (1953) found that greatest infection spread occurred from overstory to understory, that very little spread occurred on sites where an infected overstory was absent (even-aged stands), and determined that a maximum spread of 130 feet occurred in the direction of the prevailing winds. Hawksworth (1961) correlated infection incidence with tree size, attributing the lower incidence in seedlings to their small "target area."

The age composition of forest stands and the canopy conditions prevailing after the initial infection occurs are highly significant in determining the patterns of infection. In lodgepole pine forests, Hawksworth and Graham (1963) found that in open-canopied stands the rate of infection spread was 1.5 times greater than in stands where the canopy was closed; designated canopy condition as the most significant single factor in regulating spread of the infection; and indicated that

particularly in young stands, infection was highly correlated with the extent of canopy closure rather than with the common ecologic factors of slope, aspect, or elevation.

Parmeter and Scharpf (1963) concluded that only a relatively small proportion of infections actually intensify the spread of the parasite at a given time. Gill and Hawksworth (1954) assessed the intensification of infections following removal of infected branches and concluded that residual infections contributed significantly to reinfection and intensification.

Control methods and measures have been discussed and tested at length. The selection of the methods that will be most effective depends largely upon the condition of the uninfected stand. The methods commonly exercised in controlling dwarfmistletoes have been summarized in detail under the two broad categories "eradication methods" and "stand manipulation methods" (Kimmey and Graham, 1960). The former method consists largely of mechanical removal or poisoning of infected branches or entire trees from the stands, while the latter method entails converting the stand to support a species not susceptible to dwarfmistletoe attack.

Shea and Orr (1963) listed some of the difficulties encountered in attempting to control dwarfmistletoe infections in uneven- or all-aged stands. The spread of the parasite in stands of mixed ages has been estimated to be twice as fast as in stands of even-aged hosts (Kimmey and Graham, 1960). Leaphart (1963) alluded to the fact that cutting practices may actually intensify the losses caused by the parasite and suggested that control efforts were absurd in areas where

site quality was poor, host reproductive indexes low, the value of the stand negligible, and the dwarfmistletoe hazard great. Kimmey and Graham (1960) emphasized the importance of complete eradication in controlling the parasite and recommended frequent retreatment of areas in which eradication methods were employed. Childs and Wilcox (1966) deemed the removal of all overstory sources of infection as the most important single item in eradication procedures.

Hawksworth and Graham (1963) pointed out a difficulty inherent in most dwarfmistletoe control projects, the undetectable latent infections, and advocated that cleaning-up operations be conducted periodically to enhance effectiveness of the control project. The potential success of control measures is further reduced by the fact that dwarfmistletoe activity is stimulated by increased light (Kimmey and Graham, 1960), a factor inseparably associated with opening the stand canopy by pruning, tree removal, or poisoning of host trees.

Because the difficulties involved in controlling the parasite are so numerous, many investigators, particularly Shea and Orr (1963), have urged that critical evaluations of the effects of the treatments be made before conversions to even-aged stands by eradication methods are undertaken. Leaphart (1963) proposed that certain critical questions be answered by basic research before control projects were initiated to insure greatest effectiveness.

Studies of biological control agents of the dwarfmistletoes have been, to date, largely observational. Weir (1915) reported the damaging effects of a fungus, Walrothiella arceuthobii (Peck) Sacc., on the pistillate reproductive tissues. More recent studies (Wicker

and Shaw, 1962) cited the importance of three fungi, Septogloeum gillii Ellis, Pestalotia sp., and Walrothiella arceuthobii, in the local control of Arceuthobium spp. Also promising has been recent work (Scharpf, 1963; and Wicker, 1967) with a fungal parasite, Colletotrichum gloeosporioides Penz. Unfortunately, the ecological amplitudes of these natural parasites of Arceuthobium have not yet been elucidated nor have large scale projects utilizing these biological control agents been initiated.

In 1961 a control program designed to obliterate the dwarf-mistletoe, Arceuthobium campylopodum f. cyanocarpum, from the limber pines growing in the visitor use area of Craters of the Moon National Monument was launched by National Park Service officials. Incidence levels were determined from surveys conducted by Monument employees in the fall of 1961, and during 1962 and 1963 major control work was completed. The control methods used in the program closely fit the description of the "eradication" procedures set forth by Kimmey and Graham (1960).

III. THE HOST, PINUS FLEXILIS JAMES

Few published accounts of research on the limber pine, Pinus flexilis, have entered the literature. The sparsity of literature on this species is probably an indication of its economic insignificance which may be attributed to several factors. Bates (1923) discussed the "weedy" qualities of the tree in detail citing its extremely slow growth rate and its inability to compete as characteristics of the species. Preston (1961) described the wood of the limber pine as

"moderately light and soft; close-grained; and unimportant." The broad, open, and base-branched crown habit of the species also undoubtedly contributes to its undesirable timber qualities.

Pinus flexilis was first described by James in 1823 (Critchfield and Little, 1966). Preston (1961) listed its distinguishing taxonomic characteristics as: "needles $1\frac{1}{2}$ - 3 inches long, stout, persistent 5 - 6 years; and cones 3 - 10 inches long, subcylindrical and opening at maturity." More recent work by Steinhoff (1964) again elevated to species level (P. strobiformis Engelm.) the pine of the southwestern United States formerly known taxonomically as Pinus flexilis James var. reflexa Engelm.

Other important characteristics of the species include its reproductive and developmental cycles. Sudworth (1917) stated that cone maturation required a period of 2 years and that the wingless seeds were shed in September or October. Preston (1961) noted that the tree was very intolerant, slow growing, and required a period of 200 to 300 years to attain maturity.

Like other phases of limber pine research, distributional studies have been limited largely because of the species' commercial insignificance. Critchfield and Little (1966) illustrated the distributional limits of the limber pine in the western United States and Preston (1961) designated the typical growing site of the tree as "summits and rocky foothills."

The ecological factors governing the distribution of the limber pine have been neglected for some time. Bates (1923) correlated the distribution of the tree with its unique physiological and anatomical

features, found that the limber pine was photosynthetically inefficient and explained its slow growth rate on this basis, and stated that the tree had become adapted for growing on "bare sites where there was no competition through reduction in the number and size of its stomata." Sudworth (1917) concluded that the limber pine "preferred dry gravelly loam with no humus," required full light and subsequently did not form dense stands, and exhibited only moderate germination levels under optimal conditions. Bates (1923) concluded his comparative study of the physiological requirements of various conifers emphasizing that the limber pine "was not adapted for competition."

Largely because the lava flows at Craters of the Moon have not as yet been satisfactorily "dated," several different dendrochronological studies of the limber pine have been completed, particularly from the point of view that the tree ages are valid indicators or indexes of the flow ages. Although numerous tree molds and lava trees occur in the Monument, the mystery of whether the trees that formed these peculiar volcanic structures were actually limber pines remains unsolved. Consequently, it is impossible to determine how long the limber pine has inhabited the site. Basing his conclusion on the conspicuous absence of large dead trees, Eggler (1941) concluded that the present limber pine stands were the first to occupy the site.

Several tree ring counts have been made in the Monument (Stearns, 1963; Eggler, 1941; and Schulman, unpublished). Collectively these studies indicate that the ages of the living limber pines range from 13 (Eggler, 1941) to 1,210 (Schulman, personal correspondence) years.

CHAPTER III

METHODS

Reconnaissance methods were employed in determining the age of the dwarfmistletoe infection, the distribution of the parasite, and the extent of the dwarfmistletoe infection within the Monument. Methods of a more analytic nature were used to assess the effects of the parasite on the growth of the host, to delimit patterns of infection, to determine the effectiveness of the eradication program initiated in 1961, and to detect the vegetative changes induced by the eradication program. In addition, the role of wind in disseminating the seeds of the parasite was assessed and observations of other dispersal agents were recorded. A general survey of the limber pine stands of the Monument was completed during the summer of 1966 and a more extensive study was conducted during the summer of 1967 on a full-time basis. Throughout the study, wide-angle 7 X 35 mm binoculars fitted with yellow ocular filters were used for spotting the shoots of the parasitic plant.

Distribution of the Parasite

In order to define the distributional limits of the parasite, all forest stands except those in the most remote sections of the southeast corner of the Monument were surveyed for the incidence of the parasite (see Fig. 3, page 24). Since all reconnaissance work was done on foot, time prevented detailed analysis in the forest stands south of Big Cinder Butte. Consequently, only the presence or absence of the

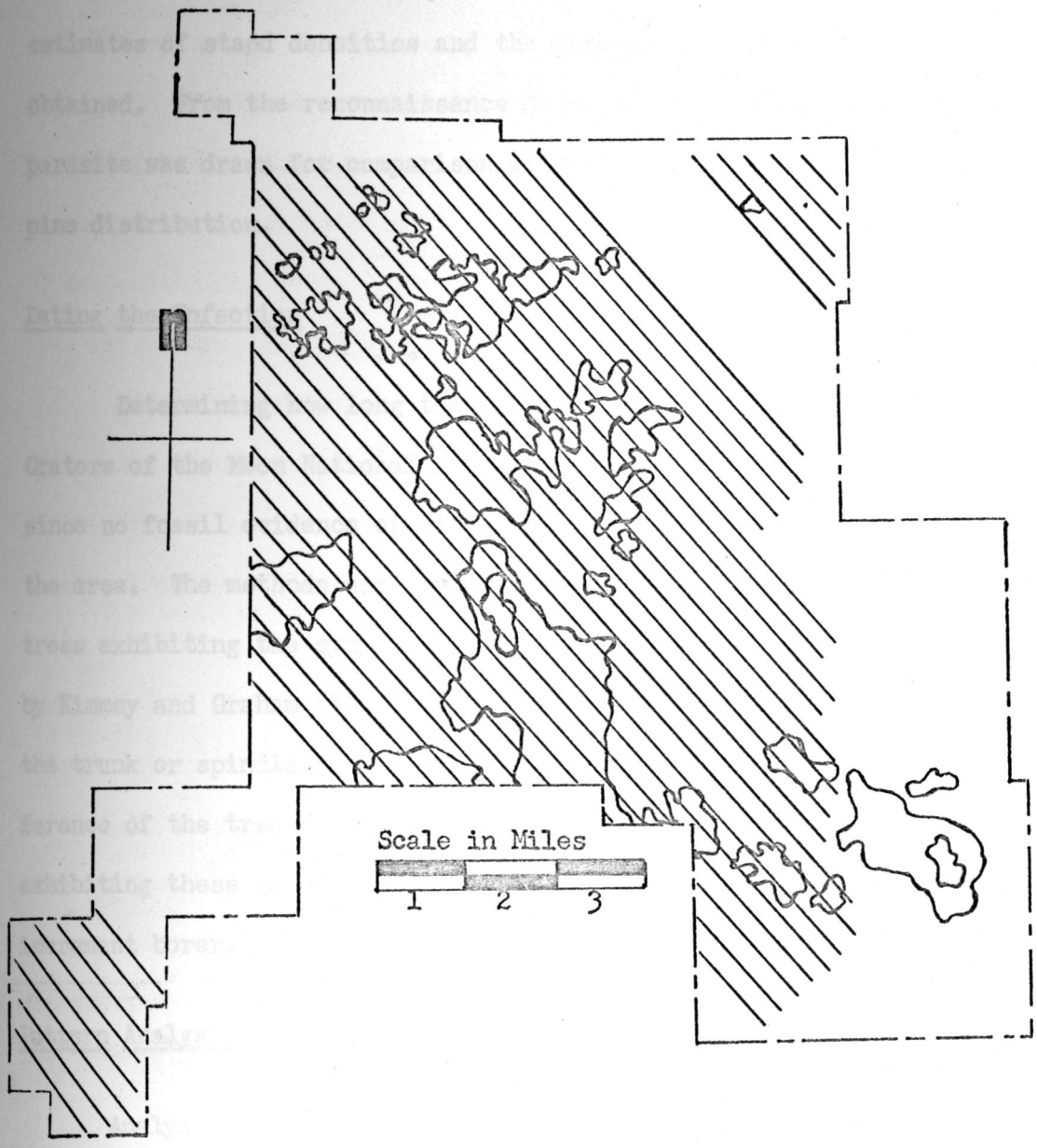


Figure 3. Area included in the reconnaissance phase of the study (shaded areas). Map of limber pine distribution adapted from the master plan vegetative map of Craters of the Moon National Monument. The most heavily forested areas (limber pine stands) are enclosed by solid lines.

parasite was recorded during the surveys of the more remote stands. Observations of stands exhibiting symptoms of heavy infection (i.e., spiketopped and stunted trees) were also recorded. When time permitted, estimates of stand densities and the percentages of infected trees were obtained. From the reconnaissance data, a distributional map of the parasite was drawn for comparison with a similar map showing limber pine distribution.

Dating the Infection

Determining how long the parasite has been a part of the flora of Craters of the Moon National Monument presented certain difficulties since no fossil evidence of either parasite or host has been found in the area. The methods used in dating the infection involved locating trees exhibiting the symptoms of old dwarfmistletoe infections described by Kimmey and Graham (1960) as "large, elongated, and flattened on. . . the trunk or spindle-shaped swellings that include the entire circumference of the tree." During the reconnaissance of forest stands, trees exhibiting these symptoms were bored and core samples extracted with an increment borer. Their ages were determined from tree ring counts.

Pattern Analysis

Analysis of the patterns of infection within forest stands presented numerous problems. Stand characteristics were particularly difficult to assess because of the base-branched growth habit and irregular crown structure of the limber pines. Canopy structure proved to be so highly variable in the relatively open and sparsely forested

stands that percent foliage crown cover (crown density) measurements were not feasible in the allotted time.

After other variable characteristics were considered for use as an index of canopy or overstory structure, tree height was selected for this purpose. Since tree height could be rapidly measured and since the dwarfmistletoe infection class ratings per tree were determined, as described below, by methods that standardize infection rating criteria by accounting for variability in tree height, the characteristic of tree height was used as an index of overstory structure.

Slight modifications of the methods Hawksworth used for determining the effects of dwarfmistletoe on even-aged stands of lodgepole pine in Colorado (Hawksworth, 1964) were employed. Because of the inaccessibility of those areas south of Big Cinder Butte, only ecologically variable sites north of this cinder cone were chosen for transect analyses (see Figure 4, page 27). Random locations within each of these sites were selected by dropping straight pins on a topographic map and marking those points on which the pin points came to rest as transect base points.

A total of twenty-eight transects $\frac{1}{2}$ chain wide and of a length dependent upon the extent of the forest stand were used to delineate sampling plots of the dimensions $\frac{1}{4}$ chain by $\frac{1}{4}$ chain (0.00625 acre) distributed in pairs on either side of a transect line running from the randomly-selected base point, which was marked by a red-and-white striped rod six feet in length, through the forest stand (see Figure 5, page 28). Further analysis consisted of determining the diameter of each tree at ground level, its vigor, height, and the type and extent of

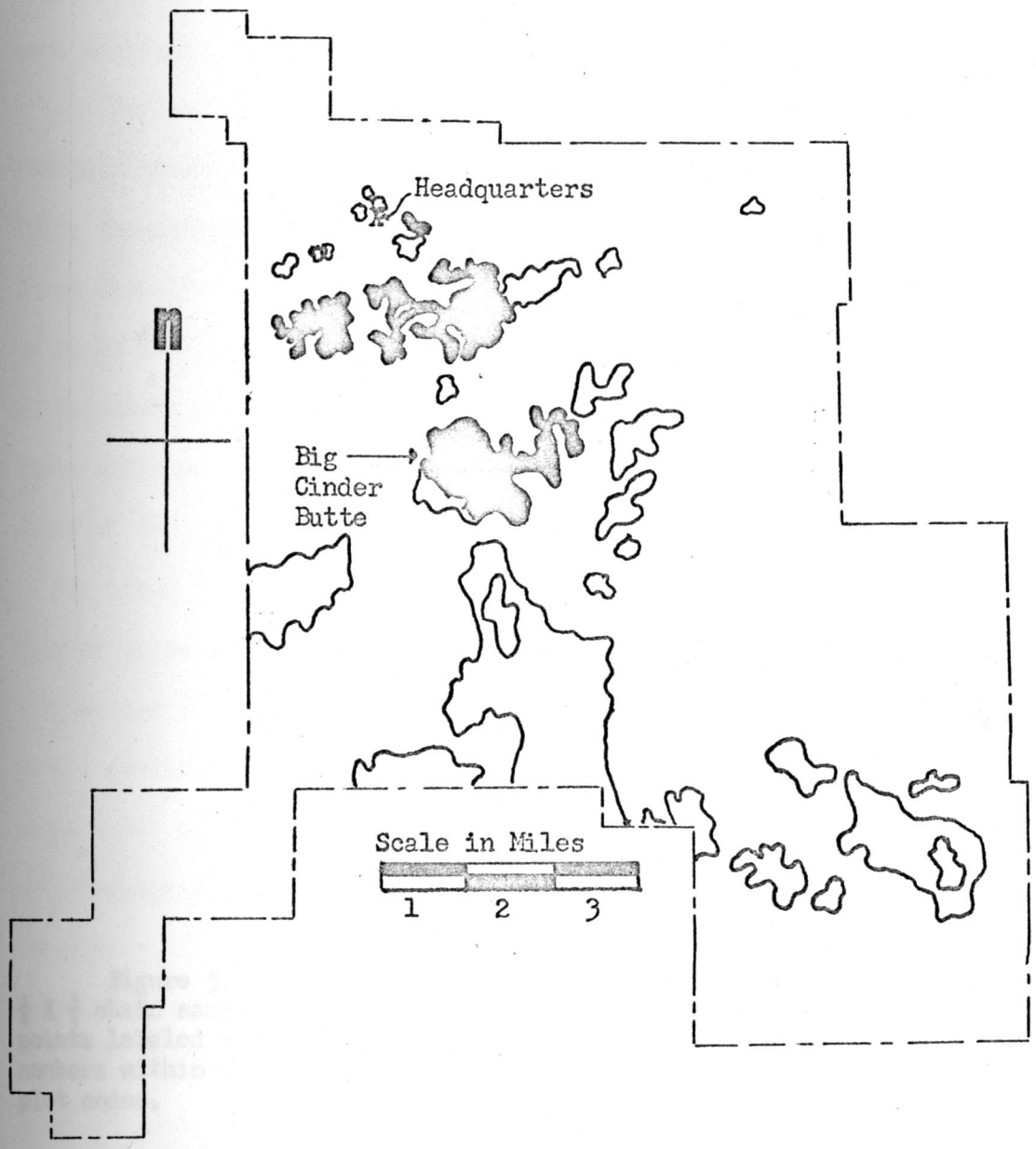


Figure 4. Relatively accessible areas of the Monument which were included in the detailed transect analyses (darkened areas). Map of limber pine distribution adapted from the master plan vegetative map of Craters of the Moon National Monument. The most heavily forested areas (limber pine stands) are enclosed by solid lines.

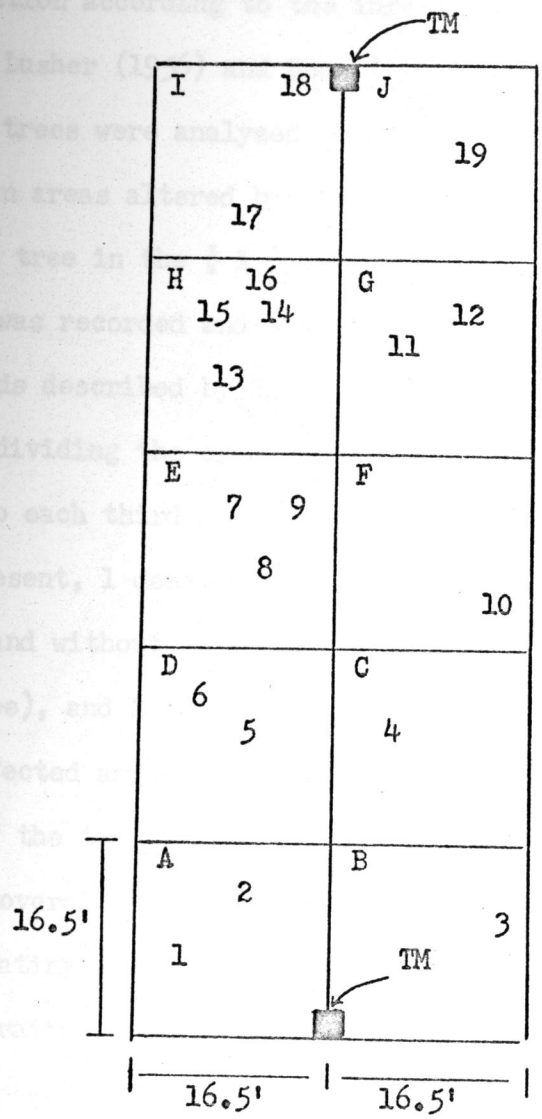
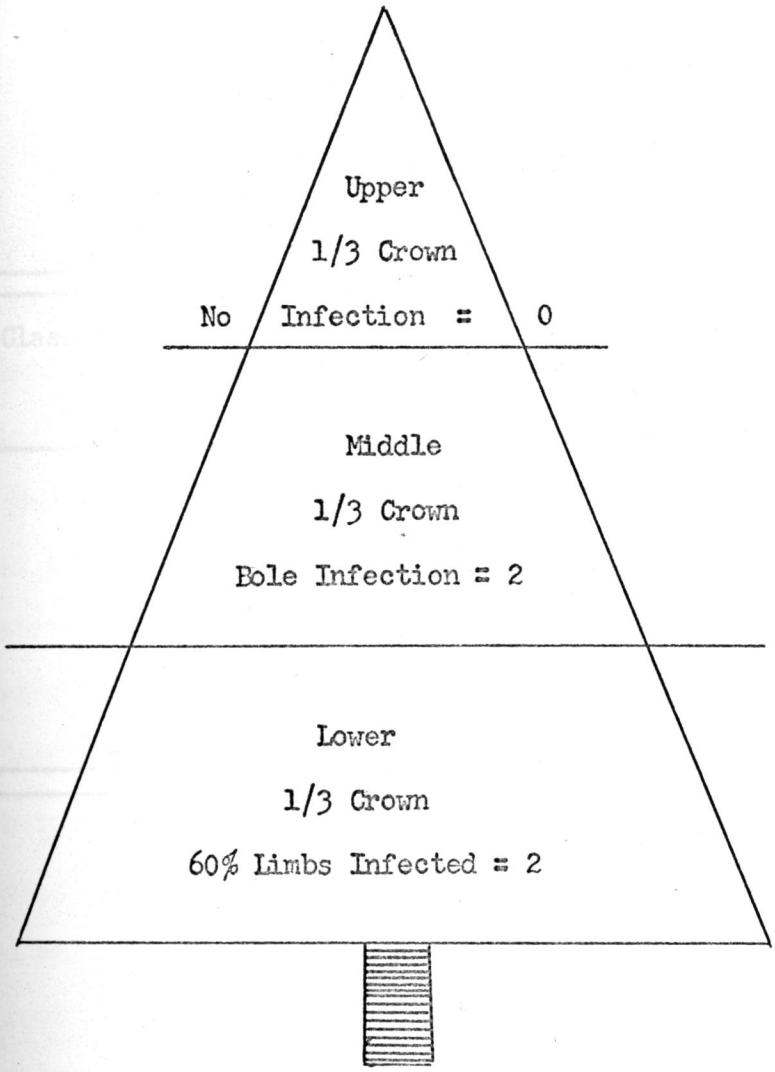


Figure 5. Schematic transect layout showing positions of the $\frac{1}{4} \times \frac{1}{4}$ chain sampling plots on either side of a transect line (between points labeled TM). Transect base points are denoted by TM; the numbers within the plots are tree numbers; and the letters are sampling plot codes.

mistletoe infection according to the infection rating scale described by Hawksworth and Lusher (1956) and Shea (1964). Within twenty-eight transects, 383 trees were analyzed in untreated areas and 307 trees were analyzed in areas altered by the eradication program.

For each tree in the $\frac{1}{4}$ X $\frac{1}{4}$ chain sampling plots, incidence of the dwarfmistletoe was recorded and the infection intensity determined. Using the methods described by Shea (1964), ratings were assessed by first visually dividing the crown into thirds and assigning a rating of 0, 1, or 2 to each third of the crown with rating 0 indicating no infection present, 1 denoting a light infection (less than 60% of the limbs infected and without an infection within 6 inches of the bole or trunk of the tree), and 2 indicating a heavy infection (more than 60% of the limbs infected and/or with an infection within 6 inches of the bole or trunk of the tree). Ratings for the third-crowns were then tallied and the overall infection levels for each tree determined with host infection rating 6 considered as the maximum. Figure 6, page 30, illustrates the rating system.

Table I, page 31, lists the four infection classes into which trees were placed depending upon their total infection ratings as determined by the rating scale criteria listed above and in Figure 6, page 30. The relationship between tree height, as an index of over-story structure, and dwarfmistletoe infection class was then statistically analyzed using a one-way classification analysis of variance for samples of unequal size (Steel and Torrie, 1960). The results of this analysis are given in Table V, page 47. Infection class means were then compared using Duncan's multiple-range test with unequal replication



Total Tree Infection Rating = 4

Figure 6. Dwarfmistletoe infection rating system.

TABLE I

INFECTION CLASSES, LEVELS, AND INTENSITIES

FOR DWARFMISTLETOE INFECTIONS PER TREE

Infection Class	Infection Level (Hawksworth & Lusher Scale)		Relative Intensity
	Minimum	Maximum	
1	0	0	Uninfected
2	1	2	Light
3	3	4	Moderate
4	5	6	Heavy

(Steel and Torrie, 1960). The relationship between sampling plot tree density and mean infection class rating was determined in the same manner.

Effects of the Parasite on the Host

The relationship between annual growth index of the host, defined as the mean increment in a radial core sample, and dwarf-mistletoe infection intensity was assessed statistically following random collection of the necessary data. A table of random numbers (Steel and Torrie, 1960) was used in determining from which of the trees within the transects (laid out for pattern analysis) core samples would be extracted. Although 19% of the limber pines analyzed in all transects were "aged" in this manner, the sample size of 133 trees was completely arbitrary. The number of trees bored and "aged" per transect varied with transect length and tree density and ranged from one to ten per transect.

Core samples were removed from each randomly-selected tree at a level 1 foot above the ground with a Swedish increment borer. The cores were stored in capped plastic tubes 3/4 inch in diameter and of desired length. Ages of the trees were determined by counting growth rings with the aid of a binocular dissecting microscope. Mean increment was assessed by dividing total core length, defined as the length in millimeters from bole center to bark, by the age.

The relationship between annual growth index and dwarfmistletoe infection class (as listed in Table 1, page 31) was analyzed statistically, again using a one-way analysis of variance for samples of

unequal size (Steel and Torrie, 1960). Duncan's multiple-range test with unequal replication (Steel and Torrie, 1960) was then used to compare the growth index means for each infection class.

Effectiveness of the Control Program

Since the original eradication program was not conducted using clearly defined experimental units within forest stands, the effectiveness of the control measures was difficult to assess accurately. Forest stands within the control area (Figure 7, page 34) were systematically sampled where stand size prohibited 100% sampling. Host trees showing residual infections were flagged and tallied on the basis of the type of infection present (i.e., whether the host was uninfected, supported a prunable infection, or supported a non-prunable infection). Percentages of infected trees per forest stand were determined for comparison with similar percentages determined during the pre-control survey conducted in 1961 by National Park Service employees, and with percentages tabulated by the dwarfmistletoe control crews during the eradication project in 1962 and 1963. In a similar manner, percentages of prunable and non-prunable infections were determined with similar figures obtained from Park Service records. Table II, page 35, lists the sample sizes in percentages of trees per forest stand, used to determine the percentages of total trees per stand which support residual dwarfmistletoe infections after the eradication project of 1962 and 1963.

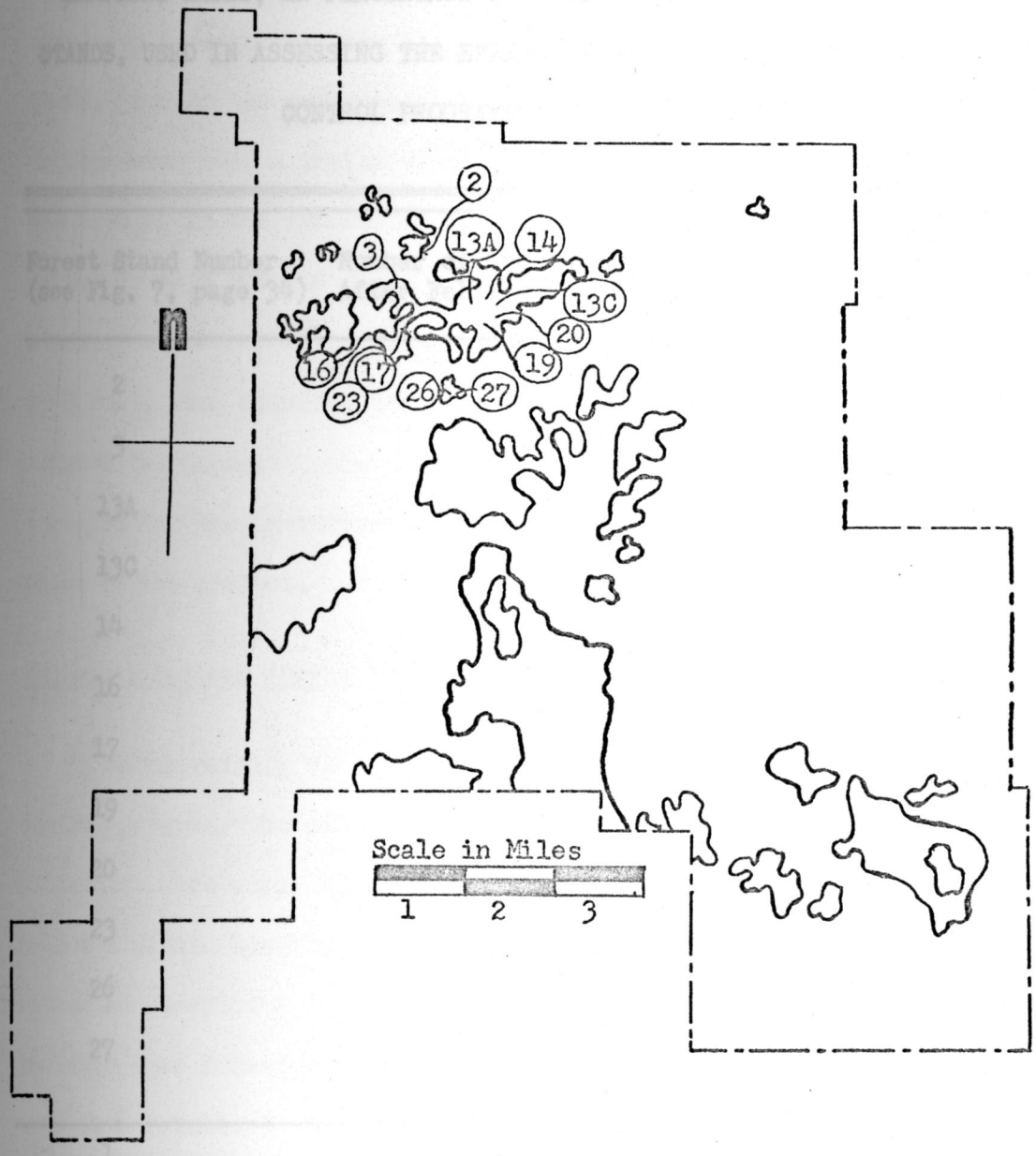


Figure 7. Location of forest stands in the visitor-use portion of the Monument. Eradication methods for controlling the dwarf-mistletoe were exercised in the numbered areas during 1962 and 1963. The most heavily forested areas (limber pine stands) are enclosed by solid lines.

TABLE II

SAMPLING BASIS, IN PERCENTAGE OF TOTAL TREES IN TREATED FOREST STANDS, USED IN ASSESSING THE EFFECTIVENESS OF THE DWARFMISTLETOE CONTROL PROGRAMS OF 1962 AND 1963

Forest Stand Number (see Fig. 7, page 34)	Number of Trees Remaining[1] After Felling and Poisoning	% Remaining Trees Sampled
2	378	60
3	1,247	97
13A	422	95
13C	312	83
14	559	82
16	1,624	62
17	224	16
19	11,970	20
20	1,289	22
23	114	91
26	137	81
27	879	39

[1]Figures obtained from control crew tally sheets. These figures represent the totals of trees left standing in the forest stands during the time the control program was being conducted.

Dispersal Agents

Both field observations of biotic factors and wind gap analyses were used to determine the dispersal agents of the dwarfmistletoe seeds. During the early autumnal seed dispersal period (August 25 to September 14), a series of four crudely-constructed cheesecloth nets was erected in the unforested wind gap between North Crater (Number 3; Figure 7; page 34) and Big Craters (Number 16; Figure 7; page 34) in an attempt to collect any sticky seeds carried by the wind. Nets, 9 feet by 3 feet, were attached to nylon cording and were then stretched between two transect poles. Other sparsely-vegetated wind gaps were surveyed for the incidence of the parasite during the reconnaissance phase of the project.

Phytosociological Appraisal

In appraising the phytosociological changes induced by the control program, the methods outlined by Phillips (1959) for successional studies were used. Eight permanent 10-meter square quadrats were laid out within heavily treated, moderately treated, and relatively untreated forested areas showing successional variation. Quadrat sites included some forested areas with only pioneer species and limber pines, some with relatively open understories of mixed seral stages, and others with relatively closed (i.e., high cover index) understories approaching the regional climax. All sites were on cinder cone slopes.

Each of the eight 100 square meter quadrats was laid out around a central point marked by a 24 inch long steel pin. The quadrat

corners were determined by direct measurement taken from the central point with a metric tape. The northeast, northwest, and southwest corners were marked with permanent metal slats. The southeast corner was marked with a wooden rod to which a metal number tag had been affixed. After the quadrat boundaries were delimited by the corner and central points, the quadrats were analyzed by quarter sections (25 square meter units).

Cover approximations for each of the quadrats were made using a grid system consisting of square meter units delimited by clothesline rope stretched between surveying pins. Where applicable (grass-forb synusia), the square meter units were further divided into square decimeter subunits with a 100 square decimeter frame device which was constructed from wood (framework) and string (grid units). Cover totals, in square centimeters, were determined for each species. Where cover was negligible, the species was assigned a cover total of 0.5 sq. cm. per stem (Phillips, 1959). Within the gridwork, the position and total cover of each plant were plotted on graph paper with a reduction scale of 30:1 (i.e., 30 sq. cm. of vegetation was equivalent to 1 sq. cm. unit on the graph paper).

The quadrats were compared on the basis of species composition, abundance, and crown cover. Successional patterns and vegetative changes resulting from the removal of the limber pines were determined from the vegetative data collected in this manner.

CHAPTER IV

RESULTS

Distribution of the Parasite

Figure 8, page 39, shows the distribution of the dwarfmistletoe with reference to limber pine distribution. Although the infection levels appeared to be highly variable from one forest stand to another, the parasite was found to be nearly as widely distributed as the host species. Five infection-free stands were located during the reconnaissance phase of the study, and numerous isolated infections, some more than one mile from the nearest infected stand or tree were found (see Figure 9, page 40).

In general, highest levels of infection were found in the forest stands of cinder cones where host density was estimated to be highest. Weathered aa lava flows supporting limber pine stands had higher infection levels than did pahoehoe flows having approximately the same stand density. Table III, page 41, compares infection levels and stand densities for those stands for which estimates of stand density and infection percentages were determined during the reconnaissance work. The sites listed in Table III, page 41, are mapped in Figure 8, page 39.

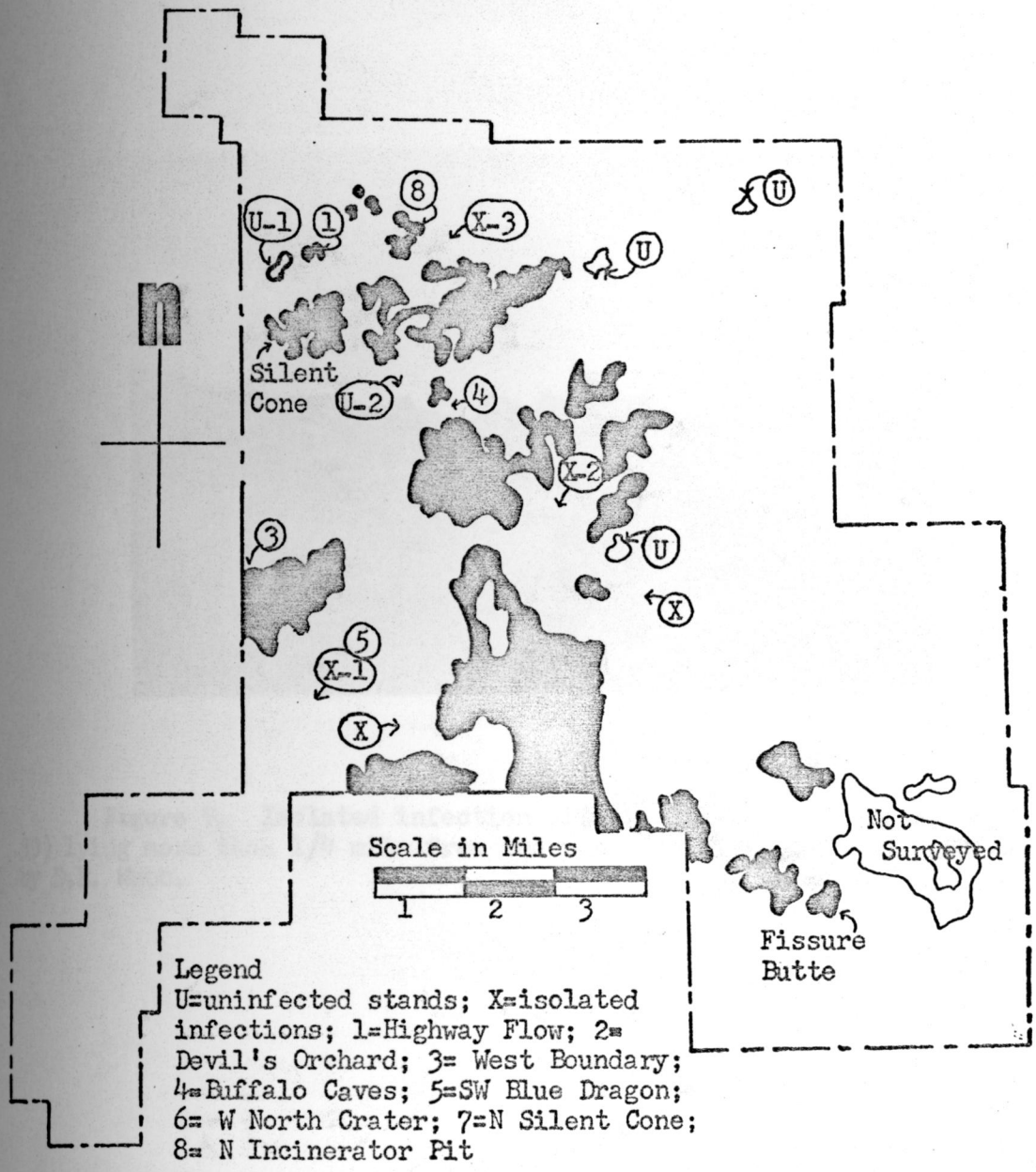


Figure 8. Distribution of the dwarfmistletoe, Arceuthobium campylopodum f. cyanocarpum (darkened areas) in comparison with the distribution of the host, Pinus flexilis. The most heavily forested areas (limber pine stands) are enclosed by solid lines.



Figure 9. Isolated infection site (point X-3; Figure 8; page 39) lying more than 1/4 mile from the nearest infected stand. Photo by D.E. Webb.

TABLE III

ESTIMATED LIMBER PINE DENSITY AND PERCENTAGES OF INFECTED TREES FOR SELECTED SITES

Location (Figure 8, page 39)	Substrate Type	Stand Density (Trees/Acre)	% Infected Trees
Highway Flow	Weathered Aa	2	10
Devil's Orchard	Weathered Aa	8	30
West Boundary	Weathered Aa	7	15
Buffalo Caves	Pahoehoe	7	1
Southwest Blue Dragon	Pahoehoe	4	1
West North Crater	Cinder Cone	9	50
North Silent Cone	Cinder Cone	312	61
North Incinerator Pit	Cinder Cone	37	66

Dating the Infection

During the reconnaissance of the forest stands, six limber pines were located that exhibited the symptoms of main stem infections that started when such trees were quite young. Figure 10, page 43, shows a tree exhibiting such symptoms.

Tree ring counts made from core samples extracted from these trees revealed that they ranged from 198 to 220 years, with an average age of 209 years. Table IV, page 44, lists the locations and ages of the trees used in "dating" the infection. The relative positions of the sites on which the trees were growing are mapped in Figure 11, page 45.



Figure 10. Young tree showing a main stem infection. Six older trees exhibiting similar symptoms were "aged" to date the dwarfmistletoe infection at Craters of the Moon National Monument. Photo by Warren Van Camp.

TABLE IV

LOCATIONS AND AGES OF THE LIMBER PINES USED

FOR DATING THE DWARFMISTLETOE INFECTION

Location	Age	Map Code (See Fig. 11, page 45)
SE¼, Sec. 22, T. 1 N., R. 24 E.	198	1
SE¼, Sec. 26, T. 1 N., R. 24 E.	199	2
SW¼, Sec. 13, T. 1 N., R. 24 E.	219	3
NW¼, Sec. 31, T. 1 N., R. 25 E.	214	4
SW¼, Sec. 31, T. 2 N., R. 25 E.	205	5
SW¼, Sec. 31, T. 2 N., R. 25 E.	220	6

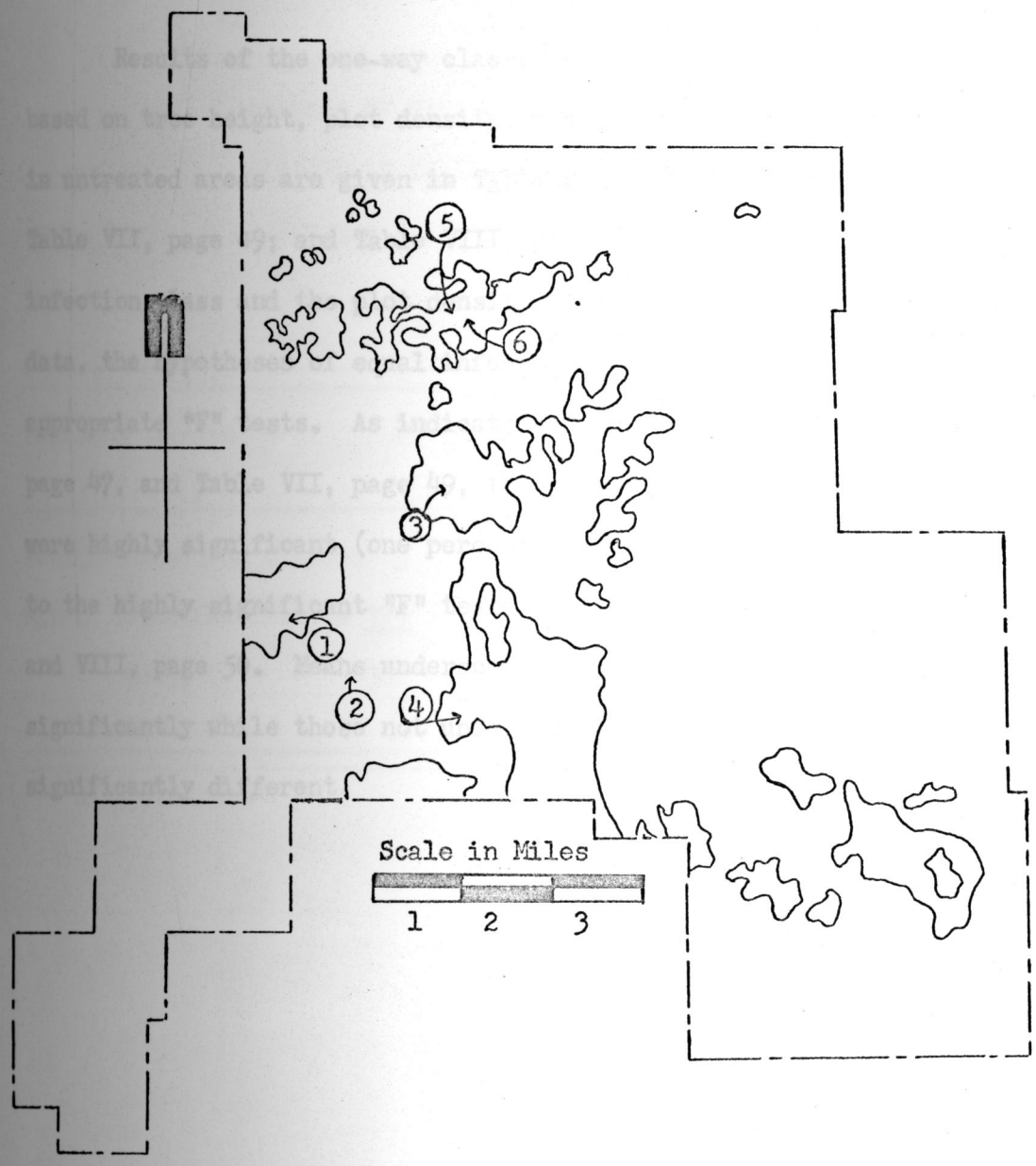


Figure 11. Locations of the limber pines used for "dating" the dwarfmistletoe infection (see Table IV, page 44). The most heavily forested areas (limber pine stands) are enclosed by solid lines. Map of limber pine distribution adapted from the master plan vegetative map of Craters of the Moon National Monument.

Patterns of Infection

Results of the one-way classification analyses of variance based on tree height, plot density, and infection class data collected in untreated areas are given in Table V, page 47; Table VI, page 48; Table VII, page 49; and Table VIII, page 50. For both the height/infection class and the plot density/plot mean infection class sets of data, the hypotheses of equal infection class means were tested using appropriate "F" tests. As indicated by the double asterisk in Table V, page 47, and Table VII, page 49, the infection class mean differences were highly significant (one percent level). Class means contributing to the highly significant "F" tests are given in Tables VI, page 48, and VIII, page 50. Means underscored by the same line do not differ significantly while those not underscored by the same line are significantly different.

TABLE V

ANALYSIS OF VARIANCE FOR TREE HEIGHT DATA CLASSED AT DIFFERENT INFECTION LEVELS FOR 383 TREES GROWING IN UNTREATED AREAS

Source of Variation	df	Sum of Squares	Mean Squares	F
Between Infection Classes	3	5,582	1,861.00	21.05**
Within Infection Classes	379	33,511	88.42	
Total	382	39,093		

TABLE VI

DUNCAN'S MULTIPLE-RANGE TEST WITH UNEQUAL REPLICATIONS FOR MEAN TREE HEIGHT IN FEET BY INFECTION CLASS

	Infection Class			
	Uninfected	Light	Moderate	Heavy
Class Mean (ft.)	6.7	9.9	13.5	15.8
No. Replications	183	46	74	80

TABLE VII

ANALYSIS OF VARIANCE FOR SAMPLE PLOT TREE DENSITY

BY MEAN INFECTION LEVELS PER PLOT

FOR 221 SAMPLING PLOTS

Source of Variation	df	Sum of Squares	Mean Squares	F
Between Mean Infection Classes	3	96.75	32.25	28.04**
Within Mean Infection Classes	217	251.12	1.15	
Total	220	347.87		

TABLE VIII

DUNCAN'S MULTIPLE-RANGE TEST WITH UNEQUAL REPLICATIONS FOR SAMPLE PLOT TREE DENSITY BY MEAN INFECTION LEVELS PER PLOT

	Mean Infection Level Per Plot			
	Uninfected	Heavy	Moderate	Light
Class Mean (No. Trees)	1.25	1.34	2.24	2.86
No. Replications	91	46	49	35

Effects of the Parasite

Treatment of the infection class/ annual increment data using a one-way classification analysis of variance based on a total of 133 core samples gave the results presented in Table IX, page 52. Differences between class means were analyzed using Duncan's multiple-range test with unequal replications (Steel and Torrie, 1960) since the "F" test test for equal treatment means was significant at the five percent level. The results of the ranked mean test are given in Table X, page 53.

TABLE IX

ANALYSIS OF VARIANCE FOR ANNUAL GROWTH INDEXES CLASSED AT DIFFERENT INFECTION LEVELS FOR 133 TREES

Source of Variation	df	Sum of Squares	Mean Squares	F
Between Infection Classes	3	3.82	1.27	3.62*
Within Infection Classes	129	44.96	.35	
Total	132	48.78		

TABLE X

DUNCAN'S MULTIPLE-RANGE TEST WITH UNEQUAL REPLICATIONS FOR MEAN ANNUAL GROWTH INDEXES (MEAN ANNUAL INCREMENTS) IN MILLIMETERS BY INFECTION CLASS

	Infection Class			
	Moderate	Heavy	Light	Uninfected
Class Mean (mm)	1.06	1.25	1.35	1.50
No. Replications	35	41	15	42

Effectiveness of the Control Program

Results of the survey of treated forest stands for the incidence of the parasite are given in Tables XI, page 55, and XII, page 56. Table XI compares percentages of infected trees within forest stands for four years. The 1961 figures were obtained from a National Park Service survey conducted prior to the initiation of the control program by Monument employees. The 1962 and 1963 figures were obtained from records maintained by the eradication crews during the control program. The 1967 percentages were obtained in the present study.

Table XII, page 57, compares the percentages of trees classed according to types of infection. The 1962 and 1963 percentages were taken from record sheets maintained by the control crews, while the 1967 percentages were obtained in the present study.

TABLE XI

COMPARATIVE DWARFMISTLETOE INFECTION LEVELS

BY PERCENTAGES OF INFECTED TREES PER CONTROL STAND FOR

THREE AND/OR FOUR YEARS

Forest Stand Number (See Figure 7, page 34)	Percentage of Infected Trees Per Year			
	1961[1]	1962[2]	1963[2]	1967[3]
2	35	42	9	12
3	61	68	-	23
13A	35	44	-	15
13C	62	64	-	22
14	65	72	-	33
16	39	45	-	20
17	51	30	-	40
18	6	11	-	11
19	22	---	22	13
20	11	---	14	8
23	27	---	33	12
26	9	18	11	14
27	22	25	27	27

[1]1961 percentages obtained from an NPS survey conducted prior to the initiation of the control program.

[2]1962 and 1963 figures represent the percentages of trees treated by the eradication crews during the control program.

[3]1967 figures obtained in the current study.

TABLE XII

COMPARATIVE PERCENTAGES OF TYPES OF INFECTION

FOR TWO AND/OR THREE YEARS

Forest Stand Number	Year								
	1962			1963			1967		
	% Total Trees			% Total Trees			% Total Trees		
	Prunable	Removable	Uninfected	Prunable	Removable	Uninfected	Prunable	Removable	Uninfected
2	13	29	58	9	0	91	8	4	88
3	9	59	32				15	8	77
13A	8	35	57				14	1	85
13C	13	51	36				22	0	78
14	12	58	30				23	10	67
16	11	34	55				18	2	80
17	12	19	69				31	9	60
18	4	7	89				11	0	89
19				7	15	78	10	3	87
20				3	11	86	5	2	93
23				10	23	67	8	4	88
26	10	8	82	10	1	89	9	5	86
27	17	8	75	25	2	73	23	4	73

Dispersal Agents

Although numerous birds and rodents frequently feed on the immature limber pine cones and seeds, only two common birds of the Monument were observed feeding on the dwarfmistletoe berries. The mourning dove, Zenaidura macroura, and the mountain bluebird, Sialia currucoides, were observed pecking at the dwarfmistletoe fruits during advanced stages of fruit maturation in late August.

Reconnaissance of wind gaps revealed that those gaps with relatively more limber pines were more heavily infected than those supporting fewer trees. Some of the wind gaps were free of infection.

For the most part, the results of the wind net study were negative, probably because of inadequate methods. A total of only five dwarfmistletoe seeds were collected in the four nets which collectively had a surface area of 108 square feet.

Phytosociological Appraisal

Results of the vegetative analyses of eight 100 square meter quadrats laid out for successional studies and for assessing the phytosociological changes induced by the removal of heavily infected limber pines are presented in Table XIII, pages 59, 60, 61, 62, and 63. The data of Table XIII is summarized by growth form class cover totals in Table XIV, page 64.

Nearly all of the limber pines in quadrats 11 and 40 had been felled during the eradication program of 1962-63. In quadrats 33, 36, and 37, almost all the trees had been poisoned but were still standing. Although the trees in quadrats 35, 38, and 39 had been pruned, relatively little alteration was apparent in these quadrats. Ironically, nearly all the trees in quadrats 35,38, and 39 bore residual dwarf-mistletoe infections.

TABLE XIII

COMPOSITION, ABUNDANCE, AND CROWN COVER (SQ. CM.) FOR EIGHT 100 SQUARE METER QUADRATS

Species	Measure	Quadrat Number 11	33	35	36	37	38	39	40
Agropyron smithii Rydb.	Abundance							4	
	Cover							713	
Bromus tectorum L.	Abundance	1							
	Cover	+							
Elymus cinereus Scribn. and Merr.	Abundance						3	8	
	Cover						3813	467	
Festuca idahoensis Elmer.	Abundance	90	1	39			45		
	Cover	13733	434	1188			3972		
Oryzopsis hymenoides (R. & S.) Ricker.	Abundance		1					4	12
	Cover		682					1612	2883
Sitanion hystrix (Nutt.) J.G. Smith.	Abundance	4	13	22	5		5	27	10
	Cover	467	7	11	747		4	321	5
Stipa occidentalis Thurb. ex S. Wats.	Abundance	1	38	15	3	1	2	1	8
	Cover	+	2021	1178	2513	1	589	+	2047
Arabis lignifera Nels.	Abundance	11	4				7	4	
	Cover	6	1179				4	2	
Aster canescens Pursh.	Abundance		5	12				2	6
	Cover		1676	1798				1	3

TABLE XIII (CONT.)

COMPOSITION, ABUNDANCE, AND CROWN COVER (SQ. CM.) FOR EIGHT 100 SQUARE METER QUADRATS

Species	Measure	Quadrat Number 11	33	35	36	37	38	39	40
Chaenactis douglasii (Hook.) H. & A.	Abundance	77		3	2	2	25	20	
	Cover	39		2	1	1	17	10	
Chenopodium album L.	Abundance	22					14		43
	Cover	319					7		477
Collinsia parviflora Dougl.	Abundance	49						10	
	Cover	25						5	
Cymopterus terebinthinus (Hook.) T. & G.	Abundance	94		47			92		
	Cover	42470		29			37327		
Delphinium andersonii Gray.	Abundance	10					6	3	11
	Cover	5					3	2	6
Eriogonum ovalifolium Nutt. var. depressum Blank.	Abundance		3	21	123	146	7	50	20
	Cover		714	12	26211	62744	1923	3627	996
Eriogonum umbellatum Torr.	Abundance	66	11	25	3	1	7	71	75
	Cover	21527	8052	18166	3100	1457	1532	22885	27838
Fritillaria atropurpurea Nutt.	Abundance						1		
	Cover						+		
Gayophytum ramosissimum Torr. & Gray.	Abundance	309	26	12			160	89	8
	Cover	155	13	5			80	45	4

TABLE XIII (CONT.)

COMPOSITION, ABUNDANCE, AND CROWN COVER (SQ. CM.) FOR EIGHT 100 SQUARE METER QUADRATS

Species	Measure	Quadrat Number 11	33	35	36	37	38	39	40
Lewisia rediviva Pursh.	Abundance			1					
	Cover			+					
Lupinus caudatus Kell.	Abundance	1							
	Cover	+							
Mentzelia albicaulis Dougl. ex Hook.	Abundance	5					5		
	Cover	3					3		
Mimulus nanus H. & A.	Abundance	138	120	7			132	136	56
	Cover	70	61	15			66	68	63
Mimulus suksdorfii Gray.	Abundance	8	4	6					
	Cover	4	2	12					
Penstemon cyaneus Penn.	Abundance	1							
	Cover	+							
Penstemon deustus Dougl.	Abundance							1	1
	Cover							+	651
Phacelia leucophylla Torr.	Abundance	120	4	16	44	450	20	19	
	Cover	553	2	12	517	736	10	10	
Potentilla glandulosa Lindl. var. pseudorepestris. (Rydb.) Keck.	Abundance							1	
	Cover							+	

TABLE XIII (CONT.)

COMPOSITION, ABUNDANCE, AND CROWN COVER (SQ. CM.) FOR EIGHT 100 SQUARE METER QUADRATS

Species	Measure	Quadrat Number 11	33	35	36	37	38	39	40
Stephanomeria tenuifolia (Torr.) Hall.	Abundance								2
	Cover								1
Amelanchier alnifolia Nutt. var. utahensis (Koehne) M.E. Jones.	Abundance						2		
	Cover						2263		
Artemisia arbuscula Nutt.	Abundance							1	
	Cover							775	
Artemisia tridentata Nutt.	Abundance							46	36
	Cover							51026	96565
Chrysothamnus nauseosus (Pall.) Britt.	Abundance	9	38				5	17	12
	Cover	16338	50186				4619	8959	7431
Eriogonum microthecum Nutt.	Abundance								1
	Cover								3100
Leptodactylon pungens (Torr.) Tydb.	Abundance		1		1			15	57
	Cover		+		1			1709	3045
Purshia tridentata (Pursh.) D.C.	Abundance	35	68	6	17	10	81	56	68
	Cover	191852	285014	2759	67644	838	290253	155967	160704
Ribes cereum Dougl.	Abundance	7	2	1	4				10
	Cover	12432	10602	+	3009				16647

TABLE XIII (CONT.)

COMPOSITION, ABUNDANCE, AND CROWN COVER (SQ. CM.) FOR EIGHT 100 SQUARE METER QUADRATS

Species	Measure	Quadrat Number 11	33	35	36	37	38	39	40
Juniperus scopulorum Sarg.	Abundance	1							
	Cover	806							
Pinus flexilis James	Abundance	5	1	14	13	16	5	4	2
	Cover	14291	+	686631	15625	28582	196819	391380	9889

TABLE XIV

PERCENTAGE COMPOSITION BY GROWTH FORM CLASS

OF THE VEGETATION IN EIGHT QUADRATS 10 METERS BY 10 METERS

Quadrat Number	Growth Form Class								Total Cover	
	Grasses		Forbs		Shrubs		Trees			
	Total Cover (Sq. Cm.)	% Total Vegetative Cover (Nearest Whole Percent)	Total Cover (Sq. Cm.)	% Total Vegetative Cover (Nearest Whole Percent)	Total Cover (Sq. Cm.)	% Total Vegetative Cover (Nearest Whole Percent)	Total Cover (Sq. Cm.)	% Total Vegetative Cover (Nearest Whole Percent)	Total Cover (Sq. Cm.)	% Total Ground Cover (Nearest Whole Percent)
11	14,200	4	65,173	21	220,621	70	15,097	5	315,093	32
33	3,143	1	14,841	4	345,802	95	0.5	0	363,787	36
35	2,736	0	20,036	3	2,759	0	686,631	97	711,803	71
36	3,260	3	29,829	25	70,654	59	15,625	13	119,268	12
37	1	0	64,938	69	838	1	28,582	30	94,359	9
38	8,378	1	40,970	8	297,135	55	196,819	36	543,302	54
39	9,531	2	26,654	7	218,435	56	136,759	35	391,380	39
40	4,935	1	30,038	9	287,492	87	9,889	3	332,354	33

CHAPTER V

DISCUSSION

Distribution of the Parasite

As indicated in Figure 8, page 39, the dwarfmistletoe is nearly as widely distributed as the limber pine. It is distributed far beyond the visitor-use portion of the Monument, and well beyond the boundaries of the forest stands in which control measures were exercised.

Also in Figure 8, page 39, it is readily evident that most of the infection-free forest stands are located east of the Great Rift Zone. This overall pattern of distribution suggests that the initial infection occurred along the Monument's western boundary and has since spread eastward. Although no records of the direction of the spread of the infection exist, the absence of the parasite in the limber pines growing approximately 8 miles east of Monument headquarters, on a lobe of North Crater Flow extending beyond the eastern boundary of the Monument, tends to support this interpretation.

Two minor exceptions may be noted in the overall west-to-east distributional pattern of the parasite. On Grassy Cone (point U-1, Figure 8, page 39) Douglas fir, rather than limber pine, is the dominant tree species in the forest stand. Apparently, the density of the susceptible limber pines is so low that either the parasite has not yet become established, or the parasite became established but failed to spread because the intercepting branches of the non-susceptible

Douglas fir minimized the effectiveness of the seed dispersal mechanism of the parasite.

Forest stand #25 (point U-2, Figure 8, page 39) represents the other exception to the overall distributional pattern. This stand is located in an isolated area which appears to be a crater wall fragment, or monolith, in the center of a pahoehoe flow. Most of the trees growing in stand #25 are shielded from the winds by the summit of the monolith. Consequently, it is highly probable that the limber pines of this stand are so far removed from infection sources and so well shielded from the winds that could carry the dwarfmistletoe disseminules, that it has remained uninfected to the present time.

Of great interest are the differential infection levels which were observed in forest stands growing on the various substrates. As indicated in Table III, page 41, the infection levels on cinder cones are considerably higher than those of either the pahoehoe flows or aa flows.

Perhaps the higher percentages of infected trees on the cinder cones can be best explained in terms of higher tree density, although pattern analysis (see page 70) failed to confirm that density was a significant variable. Since the aa and pahoehoe flows support fewer trees per acre than the cinder cones, the "target area" for the disseminules must be considerably higher on the cones.

The differential infection levels between aa and pahoehoe flows are probably of little significance. Except for the aa flows at the western boundary of the Monument, the other weathered aa flows were proximal to relatively heavily infected cinder cone forest stands.

Both of the pahoehoe flows listed in Table III, page 41, were near heavily infected cinder cones.

From the analysis of distribution it is apparent that the more densely forested slopes of the cinder cones are infection centers. It is very likely that the tree density on the flows surrounding the cones is too low to sustain intense infections.

The occurrence of isolated infections (Figure 8, page 39) is highly atypical for dwarfmistletoe infection patterns since it cannot be attributed to the seed ejection mechanism of the dwarfmistletoe fruit. Infections of an isolated nature are possibly unique to this particular form of the parasite, Arceuthobium campylopodum f. cyanocarpum (Hawksworth, personal correspondence). Since the occurrence of these infections cannot be explained adequately in terms of the seed ejection mechanism, several alternative explanations are offered.

The isolated infected trees may possibly be relicts of ancient infected stands which were destroyed by the volcanic eruptions or through other natural causes. In at least two of the areas where the isolated infections were found (points X-1 and X-2, Figure 8, page 39), the presence of lava trees and/or tree molds in the immediate vicinity of the isolated infections supports this interpretation. However, since the species of tree imprinted in the lavas of the Monument is unknown, this interpretation remains highly speculative.

A second alternative is that the isolated infections may have been initiated by disseminules carried by the wind. This is particularly tenable since the winds in the vicinity of the Monument generally prevail from one direction, the southwest, and attain average maximum daily

velocities of 30 miles per hour for the entire year.

Biotic dispersal agents could also account for the isolated infections, to be discussed later in greater detail. Although the importance of biotic agents in dispersing the parasite was not assessed adequately in this study, it is extremely difficult to explain the occurrence of the isolated infections without implicating either biotic or abiotic factors.

Dating the Infection

In the absence of fossil evidence, two assumptions were made in the dating techniques employed in this study. First, it was assumed that the six trees which exhibited the symptoms of old infections as described by Kimmey and Graham (1960) were initially infected during the first five or six years of growth. Second, the dating was based upon the assumption that the limber pine stands of the Monument are, as Eggler (1941) suggested, "the first to occupy the site."

Other methods for approximating the dates of initial infections are known, but since these methods require transverse sectioning of the bole and result in destruction of the host tree, they were not used in the current study. Such methods, discussed by Hawksworth and Hinds (1964) entail cutting the tree and tracing the endophytic system of the parasite to the innermost growth ring in the transverse section that shows sinkers of the endophytic system.

Although only six trees were located and sampled for use in dating the older infections (see Table IV, p. 44), their mean age probably represents the most reliable available figure for the age of the

dwarfmistletoe infection at Craters of the Moon National Monument. This mean age of 209 years is meaningful when compared with the 450-year age of the oldest tree sampled in this project; the oldest known living limber pine in the Monument, the age of which is 1210 years (University of Arizona Laboratory of Tree-Ring Research, personal correspondence); and the 44-year period during which the area has been administered by the National Park Service.

Pattern of Infection

Although the mean height of the uninfected tree class was determined partially from measurements of non-susceptible trees (i.e., seedlings and trees in the polycotyledonous stage of development), the ascending order of class means as shown in the multiple-range test (Table VI, page 48) cannot be explained on this basis. Three of the four significant differences between infection class means (between the uninfected class mean and the three infected class means) can be attributed to non-susceptible trees. However, the fourth significant difference, between the heavy infection class mean and the light infection class mean, must be explained in different terms.

Assuming that tree height is a reliable index of canopy cover, the more intense infections in the taller trees may be explained on the basis of greater surface or "target" areas for dwarfmistletoe seed interception. Also, the greater rate of infection intensification in a larger tree having more limbs which could potentially be infected may explain the significant difference between the heavy infection class

mean and the light infection class mean.

Since the difference between the heavy infection class mean and the moderate infection class mean is not significant, the apparent positive correlation suggested by the ascending order of the four means does not hold true beyond the moderate class. Because this difference is nonsignificant, it is likely that infection intensity (class) and canopy cover (as indicated by tree height) are correlated positively up to a critical canopy size, beyond which this relationship does not hold true. If tree height can be considered a reliable index for canopy size and "target" area, then the data of the current study concur with those of Shea (1964) who found a significant (5 percent level) interaction between area and infection level in ponderosa pines of south-central Oregon.

Thus, within infected forest stands, infection intensities may be associated with tree height and the patterns of infection with canopy size. With the exception of crown canopy, as determined by tree height, no other factors were associated consistently with infection pattern.

No consistent patterns between mean infection levels per sampling plot and sampling plot tree density were found, as indicated in Table VIII, page 50, by the irregular order of the infection class means. The absence of a positive correlation between density and infection intensity can probably be explained best in terms of the open nature of the limber pine stands of the Monument. Density of the limber pine, under the peculiar environmental conditions that prevail at Craters of the Moon (and elsewhere in its range), is negligible when compared

with the densities of trees in commercial forest stands with reference to density/infection intensity interaction.

Since density is not correlated positively with infection intensity, the differential infection levels listed in Table III, page 41, probably cannot be explained adequately in terms of tree density. Possibly another variable which differs significantly between the forest stands of the lava flows and those of the cinder cones is responsible for the differential infection levels estimated for these three substrates. Although an evaluation of the roles of many variables existing between the forest stands of the flows and cones was not attempted, it is apparent that the inclination of the cinder cone slopes may be a significant factor in infection intensity. It is unlikely, however, that any single variable can explain fully the highly irregular patterns of dwarfmistletoe infection characteristic of the limber pine stands of Craters of the Moon National Monument.

Effects of the Parasite

The significant (5 percent level) "F" test of Table IX, page 52, is the result of the difference between the uninfected class mean and the moderately infected class mean (see Table X, page 53). Since no significant differences occur between the uninfected class mean and the heavily and/or lightly infected class means, an inverse correlation between infection level and annual growth index (radial) does not apply at Craters of the Moon. If an inverse correlation could be applied, a descending class mean order (i.e., heavy, moderate, light, uninfected) would be expected.

Because cores from the stunted and spiketopped trees of heavily infected Silent Cone were included in the analysis, the conclusion that no significant decrease in radial growth occurs with increasing infection intensity applies to the trees of the two forest stands that exhibited overall symptoms of heavily infected stands (Silent Cone and Fissure Butte Vent; see Figure 8, page 39) as well as to trees of less heavily infected stands. Thus, under the peculiar environmental conditions of the Monument, it is likely that some other variable is more closely correlated with the annual increment of the slow-growing limber pine than dwarfmistletoe infection level. Although climatic records to substantiate this hypothesis are nonexistent, available precipitation is probably the variable that is most closely correlated with annual growth indexes of the limber pines.

Effectiveness of the Control Program

As indicated in Table XI, page 55, residual infections were found in all of the stands in which eradication procedures had been taken. The percentages of infected trees per forest stand are lower than those determined during either the pre-eradication survey of 1961 or the eradication programs of 1962 and 1963. The lower infection percentages can be attributed to the control measures since during the control program all prunable infections were removed mechanically and all heavily infected limber pines were felled. It is not unusual that the control program was not 100% effective in eliminating the parasite since periodic retreatments designed to remove latent and/or missed infections are normally associated with projects of this type, "depending

on management objectives" (Kimmey and Graham, 1960).

In addition to the factors of latent and missed infections, the factor of increased light intensity, which stimulates the activity of dwarfmistletoe shoots (Kimmey and Graham, 1960), must be considered. This factor, which is inevitably associated with the opening of the stand canopy through host removal, probably contributed significantly to the intensification of the residual infections in the control stands.

Another explanation for the residual infections is the uneven-aged composition of the Monument's limber pine stands. The difficulties encountered in controlling the parasite in uneven-aged stands are well known (Leaphart, 1963; and Shea and Orr, 1963). Invariably, in uneven-aged stands, all susceptible generations of the host become infected. Consequently, unless all trees are removed, the parasite is continually recycled.

From the data presented in Table XII, page 56, it is evident that definite changes occurred in the types of infection present in the forest stands following the control program. A general decline was observed in the percentage of trees which would necessarily be felled or poisoned in the event that further control work in the visitor-use portion of the Monument is undertaken. This shift toward fewer heavily infected (removable) trees could be expected since more than 6,000 heavily infected trees were felled or poisoned during the control operations of 1962 and 1963. The general increase in percentages of prunable infections probably resulted from the intensification of infections after the control operations.

Although the eradication program was not 100% effective in

obliterating the parasite from the limber pines growing in the visitor-use portion of the Monument, it did lower the percentage of infected trees present. Of greater significance is the fact that a well-defined shift in types of infection occurred as a result of the program because heavy infections predominated in the pre-eradication period whereas at the present time higher percentages of prunable infections prevail.

Dispersal Agents

It is almost impossible to explain the occurrence of isolated dwarfmistletoe infections in the Monument without suggesting that biotic factors and/or wind are involved in dispersing the seeds of the parasite. Since the maximum dispersal distance attributable to the hydrostatic pressure of the seed ejection mechanism of the fruit is 30 feet (Peace, 1962), it is highly probable that other agents, such as mammals, birds, or the wind, were involved in initiating these infections.

Despite the fact that mourning doves and mountain bluebirds were observed feeding on dwarfmistletoe berries, conclusive evidence for their role as dispersal agents was not obtained. In order to prove that these animals were acting as dispersal agents, crop analyses and post-digestion seed viability studies would have been necessary. Such detailed studies were beyond the scope of the current study, and were not attempted. For the same reason, no attempts were made to assess the role of external adhesion of seeds to rodents and birds in dispersing the seeds.

It is unfortunate that evidence for biotic dispersal was not more conclusive since reports both supporting and discrediting this means of infection spread are in the literature. Although Kimmey (1957) expressed doubt about dwarfmistletoe seed dispersal by birds, other researchers (Kimmey and Graham, 1960; Kuijt, 1955; and Weir, 1916) suggest a possible role for animals in distributing the parasite.

Because the methods used to assess the role of wind in dispersing the dwarfmistletoe seeds proved to be inadequate, a definite dispersal role for this abiotic factor was unsubstantiated in the current study. Although five dwarfmistletoe seeds were collected in the wind nets erected to catch wind-borne disseminules, it remains highly probable that the strong, unidirectional, diurnal winds characteristic of the Monument contribute to the spread of the parasite. Several accounts implicating this abiotic factor in dispersing the dwarfmistletoe seeds are known (Kimmey, 1957; Roth, 1953; and Weir, 1916).

Phytosociological Appraisal

The vegetative data collected from the eight 100-square meter quadrats concur with the successional patterns discussed by Eggler (1941). Depending upon the microhabitat, the limber pine represents either the second or third seral stage in primary plant succession on the recent volcanics of the Monument. The tree successfully invades habitats supporting pioneer and/or ephemeral communities (Figure 12, page 76), but in the course of succession it is replaced by bitterbrush (Figure 14, page 77) and ultimately by the regional climax community of sagebrush and grass (Figure 15, page 77). The tree also competes



Figure 12. Pioneer community (foreground) in transition stage to limber pine community. Photo by Warren Van Camp.



Figure 13. Mature limber pine community not yet invaded by shrub understory. Photo by Warren Van Camp.



Figure 14. Limber pine - bitterbrush community with closed shrub understory. Photo by D.E. Webb.



Figure 15. Regional climax community of sagebrush. The trees in the foreground are Rocky Mountain juniper and limber pine. Photo by D.E. Webb.

successfully in open tree-shrub communities but fails to reseed as the shrub understory closes.

Further evidence of the seral position of the limber pine is the absence of the species from the vegetative communities of the older volcanics of the surrounding Snake River Plain. Only the comparatively recent lavas within the boundaries and in the immediate vicinity of the Monument support stands of Pinus flexilis. Undoubtedly the inability of the tree to compete (Bates, 1923) with the shrubs of the regional climax community results in its seral status and gradual elimination.

Removal of the limber pines from the various plant communities has pronounced effects on successional dynamics. On sites where the shrub understory is essentially closed (quadrats 33, 38, and 40; Table XV, page 65), tree removal accelerates normal succession. In quadrat 40, all but two small saplings were felled during the eradication program. By the time these saplings are old enough to produce cones, providing they can withstand competition for that period of time, the shrub understory will be so dense that establishment of any pine seedlings will be impossible.

In quadrat 33, the limber pines had been poisoned but were still standing. This enabled pre-eradication cover estimates for the pine to be determined in the present study. Before the eradication program was initiated, the limber pine covered at least 102,321 sq. cm. of quadrat 33. As indicated in Table XIII, page 63, the present cover for the single limber pine seedling (in the polycotyledonous stage of development) is less than 1 sq. cm. If this seedling survives long enough to

produce seeds, its reproductive potential will be nullified by the closure of the shrub understory which will undoubtedly accompany maturation of this single seedling.

Although the trees in quadrat 38 have been pruned, they still bear limb infections of dwarfmistletoe. In this quadrat the shrub understory is closing. However, since the limber pines were not removed from this site, the shrub:tree cover ratio remains favorable for limber pine reproduction. With 54% of the ground surface of this quadrat occupied by vegetation at the present time, and with two cone-bearing limber pines present, the conditions are such that the limber pine can seed another generation of trees before the shrub understory closes.

From the vegetative analyses of these three quadrats (33, 38, and 40) it is apparent that normal succession is accelerated on sites where the shrub understory was nearly closed before the limber pines were removed. Because the removal of the seed source reduced the reproductive potential of the pine below a critical level, or because existing seedlings cannot compete successfully with the shrub synusia, the limber pine is not reforesting such sites (quadrats 33 and 40).

On sites where the transition from tree to shrub communities has been initiated but has not yet advanced to the stage in which the shrub synusia is dominant (quadrats 11 and 39; Table XIV; page 64), conditions are favorable for limber pine reproduction. However, seedling crops of the limber pine were not evident in these two quadrats.

For sites which are essentially in the pioneer stages of

succession (quadrats 35,36, and 37; Table XV; page 65), tree removal retards the normal successional rate. This may be attributed to the retardation of soil development brought about by the removal of the pine which is singularly the most important species contributing to the organic increment of the immature volcanic soils of the Monument. In such sites, particularly in quadrats 35 and 37, relatively large seedling crops of the limber pine were observed.

The effects of tree removal on successional dynamics in this unusual area are pronounced. In the pioneer communities, tree removal reduces the normal successional rate because soil development is retarded in the absence of the organic material supplied by the pine. For areas supporting closing or maturing shrub communities, the removal of potential seed sources prevents reforestation and thereby accelerates normal plant succession. The closure of the shrub understory further reduces the reproductive potential of the limber pine since the tree seedlings, with an extremely low survival index and a requirement for full sunlight (Bates, 1923), cannot compete successfully with the shrub synusia.

CHAPTER VI

SUMMARY AND SUGGESTIONS FOR FURTHER RESEARCH

I. SUMMARY

In 1962 and 1963 a management policy designed to obliterate the parasitic dwarfmistletoe, Arceuthobium campylopodum f. cyanocarpum, from the limber pine (Pinus flexilis) stands of the visitor-use portion of Craters of the Moon National Monument, Idaho, was activated. At that time very little was known about the extent of the dwarfmistletoe infection within the Monument and the factors that contribute to its spread. Prior to the initiation of the control project, no attempts were made to assess the ecological impact of host removal on the unusual plant communities of the Monument. In the course of the current study, seven aspects of the dwarfmistletoe problem at Craters of the Moon National Monument were studied in an attempt to provide a broader scientific base upon which future management objectives could be formulated.

The distribution of the dwarfmistletoe in the limber pine stands of the Monument was determined through reconnaissance methods. From the reconnaissance work it is evident that the parasite is distributed far beyond the limits of the visitor-use portion of the Monument, and, with several exceptions, it is as widely distributed as the host tree. The parasite is not restricted to trees growing on one particular substrate (pahoehoe, aa, or cinders), nor is it restricted to the densest forest stands. Although highly atypical and possibly unique

to this form of the dwarfmistletoe, numerous isolated infections occur within the Monument.

Six trees having spindle-shaped bole infections were bored and "aged" to determine the approximate age of the dwarfmistletoe infection. The mean age of the six trees was 209 years, which indicates that the limber pines of the Monument have been infected with the parasite since before white man explored the western United States.

Analysis of infection patterns, as determined from detailed transect studies, revealed that virtually no consistent patterns of dwarfmistletoe infection prevail in the limber pine stands of the Monument. Canopy size, as indicated by tree height, is most closely correlated with infection intensity. Both of these variables (canopy size and host density) show no consistent pattern from one stand to another.

Effects of the dwarfmistletoe on the annual radial growth increment of the host were analyzed statistically with a one-way analysis of variance. Neither a positive nor a negative correlation between infection intensity and growth exists. It is suggested that an environmental variable such as annual available precipitation is more closely correlated with the annual increment of the slow-growing limber pine than is the intensity of dwarfmistletoe infection.

Treated forest stands were surveyed to determine the current levels of residual infection. Infections are present in all of the treated stands and in nearly every stand the percentage of infected trees is below a comparable figure from pre-eradication data. Since more than 6,000 heavily infected limber pines were removed in 1962-63,

fewer heavily infected trees are found in the treated stands but a higher percentage of lightly and moderately infected trees are present.

Dispersal agents were inadequately evaluated in this study. It is quite likely, however, that the following agents are involved in disseminating the seeds of the parasite: (1) the seed ejection mechanism of the dwarfmistletoe; (2) wind; and (3) birds and rodents. The seed ejection mechanism of the dwarfmistletoe is unquestionably the single most important dispersal agent. Wind and biotic factors probably are of minor importance but possibly are responsible for the isolated infections.

The effects of host removal on plant community structure and successional dynamics were analyzed with permanent quadrat methods. The vegetative analyses indicate that limber pine removal from communities supporting closed shrub understories actually accelerates plant succession and such sites cannot be expected to become reforested with the highly noncompetitive limber pine. Conversely, because the limber pine is a major source of organic matter which is vital to soil development, removal of the tree from communities in the pioneer stages of succession actually retards this natural process. Clearly, the limber pine is a seral, rather than a climax, species, and its removal profoundly alters the course of primary plant succession on the recent lava flows of Craters of the Moon National Monument, Idaho.

II. SUGGESTIONS FOR FURTHER RESEARCH

Perhaps the formidable terrain of Craters of the Moon has been responsible for the apparently insufficient quantity of scientific

research that has been completed in this unique area to date. Or perhaps the remaining problems are insurmountable. Before research projects in other disciplines can be contemplated, basic answers must be supplied from research projects in geology and volcanology. Since the exact ages of the lava fields of the Monument are unknown, dating the flows with appropriate chemical methods would be highly desirable. In addition, research directed toward identifying the species imprinted in the tree molds and/or lava trees would be of importance in contributing to an understanding of pre-eruption vegetation.

Since very little is known about the mortality rates of limber pine seedlings under controlled and natural conditions, research projects designed to determine these rates would be of great value. Also, the relative rates of plant succession should be determined through long term successional studies. Both the relatively open limber pine stands and the isolated dwarfmistletoe infections provide ideal conditions for studies of the dispersal agents of the parasite. Consequently, projects dealing solely with the dispersal agents of the dwarfmistletoe should be initiated. Such studies would be of great importance in predicting the success or failure of control measures initiated and exercised by an agency dedicated to the preservation of America's natural heritage, the National Park Service.

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